What We Need to Know to Improve the Utilization of Fat in Diets

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Abstract

High fat ingredients are commonplace in diets fed to dairy cattle and include commercial fat supplements designed for convenient transport and mixing, oilseeds such as cottonseed or soybeans, or byproducts such as distillers grains, tallow, or food processing wastes. Strategies for optimizing benefits from feeding additional fat remain focused today, as in the past, on minimizing problems with intake, rumen function, and digestibility. All of these limitations are a function of several important fat attributes, including its fatty acid content, the relative proportions of saturated and unsaturated fatty acids, the concentration of free fatty acids, accessibility of the fat to microbial exposure, and the extent of chemical alteration such as calcium salts. When fed properly, animal performance benefits from feeding additional fat are well documented and extend beyond just the expected improvements in lactation performance based solely on the fat energy value. These additional benefits have included improvements in efficiency, reproductive performance, and even the immune system and disease resistance. However, many exciting future benefits of feeding additional fat to dairy cattle may be on the horizon. These might include managing the rumen production of biohydrogenation trans intermediates to take advantage of metabolic benefits, or managing the absorption of selected fatty acids to enhance their function as precursors for signaling molecules, and perhaps even feeding fatty acids prepartum for fetal imprinting and potential lifetime production benefits.

Introduction

The information needed to improve the utilization of fat for dairy cows is dependent on whether the timeframe for utilization is on the present or on the future.

Present day fat uses:

- Maximize fat as an energy source for milk yield or to restore body weight,
- Avoid problems with intake, rumen function, or milk components, and
- Take advantage of reproduction and possible immune benefits.

Possible future fat uses:

- All the above present day benefits plus,
- Manage the rumen production of biohydrogenation trans intermediates to take advantage of their physiologic and metabolic benefits,
- Manage ratios of selected fatty acids to control interactions that enhance their function as precursors for signaling molecules, and
- Feed selected fatty acids prepartum for fetal imprinting and potential lifetime production benefits.

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Future fat benefits are backed by scientific findings and already have documented benefits in nonruminant species, including humans. The prospects for dairy cattle are even more exciting given the complexity of fatty acid isomers synthesized daily by the rumen microbial population and their possible transfer to body tissues. However, because the volume of information is too large to cover both present and future aims, and there remains a need to better utilize fats for present day needs, this paper will focus only on some main points that enhance present day fat utilization opportunities.

To address present day issues, this paper will take the approach that a nutritionist is presented with an unknown fat source for possible inclusion in a dairy total-mixed ration (**TMR**) and examines the information that should then be obtained to improve its utilization. Some of the key points and a brief explanation are given below.

Understand the Fat Characteristics Affecting Utilization

Total fatty acid content

The fatty acid portion of fat supplements provides all the energy and tissue benefits so it is important to verify its content. Caution is advised when obtaining fats from unknown vendors to be sure that considerable impurities do not still remain in the product that lower the fatty acid and energy contents. Fatty acid content of fat supplements can be diluted by nonfatty acid components that have lower or no energy value. Fat content has traditionally been determined as the ether-extractable component of the feed. When defined in this manner, there can be considerable variation in fat content among feed ingredients. Among the lowest is the ether extract in grains and forages. In addition to extracting fat, ether also extracts some carbohydrate, vitamins, and pigments. Therefore, the ether extract in cereal grains, forages, and the total mixed ration often contain less than 60% fatty acids (Palmquist and Jenkins, 2003). Because of the problems inherent with ether extract, many laboratories have moved to determining fatty acid content of feeds instead of ether extract.

Most plant oils contain 100% ether extract, with a high percentage of fatty acids. The impurities extracted, such as water and pigments, are removed during refining, leaving the commercial plant (soybean oil, canola oil, corn oil, etc) and animal (tallow, grease, etc.) fats with mainly triglycerides consisting of 90 to 93% fatty acids. The remaining 7 to 10% is mainly glycerol. Glycerol is readily utilized as an energy source, but only contains the energy of carbohydrates. Rather than guessing, it pays to have a sample of the fat analyzed for fatty acid content and profile.

Fatty acid composition

Fatty acids are chains of carbons that end in an acid group, or carboxyl group as is referred to in biochemistry. An example of a common fatty acid is stearic acid with 18 carbons and no double bonds.

