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Understanding and Optimizing the Jungle of Bypass Fats

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ABSTRACT

Nutritionists attempt to meet nutrient requirements and regulate energy balance through dietary interventions. Traditionally, fat supplementation has been used to increase dietary energy density without increasing diet fermentability. Nearly all dietary ingredients contribute some fat to the diet and ingredients with a low fat intake that are fed at high rates are commonly overlooked, but contribute greatly to fat intake. Feeding high fat byproducts and the development of varieties selected for a specific fatty acid (**FA**) profile is quickly changing the FA profile of many fat sources. Fatty acids are well known to be bioactive nutrients that modify metabolism and physiology. The use of lipids as an energy source, substrate for cellular membrane synthesis, substrate for signaling factor synthesis, and their bioactivity make determination of *requirements* difficult. Important aspects of fat supplements are their digestibility, effect on intake and milk production, and their ability to modify physiology. The massive growth in the palm oil industry has broadened the type of products available and highlighted additional differences in metabolism of FA. Selection of fat supplements should consider the basal diet, rumen available fat sources, and the goal of using the fat supplement. Our understanding of FA continues to grow and provides tools to increase production, efficiency, and health of dairy cows.

INTRODUCTION

Lipids are a broad group of compounds that are soluble in organic solvent including waxes, sterols, and compounds that include fatty acids (**FA**) including triglycerides, phospholipids, and glycolipids. Dietary FA are the nutritionally important compoenent 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 yr 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.

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 (Kellner, 1907). It is interesting that over 100 yr 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 (Staples et al., 1998), and modifying FA profile of milk (Glasser et al., 2008a; Shingfield et al., 2013). The field of ruminant FA metabolism underwent tremendous growth with the Biohydrogenation Theory of milk fat depression (**MFD**) and the identifaction of bioactive conjugated linoleic acid (**CLA**) isomers. Most recently, availability of enriched palmitic acid supplements provides additional options.

Fat Digestion and Metabolism

Fatty acids are not fermented 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 currently is growing interest in the positive human health attributes of these FA and ruminant meat and milk is the predominant source in the human diet. Ruminal synthesis of FA is increased when feeding low fat diets as 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 they are toxic and because they 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 limits the amount of unsaturated FA that can be fed to dairy cows [see Harvatine et al. (2009) and below]. Biohydrogenation also severely limits absorption of the essential polyunsaturated FA by the cow.

Rumen Availability of FA

Increasing unsaturated FA increases the toxic effect on microbial populations and also increases the substrate required for biohydrogenation. The first step in balancing any nutrient is considering diet concentration and Jenkins (2011) 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. Traditionally, the second step in balancing nutrients is consideration of rates. Although considerable effort has been put towards determining rates of fiber and starch digestion in the rumen, little 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 (**DGS**) is rapidly available and has a large impact in the rumen compared to whole cottonseed that is slowly released. Previous work has demonstrated that increased grinding of oilseeds increases their risk of diet-induced MFD. Jenkins et al. (2016) 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 fiber digestion as they are insoluble salts that block FA metabolism by microbes (Palmquist and Jenkins, 1980). It appears that 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 (Sukhija and Palmquist, 1990). However, calcium salts are far less disruptive to rumen fermentation than feeding a free oil.

Digestibility of FA

Intestinal absorption of FA is quite different in the ruminant as duodenal flow is predominantly saturated free FA. Non-ruminants depend on monoglycerides and unsaturated FA for formation of miscelles, while the ruminant lysolecithin aids formation of micelles as a very potent emulsifier (Doreau and Chilliard, 1997). In the ruminant, there is a large decrease in total tract digestibility when saturated triglycerides (**TG**) are fed as they are more resistant to ruminal and intestinal lipolysis than unsaturated TG (Elliott et al., 1994; Elliott et al., 1999). There is significant variation in total tract digestibility in the literature that reflects both variation between diets and the technical challenges of digestion studies. Total tract FA absorption is roughly between 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 using different approaches have observed little difference in digestibility between FA, although FA digestibility decreases with increasing fat intake (Glasser et al., 2008b; Schmidely et al., 2008; Boerman et al., 2015). More attention should be paid to FA digestibility, but will require a dedicated effort to conduct well-controlled experiments.

Metabolic Fate of FA

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 and are energetically efficient processes as FA can be directly deposited and do not have any energy loss. The metabolic fate of absorbed FA is expected to depend 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; (Mosley et al., 2007)], but also have been observed with oilseeds and other FA supplements (Weiss and Pinos-Rodriguez, 2009). After peak lactation, dietary FA will be increasingly partitioned towards body reserves. Importantly, oxidization of FA spares other nutrients from oxidation, which creates a complicated discussion of the metabolic impact of dietary FA.

