Fatty Acid Digestibility and Dairy Cow Performance

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Take Home Messages

- Fat supplementation can increase dietary energy density without increasing diet fermentability, but also has other physiological effects.
- Nearly all dietary ingredients contribute some fat to the diet. Ingredients with a low fat content are commonly overlooked, but some are fed at high rates and contribute greatly to fat intake.
- Feeding high fat byproducts, and the development of plant varieties selected for a specific fatty acid profile complicate ration balancing.
- The bioactivity of lipids, and their use as an energy source and as a substrate for cellular membrane synthesis and for signaling factor synthesis make determination of requirements difficult.
- Digestibility of hydrogenated triglycerides is low, but research summaries report little difference between digestibilities of individual fatty acids.
- Increasing fat supplementation is expected to decrease total fatty acid digestibility.
- Important aspects of fat supplements are their digestibility, their effect on intake and milk production, and their ability to modify physiology.
- Enriched palmitic acid increases milk fat more than other long-chain fatty acids.
- Selection of fat supplements should consider the basal diet, rumen available fat sources, and the goal of using the fat supplement.

Introduction

Dietary fatty acids (FA) are the nutritionally important component of lipids and serve a number of functions in animal nutrition. Fatty acids are a concentrated source of energy, but also serve as integral structural components of cellular membranes and regulatory molecules. Over the past 25 years, we have come to appreciate that some FA are bioactive compounds that modify physiology and metabolism. The dairy cow experiences very different metabolic demands and physiological conditions across lactation, and it is reasonable to expect that the role of FA differ during these states. It is impossible to make a one-size-fits-all recommendation for dietary fat feeding or expectation on the response to dietary fat. However, current knowledge of fat supplements can direct their use to modify a number of important production parameters.

Palmquist and Jenkins (1980) reviewed the history of fat research in dairy cows starting from a 1907 review of the effect of fat on milk and milk fat yield. It is interesting that over 100 years later we still are asking some of the same questions, but in the context of a cow with much higher metabolic demands. Interest in fat supplementation has traditionally centered around increasing dietary energy density without increasing dietary fermentability to support energy requirements of high producing cows. More recently, interest in fat supplementation has broadened to increasing milk or milk fat yield, increasing reproductive efficiency, and modifying the FA profile of milk. The field of ruminant FA metabolism underwent tremendous growth with the Biohydrogenation Theory of milk fat depression (MFD) and the identification of bioactive conjugated linoleic acid (CLA) isomers. Most recently, availability of enriched palmitic acid supplements provides additional options for fat feeding.

▪ Fat Digestion and Metabolism

Fatty acids are not broken down in the rumen, and normally, duodenal flow of FA is similar to intake. Rumen microbes synthesize some FA, resulting in ruminal outflow of odd and branch-chain FA. There is growing interest in the positive human health attributes of these FA, and ruminant meat and milk are the predominant source in the human diet. Ruminal synthesis of FA is increased when feeding low fat diets because the microbes require FA for synthesis of their cellular membranes. The majority of FA in forage and grain feedstuffs are unsaturated, and the rumen microbes will biohydrogenate these unsaturated FA forming *trans-FA* intermediates. Complete biohydrogenation results in saturated FA, but biohydrogenation is commonly incomplete. Rumen microbes biohydrogenate unsaturated FA because these FA are toxic, and the microbes prefer saturated and *trans-FA* for their cellular membranes. The pathways of biohydrogenation are dynamic and responsive to nutritional factors and rumen environment. Specific *trans-FA* formed in alternate biohydrogenation pathways can cause diet-induced MFD, and limit the amount of unsaturated FA that can be fed to dairy cows [see Harvatine et al. (2009)]. Biohydrogenation also severely limits absorption of the essential polyunsaturated FA by the cow.

Rumen Availability of Fatty Acids

Increasing the amount of unsaturated FA in the diet increases the toxic effect on rumen microbial populations and also increases the substrate required for biohydrogenation. Dr. Tom Jenkins developed the concept of Rumen Unsaturated Fatty Acid Load (RUFAL), which is the sum of unsaturated FA in the diet, and provides insight into the risk of altering fermentation. The rates of FA availability must also be considered, but little research has been directed towards understanding the rate of FA availability. The rate of rumen availability is drastically different between some feeds. For example, unsaturated FA in distiller's grains with solubles is rapidly available and has a large impact in the rumen compared to whole cottonseed that is slowly released. Increased grinding of oilseeds increases the risk of diet-induced MFD. Dr. Jenkins recently presented the initial development of a laboratory method to estimate FA availability, and future analytical progress in this area is expected.