Fatty acids, such as stearic acid, are referred to as saturated (Figure 1) because all the carbons are holding the maximum number of hydrogens possible, or the fatty acid is “saturated” with hydrogen. Stearic acid is low in plant oils but present in higher amounts in animal fats, particularly in fats obtained from ruminant species, such as beef tallow.

Oleic acid and linoleic acid are examples of unsaturated fatty acids containing one or more double bonds. Oleic acid has a single double bond between carbons 9 and 10, and

is referred to as a monounsaturated fatty acid. Linoleic acid is a polyunsaturated fatty acid containing two double bonds between carbons 9 and 10, and between carbons 12 and 13. Oleic acid is the predominant fatty acid in animal fats and some plant oils (Table 1). Linoleic acid is the predominant fatty acid in many plant oils, including cottonseed oil, soybean oil, and corn oil. Linolenic acid is the predominant fatty acid in most forage species, followed by linoleic acid (Hatfield et al., 2007). Linolenic acid follows a similar seasonal pattern (Bauchart et al., 1984); as linolenic acid declines over the summer months, percentages of palmitic and linoleic acid increases.

Saturated and unsaturated fatty acids have different effects on rumen function and also do not have equal intestinal digestibilities. Therefore, information on fatty acid composition will help users to develop reasonable expectations on utilization of the fat source and animal performance.

Percentage of free fatty acids

Lipid extracted from plants contains fatty acids that are predominately bound to the carbon backbone of glycerol. In vegetable oils all three glycerol carbons have fatty acids attached giving the name triglycerides. Forage lipids more commonly have fatty acids attached to only two of the three glycerol carbons. Fatty acids released from the glycerol backbone are called free fatty acids (**FFA**). Fatty acids can be released from glycerol by lipase enzymes of plant or ruminal origin.

Triglycerides often exhibit reduced antibacterial effects compared to an equal quantity of free acids. Methane production in cultures of washed ruminal microbes, for example, was inhibited more by the addition of linseed oil fatty acids than by the addition of an equal amount of linseed oil triglycerides (Demeyer and Henderick, 1967). In another in vitro study, tallow added to cultures as free acids reduced the ratio of acetate to propionate by 43 to 66% compared to only a 4 to 6% reduction in the ratio when tallow was added in triglyceride form (Chalupa et al., 1984). A recent study with lactating dairy cows showed no differences in milk or components when diets were supplemented with 2% soybean triglycerides or soybean FFA (Boerman and Lock, 2014). Discrepancies between in vitro rates of lipolysis versus in vivo rates may account for part of the esterification effect. Lower rates of lipolysis would release FFA over a longer time period, thus diminishing the effects on fermentation and rumen lipid metabolism.

Calcium salts

Calcium salts of fatty acids were originally developed in the early 1980's at The Ohio State University as a form of rumen-inert (by-pass) fat to avoid ruminal fermentation and digestion problems. As long as the bond with Ca is maintained in the rumen, fatty acids do not express antimicrobial effects or interfere with the microbial population. Release of fatty acids from the Ca bond is enhanced as ruminal pH declines. The release by low pH also is greater as unsaturation increases.

By the early 1990's, calcium salts were receiving some attention for partially escaping biohydrogenation. For instance, Wu et al. (1991) reported 49% biohydrogenation of fatty acids from calcium salts of palm oil compared to 80 and 62% biohydrogenation for animal-vegetable fat and the control diet, respectively. Klusmeyer and Clark (1991) similarly found lower biohydrogenation for diets supplemented with calcium salts compared to a control diet. Based on the results of these early studies, several rumen-protected fat products have

emerged commercially in recent years that vary in the type and concentration of polyunsaturated fatty acids. If oilseeds are excluded, it is difficult to locate rumen-protected fat sources that are commercially available other than those containing calcium salts of unsaturated fatty acids.

How Fat Characteristics Can be Used to Overcome Limitations and Improve Utilization

Intake limitations

Fat added to dairy rations can reduce feed intake, which can greatly reduce or even eliminate a positive production response. Even as little as 0.5 kg (1.1 lb) less feed intake can neutralize any energy advantage coming from typical levels of added fat, thus preventing a positive production response. Reductions in feed intake have been reported for a wide variety of fat sources, and often the intake depressions are less severe for animal fats than for vegetable oils or some commercial fat supplements. In general, intake depression problems were more severe when fat supplements were higher in unsaturated fatty acids than when they were higher in saturated fats acids.