Essential FA

Fatty acids can be categorized as essential or nonessential based on the animals capacity to synthesize or conserve the required amounts and linoleic (C18:2 n-6) and linolenic (C18:3 n-3) acid are traditionally considered the two essential FA (Cunnane, 2000). 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. This overlap and 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 what is required 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 effect of individual FA. This includes their effect on hard to research processes such as immunology and reproduction. Essential FA have been a subject of conversation in many species, including ruminants, for many years. Absorption of essential FA is very limited in ruminants, but there are no reports of classical FA deficiency in adult ruminants and 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 (Drackley, 2000). It appears that essential FA are normally available in adequate concentrations based on production requirements, however there may be benefits to FA supplementation to health including improving reproductive efficiency and immunology.

Effect on Intake

A main goal of fat supplementation is to increase energy intake and 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 (Allen, 2000). 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. Abomasal infusions of unsaturated FA with a lower C16:C18 FA ratio decreased DMI and energy intake (Drackley et al., 1992, Christensen et al., 1994). Finally, 4-d continuous intravenous infusion of both palmitic and oleic acid significantly decreased intake, while stearic acid only numerically decreased intake (Vandermeerschen-Doize and Paquay, 1984). Recent work with enriched palmitic acid supplements have observed decreased intake compared to no fat controls (Lock et al., 2013; Rico et al., 2014a), although the overall decrease in DMI was not significant and energy intake was increased in a recent meta-analysis (deSouza et al., 2016)

Fats in the Basal Diet

Nearly all feed ingredients contain FA and it is best to think about diet FA starting with the base diet through high fat feeds and then 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 n3, reviewed by Glasser et al., 2013). Forages would be a great source of essential FA, but they 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 rather 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 and varies with variety including specially bred high-oil corn. In a recent characterization of a field test 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 (C18:2 n-6). In corn, the majority of the FA is in the germ and it is expected that processing methods that increase rate of digestion will 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) 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, which was raised in 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

Oilseeds are 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 dictates 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 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. For example, canola is a low erucic acid (C22:1) rapeseed. To aid the movement away from partially hydrogenated frying oils, low α-linolenic acid (18:3 n-3) soybean oil was developed in the mid-2000s, which allows increased oil frying life and oxidative stability. The next step has been development of high-oleic acid soybeans (> 70 % C18:1) that are currently under limited commercial production in the US. Once final approvals in key export countries are received it is expected to become a major part of the US soybean acreage. 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, including DGS and bakery byproducts. These byproducts vary considerable in amount and profile of FA. The FA in many of these byproducts is rapidly available. For example, condensed corn solubles is a high fat stream in distillers plants that is added back to distillers grains in making DGS. This fat is thus adhered to the outside of the grain and rapidly available in the rumen. Arguably, many of the issues with diet-induced MFD when DGS 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 of DGS. The key element to any byproduct feed is knowing the source and managing the variation to take maximal advantage of their value.

Liquid Fats

Liquid fats can be an economical source of FA, but require specialized equipment. Liquid fats 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. Importantly, the FA profile of lard and tallow changes as feeding practices change and the recent increase in DGS feeding has increase unsaturated FA in these oils. Changes in oilseed FA profile also impacts 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 the quality of the fat.

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. 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 would be expected in products that are high 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. Hydrogenation adds the risk of presence of bioactive *trans*-FA, if the process is not complete, and some methods may result in addition of small amounts of metals used as a catalyst. 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 yr 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 %; (Piantoni et al., 2013; Rico et al., 2014b; Piantoni et al., 2015)]. 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 FA

Calcium salts of palm FA was developed in the 1980's to allow feeding unsaturated FA without negative effects on fiber 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. Calcium salts are the only method currently available to increase rumen bypass of unsaturated FA, however their effectiveness 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.

Recommendation on Fat Feeding

The strategy for balancing FA in a diet should be based on your goal and the feeds available. It is best if total dietary FA does not exceed 7 % of DM. First consideration should be given to the FA entering from forages and cereal grains and note the rate of availability of these FA. Next, use economical sources of rumen available FA including high fat byproducts, liquid fats, and oilseeds. It is especially important to note the profile and rate of availability of these sources and their interaction with the basal diet. The amount of these that can be incorporated will be limited as to not disrupt rumen fermentation and cause diet-induced MFD. Lastly, dry fat supplements should be selected based on your goal. For example, supplements highly enriched in palmitic acid provide the most consistent increase in milk fat yield, prilled saturated blends of palmitic and stearic may increase energy intake most effectively, and calcium salts have the potential to increase unsaturated FA flow to the duodenum, although the level of protection is low.

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 expect that we will continue to move towards balancing for specific FA as our knowledge of ruminal biohydrogenation, specific roles of individual FA, and strategies to protect unsaturated FA improve.

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