Calcium salts of FA were developed to reduce the inhibitory effects of unsaturated FA on fibre digestion because they are insoluble salts that block FA metabolism by microbes (Palmquist and Jenkins, 1980). A main mechanism of calcium salts is slowing rumen availability, rather than true protection, as bypass rates of unsaturated FA fed as calcium salts are rather low. The dissociation of the calcium salt in the rumen is dependent on the dissociation constant of the FA and rumen pH, and increasing unsaturation decreases the strength of the calcium salt. However, calcium salts are far less disruptive to rumen fermentation than are free oils.

Digestibility of Fatty Acids

Intestinal absorption of FA is quite different in the ruminant compared with the non-ruminant, as duodenal flow is predominantly saturated free FA. Non-ruminants depend on monoglycerides and unsaturated FA for formation of micelles, while in the ruminant lysolecithin is a very potent emulsifier and aids formation of micelles. In the ruminant, there is a large decrease in total tract FA digestibility when feeding hydrogenated saturated triglycerides (TG) because they are more resistant to ruminal and intestinal lipolysis than are unsaturated TG (e.g. Elliott et al., 1999). Hydrogenated TG may have a digestibility below 40%. Research studies report significant variation in total tract digestibility that reflects both variation between diets and the technical challenges of digestion studies. Total tract FA absorption is roughly 70 and 80% in dairy cows. Differences in digestibility of individual FA is controversial and is difficult to investigate because of rumen and hindgut biohydrogenation. Meta-analysis studies using different approaches have observed little difference in digestibility between FA, although FA digestibility decreases with increasing fat intake (Glasser et al., 2008, Schmidely et al., 2008, Boerman et al., 2015). The decrease in digestibility with increased intake has important implications as it represents diminishing returns. More attention should be paid to FA digestibility, but this will require a dedicated effort to conduct well-controlled experiments.

Metabolic Fate of Fatty Acids

Fatty acids can be oxidized to provide energy for maintenance and production and provide 2.5 times more energy than carbohydrate. Fatty acids can also be used for body storage and milk fat production; these are energetically efficient processes as FA can be directly deposited and do not have any energy loss. The metabolic fate of absorbed FA depends on the physiological state of the cow and the FA. During peak lactation, FA are directed towards meeting energy requirements for milk production. In some cases, fat supplementation increases milk fat yield and the response appears to be dependent on FA profile. Kadegowda et al. (2008) observed a 243 g/d increase in milk fat yield with abomasal infusion of 400 g/d of butter oil and the increase was predominantly short and medium chain FA. More recently, milk fat responses have been commonly reported when feeding enriched palmitic acid (C16:0), but also have been observed with oilseeds and other FA supplements. After peak lactation, dietary FA will be increasingly partitioned toward body reserves. Importantly, oxidization of FA spares other nutrients from oxidation, which creates a complicated discussion of the metabolic impact of dietary FA. The milk production responses to fat supplements are variable, normally of small magnitudes, and are expected to depend on the interactions discussed above.

Essential Fatty Acids

Fatty acids can be categorized as essential or nonessential based on the animal's capacity to synthesize or conserve the required amounts. Linoleic (C18:2 n-6) and linolenic (C18:3 n-3) acid are traditionally considered the 2 essential FA. Some consider the very long chain omega-3 FA (e.g. eicosapentaeonic acid (EPA**)** and docosahexaenoic (DHA)) to be conditionally essential as they can be synthesized by elongation and desaturation, but the capacity of their synthesis is highly limited in most production animals. There is overlap in the ability to utilize omega-3 and omega-6 FA as substrate in some pathways; however, signaling molecules originating from omega-3 are more anti-inflammatory and omega-6 FA are more pro-inflammatory. Competition for elongation and desaturation has led to the concept of omega-3 to omega-6 ratios, although the importance of these measures is still uncertain.

The requirement for essential FA is different based on the amount needed for maintenance and sustained production vs. the amount that may stimulate maximum production through changing physiology and metabolism. The first definition is easier to define based on metabolic use, but the second demands an understanding of the physiological and metabolic effects of individual FA, including their effect on hard to research processes such as immunology and reproduction. Absorption of essential FA is very limited in ruminants, but there are no reports of classical FA deficiency in adult ruminants. Mattos and Palmquist (1977) determined that linoleic acid was available to the cow at twice the requirement for female weanling rats on a metabolic body weight basis. In addition, ruminants may be adapted to conserving essential FA as they are less available for oxidation. It appears that essential FA are normally available in adequate concentrations based on production requirements; however, there may be benefits of FA supplementation to health including improving reproductive efficiency and immunology.