For instance, across a summary of more than 20 dairy studies feeding tallow or grease, only two studies showed significant depressions in feed intake (Allen, 2000). A summary of the literature by Onetti et al. (2004) showed that the intake effects of tallow were dependent on forage source. Tallow added to corn silage diets reduced intake and failed to increase milk production. However, a positive milk production response was seen when tallow was fed in alfalfa-based diets, or in diets with similar alfalfa and corn silage proportions. Rabiee et al. (2012) also reported greater decreases in DMI for oilseeds and Ca salts of unsaturated fatty acids than for saturated fatty acids or tallow (Figure 2).

Several causes for the depression in feed intake by unsaturated fatty acids are under consideration. These include reduced gut motility, reduced acceptability of diets with added fat, release of gut hormones, and oxidation of fat in the liver (Allen, 2000). Refer to Allen (2000) for a description of each factor and a comparison of fat sources. Gut hormones continue to receive considerable attention as regulators of food intake. Depressed feed intake in cows fed fat supplements has been attributed to changes in cholecystokinen (Choi and Palmquist, 1996) and glucagon-like peptide 1 (Benson and Reynolds, 2001). Other peptides of gut origin, such as peptide YY, pancreatic glucagons, glicentin, and oxyntomodulin, have been linked to reduced feed intake patterns in animals fed fat (Holst, 2000). Past work has shown that abomasal infusion of unsaturated fatty acids causes greater feed intake depression than infusion of saturated fatty acids (Drackley et al., 1992; Bremmer et al., 1998). A study by Litherland et al. (2005) showed that the intake depression was greater following abomasal infusion of unsaturated free fatty acids than it was following infusion of unsaturated triglycerides. Also, as intake declined in the study by Litherland et al. (2005), the concentration of plasma glucagon-like peptide 1 increased but plasma concentration of cholecystokinen did not change.

Rumen limitations

Fat supplements must be limited to just a few percentage units in ruminant diets to avoid ruminal digestibility problems resulting from antimicrobial activity of their constituent fatty acids (Stoeffel et al., 2015). Fat sources that have the potential to cause ruminal fermentation problems are referred to as rumen-active fats. Antibacterial effects of fatty acids in the rumen are complex and depend on interrelationships among fatty acid structure, fatty acid concentration, the presence of feed

particles, and rumen pH (Jenkins, 2002). Fatty acid structural features that enhance antibacterial activity in the rumen include a free acid group on the carbon chain and the presence of one or more double bonds (Table 2). Therefore, enhancing FFA and fatty acid unsaturation in fat sources generally reduces the amount that can be included in cattle diets. Several commercial fats minimize ruminal fermentation problems by enhancing the concentration of the less antibacterial saturated fatty acids. These are referred to as rumen-inert fats to signify their lower antimicrobial effects in the rumen.

The microbial population in the rumen also is responsible for extensive transformation of dietary lipid. Lipid transformations include lipolysis to release free fatty acids from complex plant lipids, and biohydrogenation to convert unsaturated fatty acids in plant matter to more saturated lipid end products. The biohydrogenation of linoleic acid in the rumen (Figure 3) begins with its conversion to conjugated linoleic acid (**CLA**). In this initial step, the number of double bonds remains the same but one of the double bonds is shifted to a new position by microbial enzymes. Normally, the double bonds in linoleic acid are separated by two single bonds, but in CLA, the double bonds are only separated by one single bond. Many types of CLA are produced in the rumen of dairy cows (Bauman and Lock, 2006), but a common CLA produced from biohydrogenation of linoleic acid is *cis*-9, *trans*-11 C18:2. Recent research results link milk fat depression with the formation of bioactive *trans* fatty acid intermediates produced from biohydrogenation (**BH**) of unsaturated fatty acids by the rumen microbial population. Among the most potent intermediates causing milk fat deprression are several CLA isomers, such as *trans*-10, *cis*-12. Baumgard et al. (2000) reported that *trans*-10, *cis*-12 infused post-ruminally in lactating dairy cows decreased milk fat content 42% and milk fat yield 48%. *Trans*-9, *cis*-11 CLA and *cis*-10, *trans*-12 CLA were also reported to inhibit milk fat synthesis in dairy cows (Sæbø et al., 2005; Perfield II et al., 2007), with the former causing a 15% reduction in milk fat yield.