Effect on Intake

A main goal of fat supplementation is to increase energy intake, but depression of dry matter intake (DMI) can limit the benefits of fat supplements. Intake is highly regulated by animal nutrient requirements and metabolic state, and also by the type and temporal pattern of fuels absorbed. Fat source, form, and FA profile are significant predictors of intake response. In a meta-analysis, Allen (2000) reported a linear decrease in intake with calcium salts of palm distillate, while saturated FA had no effect on intake. Benson et al. (2001) summarized 11 infusion studies and observed a negative relationship between infused C18:1 and C18:2 FA concentration and intake, with C18:2 creating greater intake depression. Some studies with enriched palmitic acid supplements have shown decreased intake compared with no fat controls (Lock et al., 2013, Rico et al., 2014), although the overall decrease in DMI was not significant, and energy intake was increased in a recent meta-analysis (deSouza et al., 2016).

▪ Important Consideration in Fat Sources

It is best to think about diet FA starting with the base diet through to high fat feeds and fat supplements. Feeds vary in type and FA profile and have different effects in the rumen. Forages and cereal grains have a low concentration of fat, but their high feeding rates make them a major dietary source of FA. Oilseeds, high fat byproduct feeds, and liquid fats are economical sources of FA, but care must be taken to not disrupt rumen fermentation. Lastly, dry fats are convenient to add on farm and provide the opportunity to customize absorbed FA profile, but are expensive and differ greatly in FA profile, risks, and benefits.

Forages

Lipids in forages are predominantly in the plant leaf in the form of glycolipids. Total FA concentration in forages is only around 50% of the ether extract value because of the large non-FA content of glycolipids. Fatty acids in forages are highly unsaturated and normally contain more than 50% α-linolenic acid (C18:3). Forages would be a great source of essential FA, but these FA are readily available in the rumen and extensively biohydrogenated. Grasses contain higher levels of FA in the early growth stages (can exceed 5%) and are a common culprit in diet-induced MFD with intensive grazing. Lastly, wilting and drying before harvest decreases the availability of unsaturated FA in forages because of the formation of indigestible resins.

Cereal Grains

Corn, wheat, barley, and oats all have similar FA profiles and contain approximately 55% linoleic acid (C18:2 n-6) and less than 1% omega-3 FA. Corn grain is higher in total fat than small grains. In a recent characterization of test plots of 36 commercial hybrids we observed a range of 3.3 to 3.9% total FA (10^{th} to 90^{th} percentile) and 55.7 to 60.0% linoleic acid. In corn, the majority of the FA is in the germ and processing methods that increase rate of digestion will likely increase the rate of rumen availability of the unsaturated FA.

Corn Silage

Corn silage is a mixture of grain and forage and thus has a combination of the forage and grain attributes discussed above. We recently found that 80% of the total fat and over 90% of the oleic (C18:1 n-9) and linoleic (C18:2 n-6) acid was found in the kernel and over 70% of the α-linolenic acid (18:3 n-3) was in the leaves. Therefore, grain concentration is going to impact the FA concentration and profile. Additionally, we expect that unsaturated FA in the kernel are rapidly available in well processed and ensiled silage. We also observed moderate variation in FA concentrations and profiles of corn silage test plots with C18:2 ranging from 0.94 and 1.60% of DM (10^{th} and 90^{th} percentile). Fatty acid profile of corn silage is going to be highly dependent on genetics. Routine analysis is probably not needed, but it is advisable to determine each crop’s profile or when trouble-shooting diet-induced MFD.

Oilseeds

Feeding oilseeds is commonly an economical and convenient method to increase FA intake. The FA are highly unsaturated and are mostly found in triglycerides in the fruit contained inside the seed coat. The seed coat and processing method dictate the rate of rumen availability, which has a large impact on the associative effect of the FA on the rumen. Although the release rate of FA in the rumen can be decreased by less aggressive processing, oilseed unsaturated FA are normally extensively biohydrogenated and it is difficult to bypass unsaturated FA in oilseeds.

Expeller oilseed meals are normally higher in fat (~9%) than solvent extracted meals (<3%), but this depends on the seed, processing plant, and batch. Some facilities may also add phospholipids and free recovered oil back to the meal, which may change rumen availability and risk for oxidative rancidity.

Oilseed FA profile has and continues to undergo strong genetic selection to modify FA profile for human health and processing characteristic. The recent development of high-oleic acid soybeans (>70% C18:1) is expected to have an impact on animal feeds. These specialty oilseeds are commonly processed in specific facilities allowing identification, but as the market grows they may become mixed within the commodity market.

Byproducts

Many high fat byproduct feeds are available at a reasonable cost and vary considerably in amount and profile of FA. The FA in many of these byproducts is rapidly available. Arguably, many of the issues with diet-induced MFD when distiller's grains with solubles is fed may be due to the rapid availability of the unsaturated FA and may not be the amount of unsaturated FA. Many ethanol plants are now recovering some of the lipid to be sold as oil, which has decreased fat concentration. The key element to any byproduct feed is managing the variation to take maximal advantage of its value.

Liquid Fats

Liquid fats can be an economical source of FA. They adhere to feed particles and are expected to be rapidly available in the rumen. Liquid fats vary in their FA profile depending on their source, and changes in oilseed FA profile also impact vegetable oil streams. Quality can be an issue in liquid fats as unsaturated FA are more susceptible to oxidation once extracted and some processing streams include heating. Antioxidants are commonly added to liquid fats, especially when they are highly unsaturated. Measuring unsaponifiable matter can also provide some indication of quality.

Dry Fat Supplements

Dry fat supplements are convenient because they are concentrated sources of FA that are easy to handle on farm. They differ greatly in their source, FA profile, and metabolic effects. Some dry fat supplements may melt in extreme temperature conditions.

Prilled Saturated Fats

Saturated FA are naturally ruminal inert as they are not toxic to microbes and do not require biohydrogenation. The first major difference in prilled fats is their free FA concentration. Hydrogenated (saturated) TG are poorly digested as they are not hydrolyzed in the rumen and the cow has poor lipase activity in the intestine. Most prilled supplements on the market are high free FA products (80 to 99%) and decreased digestibility may occur in products that are higher in TG. The second major difference is FA profile. Traditionally, prilled products were a mixture of palmitic and stearic with a lower concentration of oleic. More recently, enriched palmitic acid (> 80% C16:0) products have become available as a byproduct of palm oil manufacturing. Additional differences exist in FA source and manufacturing. For example, saturated FA can be enriched by separation from unsaturated FA or unsaturated oils or made by partial or full hydrogenation of unsaturated FA. Partial hydrogenation adds the risk of presence of bioactive *trans*-FA. Also, some plant-based sources have an increased risk for contamination of residues including dioxins. Prill size can also differ between manufacturing processes and the impact on digestibility has not been extensively investigated, but appears to be minor.

Prilled free FA blends of palmitic and stearic acid have the longest history in the literature and generally do not decrease DMI and are well digested. Enriched palmitic acid products (80 to 90% C16:0) have been extensively investigated in the past 6 years, and generally result in a small increase in milk fat (~0.2-unit increase when fed at 1.5 to 2% of diet) and are also well digested. Limited research has been done with highly enriched palmitic and stearic acid products (> 95%). The highly enriched product used in these experiments decreased diet FA digestibility considerably, although it is unclear if this is attributed to specific attributes of the product fed, such as prill size, or the high enrichment.

Calcium Salts of Fatty Acids

Calcium salts of palm FA were developed in the 1980's to allow feeding unsaturated FA without negative effects on fibre digestion. Traditionally, calcium salts were made from palm oil distillate, but specialty blends that include n-6 and n-3 FA are now available. More recently, there has been interest in using calcium salts to protect unsaturated FA in the rumen and increase essential FA absorption. Using calcium salts is the only method currently available to increase rumen bypass of unsaturated FA; however, the effectiveness of calcium salts is limited. The release of highly unsaturated FA in the rumen increases the risk of diet-induced MFD when feeding calcium salts enriched in polyunsaturated FA compared to feeding a prilled saturated FA supplement.

■ Conclusions

Fat supplementation continues to evolve with changes in oilseed FA profile through selection and new dry fat supplements available from palm oil processing. Fatty acids have been appreciated as bioactive FA for some time with great interest in CLA-induced MFD and essential FA, but there also appears to be differences between saturated FA. We will continue to move toward balancing for specific FA as our knowledge of ruminal biohydrogenation, specific roles of individual FA, and strategies to protect unsaturated FA improves.

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