As biohydrogenation progresses, double bonds in the CLA intermediates are then hydrogenated further to trans fatty acids having only one double bond. *Trans* double bonds only differ from *cis* double bonds in the placement of the hydrogens. The hydrogens are located on opposite sides of the double bond for *trans* fatty acids, but on the same side of the double bond for *cis* fatty acids. Although the difference in structure between *trans* and *cis* fatty acids appears small, it causes significant differences in their physical and metabolic properties. A final hydrogenation step by the ruminal microbes eliminates the last double bond yielding stearic acid as the final end product. As a result of biohydrogenation, there is extensive loss of unsaturated fatty acids from the mouth to the duodenum of the animal.

Intestinal digestibility limitations

Low intestinal digestibility of fatty acids in fat supplements can be another factor reducing their digestible energy (**DE**) value for ruminant diets. Differences in DE values among fat sources published in NRC for Dairy Cattle (2001) are due mainly to differences in their true digestibilities. True digestibilities assumed by NRC for Dairy Cattle (2001) ranged from a high of 86% for vegetable oils and calcium salts to a low of 43% for partially-hydrogenated tallow. Tallow was assigned an intermediate digestibility of 68% in NRC for Dairy Cattle (2001).

It was not surprising, based on results from previous studies, that feeding partially hydrogenated tallow reduced fatty acid

digestibility. Hydrogenation of yellow grease to reduce its iodine value (**IV**) from 56 to 18 reduced apparent fatty acid digestibility in the total tract from 67.8 to 47.4% (Jenkins and Jenny, 1989). Fatty acid digestibilities pooled from 11 studies were normal (similar to control values) when IV exceeded 40 (Firkins and Eastridge, 1994), but below IV 40 fatty acid digestibility progressively dropped as IV declined.

Lower digestibility of hydrogenated fats may be related to their higher content of saturated fatty acids. The presence of 1, 2, or 3 double bonds increased fatty acid digestibility a similar amount. Grummer and Rabelo (1998) also reported similar improvements in apparent fatty acid digestibility from the presence of one or more double bonds. True digestibility of stearic acid was 53% and lowest among the 18 carbon fatty acids. Introducing a single double bond improved true digestibility to 78.4%. It should be pointed out that some studies did not distinguish between flows of *cis* or *trans* 18:1 to the duodenum, which might tend to lower 18:1 digestibilities.

Jenkins (2006) summarized fatty acid digestibilities from studies that included data only on lactating dairy cows fed a control diet with no high fat ingredients and fat sources that were not combined with other fats. A total of 32 published studies met all criteria and 45 studies were rejected. The selective criteria limited the number of observations for some fat sources, especially oilseeds and vegetable oils that were usually fed in combination with other fat sources.

Among the fat sources examined, only tallow and calcium salts of palm fatty acids had mean total tract digestibilities that were numerically higher than the control diets. The ranking was similar when digestibilities of the fat sources were estimated by difference. Conversely, the hydrogenated fat sources had substantially lower fatty acid digestibilities whether expressed as apparent digestibilites, or were calculated by difference. The hydrogenated fat sources also had the highest standard deviations, suggesting that wider variation exists in digestibility values of hydrogenated fats compared to other fat sources. Further examination of the data revealed that about 80% of the hydrogenated fat cases depressed diet fatty acid digestibilities more than 5%. Tallow depressed diet fatty acid digestibilities more than 5% from control fatty acids in only 27% of the cases examined.

There have been several other summaries of fatty acid digestibility reported in ruminants, including dairy cows, over the last 12 years (Table 3). Duodenal to feces digestibilities in dairy cattle were reported by Moate et al. (2004) from 8 studies, giving a total of 36 observations. Their summary excluded hydrogenated tallow and whole soybeans. Glasser et al. (2008) did a meta-analysis of C18 fatty acid digestibilities involving 294 observations in 77 studies. They included duodenal to ileal digestibilities for dairy, beef, and sheep data but found no significant species difference. They also excluded data on hydrogenated tallow. A more recent meta-analysis on duodenal to ileum digestibilites in lactating dairy cows had up to 18 observations and excluded partially-hydrogenated tallow (Boerman et al., 2015). When digestibility data was averaged across all studies, digestibility of unsaturated fatty acids were higher than saturated fatty acids, and stearic acid had the lowest digestibility.

Fatty Acid Outflow from the Rumen and Animal Performance

Meeting essential fatty acid demands

Omega fatty acids belong to one of three families, the ω-9, ω-6, or ω-3 family. Each family has a parent fatty acid that is converted to other biologically-active acids within the same omega family (Figure 4). The only parent fatty acid that can be made by body tissues is oleic acid. The ω-6 and ω-3 parent compounds (linoleic and linolenic acids) cannot be synthesized by body tissues and, therefore, must be supplied in the diet. Thus, linoleic and linolenic acids are regarded as essential because they are required for normal tissue function but cannot be synthesized by body tissues.

A typical total mixed ration of grains and forages generally contains adequate essential fatty acids to meet the needs of the animal. However, the majority of the dietary essential fatty acids are destroyed by microorganisms through biohydrogenation.

Part of the interest in omega fatty acids in dairy cattle is to enhance their concentration in milk for value-added opportunities, and part of the interest is to enhance their concentration in body tissues of the cow to enhance production and health. Omega fatty acids in milk are increased to improve manufacturing properties and to increase fatty acid nutraceuticals known to enhance human health. Increasing omega fatty acids in tissues of the cow has potential benefits on reproductive performance, immunity, and disease resistance, and positive hormonal shifts.

In a few studies, feeding fat to lactating dairy cows has improved reproductive performance, implying possible benefits on lifetime production potential. Reported improvements of reproductive performance from added fat include higher conception rates (Schneider et al., 1988; Sklan et al., 1989), increased pregnancy rates (Schneider et al., 1988; Sklan et al., 1991), and reduced open days (Sklan et al., 1991). However, supplemental fat has had little or no benefit on reproductive efficiency in other studies (Carroll et al., 1990). An extensive meta-analysis (Rodney et al., 2015) of 17 studies examining fat effects on reproductive performance in cows reported that fat caused a 27% increase in pregnancy to service and a reduction in calving to pregnancy interval. They also reported from the meta-analysis that feeding fat has a positive effect on fertility and production when fed during the transition period.

The mechanism of how fat supplements alter reproductive performance is not clear. Fat may function in one capacity by providing additional energy during early lactation to support improved productive functions, including reproduction. Negative energy balance delays ovulation and the initiation of the first normal luteal phase (Butler et al., 1981). However, recent studies also suggest that the mechanism involves an energy independent response to fat.

When an equal quantity of energy from glucose, saturated animal fat (tallow), or unsaturated fat (yellow grease) were infused into lactating dairy cows via the abomasum, the fat but not carbohydrate decreased plasma estradiol and increased progesterone (Oldick et al., 1997). The study by Oldick et al. (1997) also demonstrated the potential to decrease prostaglandin $F_{2\alpha}$ (**$PGF_{2\alpha}$**) synthesis by supplying elevated concentrations of polyunsaturated fatty acids (**PUFA**). These results were similar to previous reports that intravenous infusion of unsaturated fatty acids from a soy oil emulsion increased plasma $F_{2\alpha}$ and number and size of follicles (Lucy et al., 1990, 1991). Ovarian follicular growth was

also stimulated more in Brahman x Hereford cattle by fat compared to equal energy from carbohydrate, with a greater effect observed for fats with higher PUFA (Thomas et al., 1997). Hinckley et al. (1996) provided further support of the role of PUFA on reproductive function in ruminants. In their study, dispersed bovine luteal cells had a dose-dependent decline in progesterone production and an increase in production of prostaglandin as PUFA in the media increased. Results such as these continue to demonstrate a reproductive advantage from increased absorption of PUFA compared to other fat sources, such as monounsaturated fats.

Immune system

CLA decreased the growth rate in chicks and rats after they were injected with endotoxin (lipopolysaccharide; **LPS**). This probably was caused by release of cytokines and the prevention of the catabolic effects (Cook et al., 1993). Miller et al. (1994) examined endotoxin-induced growth suppression in mice fed with 0.5% fish oil and CLA. The fish oil fed-group lost twice as much body weight after the inoculation with endotoxin than the CLA-fed groups. These researchers found that the CLA in the endotoxin injection inhibited anorexia (a decreased sensation of appetite) and increased splenocyte blastogenesis, concluding that it might inhibit arachidonic acid synthesis, thus preventing the catabolism of tissue by removing eicosanoid precursors. In addition, Bontempo et al. (2004) examined the effects of CLA on the immunological variables of lactating sows and piglets fed with a 0.5% CLA diet. They found that CLA-fed sows exhibited increased colostrum IgG and serum leptin, and IgG and lysozyme. Nursing piglets of CLA-fed sows also exhibited higher levels of IgG and lysozyme. As these results show, dietary CLA enhanced the effect of immunological variables in lactating sows and piglets.

References

Allen, M.S. 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cattle. J. Dairy Sci. 83:1598-1624.

Bauchart, D., R. Verite, and B. Remond. 1984. Long-chain fatty-acid digestion in lactating cows fed fresh grass from spring to autumn. Can. J. Anim. Sci. 64:330-331.

Bauman, D.E. and A.L. Lock. 2006. Concepts in lipid digestion and metabolism in dairy cows. Proc. Tri-State Dairy Nutr. Conf. pp. 1-14. Available at: http://tristatedairy.org.

Baumgard, L.H., B.A. Corl, D.A. Dwyer, A. Saebo, and D.E. Bauman. 2000. Identification of the conjugated linoleic acid isomer that inhibits milk fat synthesis. Am. J. Physiol. Regul. Integr. Comp. Physiol. 278:R179-R184.

Benson, J.A., and C.K. Reynolds. 2001. Effects of abomasal infusion of long-chain fatty acids on splanchnic metabolism of pancreatic and gut hormones in lactating dairy cows. J. Dairy Sci. 84:1488-1500.

Boerman, J.P., J.L. Firkins, N.R. St-Pierre, and A.L. Lock. 2015. Intestinal digestibility of long-chain fatty acids in lactating dairy cows: A meta-analysis and meta regression. J. Dairy Sci. 98:1-15.

Boerman, J.P., and A.L. Lock. 2014. Effect of unsaturated fatty acids and triglycerides from soybeans on milk fat synthesis and biohydrogenation intermediates in dairy cattle. J. Dairy Sci. 97:7031-7042.

Bontempo, V., D. Sciannimanico, G. Pastorelli, R. Rossi, F. Rosi, and C. Corino. 2004. Dietary conjugated linoleic acid positively affects immunologic variables in lactating sows and piglets. J. Nutr. 134:817-824.

Bremmer, D.F., L.D. Ruppert, J.H. Clark, and J.K. Drackley. 1998. Effects of chain length and unsaturation of fatty acid mixtures infused into the abomasum of lactating dairy cows. J. Dairy Sci. 81:176-188.

Butler, W.R., R.W. Everett, and C.E. Coppock. 1981. The relationships between energy balance, milk production and ovulation in postpartum Holstein cows. J. Anim. Sci. 53:742-748.

Carroll, D.J., M.J. Jerred, R.R. Grummer, D.K. Combs, R.A. Pierson, and E.R. Hauser. 1990. Effects of fat supplementation and immature alfalfa to concentrate ratio on plasma progesterone, energy balance, and reproductive traits of dairy cattle. J. Dairy Sci. 73:2855-2863.

Chalupa, W., B. Rickabaugh, D.S. Kronfeld, and D. Sklan. 1984. Rumen fermentation in vitro as influenced by long chain fatty J. Dairy Sci. 67:1439-1444.

Choi, B.R., and D.L. Palmquist. 1996. High fat diets increase plasma cholecystokinin and pancreatic polypeptide, and decrease plasma insulin and feed intake in lactating dairy cows. J. Nutr. 126:2913-2919.

Cook, M.E., C.C. Miller, Y. Park, and M. Pariza. 1993. Immune modulation by altered nutrient metabolism: Nutritional control of immune-induced growth depression. Poult. Sci. 72:1301-1305.

Dasilva, G., M. Pazos, E. Garcia-Egido, J.M. Gallardo, I. Rodriquez, R. Cela, and I. Medina. 2015. Healthy effect of different proportions of marine w-3 PUFAs EPA and DHA supplementation in Wistar rats: Lipidomic biomarkers of oxidative stress and inflammation. J. Nutr. Biochem. 26:1385-1392.

Demeyer, D.I., and H.K. Henderick. 1967. The effect of C18 unsaturated fatty acids on methane production in vitro by mixed rumen bacteria, Biochim. Biophys. Acta 137:484-497.

Drackley, J.K., T.H. Klusmeyer, A.M. Trusk, and J.H. Clark. 1992. Infusion of long-chain fatty acids varying in saturation and chain length into the abomasums of lactating dairy cows. J. Dairy Sci. 75:1517-1526.

Firkins, J.L., and M.L. Eastridge. 1994. Assessment of the effects of iodine value on fatty acid digestibility, feed intake, and milk production. J. Dairy Sci. 77:2357-2366.

Glasser, F., P. Schmidely, D. Sauvant, and M. Doreau. 2008. Digestion of fatty acids in ruminants: A meta-analysis of flows and variation factors: 2. C18 fatty acids. Animal 2:5 691-704.

Grummer, R., and E. Rabelo. 1998. Factors affecting digestibility of fat supplements. Pages 69-79 in Proc. Southeast Dairy Herd Management Conference, November 9 & 10, Macon, GA.

Hatfied, R., H.G. Jung, G. Broderick, and T.C. Jenkins. 2007. Nutritional chemistry of forages. In *Forages, Volume 2. The Science of Grassland Agriculture, Sixth Edition*. R.F. Barnes (Ed.), Blackwell Publishing, Iowa State Press, Ames. Hinckley, Sr., T., R.M. Clark, S.L. Bushmich, and R.A. Milvae. 1996. Long chain PUFA and bovine luteal cell function. Biol. Reprod. 55:445.

Holst, J.J. 2000. Gut hormones as pharmaceuticals. From enteroglucagon to GLP-1 and GLP-2. Reg. Peptides 93:45-51.

Jenkins, T.C. 2002. Lipid transformations by the rumen microbial ecosystem and their impact on fermentative capacity. pp 103-117 in *Gastrointestinal Microbiology in Animals*, S.A. Martin (Ed.), Research Signpost, Kerala, India.

Jenkins, T.C. 2006. Rendered products in ruminant nutrition. In *Essential Rendering*, D.L. Meeker (Ed.), National Renderer's Association, Alexandria, VA.

Jenkins, T.C., and B.F. Jenny. 1989. Effect of hydrogenated fat on feed intake, nutrient digestion, and lactation performance of dairy cows. J. Dairy Sci. 72: 2316-2324.

Klusmeyer, T.H., and J.H. Clark. 1991. Effects of dietary fat and protein on fatty acid flow to the duodenum and in milk produced by dairy cows. J. Dairy Sci. 74: 3055-3067.

Litherland, N.B., S. Thire, A.D. Beaulieu, C.K. Reynolds, J.A. Benson, and J.K. Drackley. 2005. Dry matter intake is decreased more by abomasal infusion of unsaturated free fatty acids than by unsaturated triglycerides. J. Dairy Sci. 88:632-643.

Lucy, M.C., T.S. Gross, and W.W. Thatcher. 1990. Effect of intravenous infusion of a soybean oil emulsion on plasma concentration of 15 keto 13, 14 dihydro prostaglandin F2a and ovarian function in cycling Holstein heifers. In: Livestock Reproduction in Latin America. Int. Atomic Energy Agency, Vienna, Austria.

Lucy, M.C., C.R. Staples, F.M. Michel, W.W. Thatcher, and D.J. Bolt. 1991. Effect of feeding calcium soaps to early postpartum dairy cows on plasma prostaglandin F2a, leutinizing hormone, and follicular growth. J. Dairy Sci. 74:483-489.

Miller, C.C., Y. Park, M.W. Pariza, and M.E. Cook. 1994. Feeding conjugated linoleic acid to animals partially overcomes catabolic responses due to endotoxin injection. Biochem. Biophys. Res. Commun. 198:1107-1112.

Moate, P.J., W. Chalupa, T.C. Jenkins, and R.C. Boston. 2004. A model to describe ruminal metabolism and intestinal absorption of long chain fatty acids. Anim. Feed Sci. Technol. 112:79-115.

National Research Council. 2001. Nutrient requirements of dairy cattle. 7th rev. ed. Natl. Acad. Sci., Washington, DC.

Oldick, B.S., C.R. Staples, W.W. Thatcher, and P. Gyawu. 1997. Abomasal infusion of glucose and fat-effect on digestion, production, and ovarian and uterine functions of cows. J. Dairy Sci. 80:1315-1328.

Onetti, S.G., S.M. Reynal, and R.R. Grummer. 2004. Effect of alfalfa forage preservation method and particle length on performance of dairy cows fed corn silage-based diets and tallow. J. Dairy Sci. 87.:652-664.

Palmquist, D.L., and T.C. Jenkins. 2003. Challenges with fats and fatty acid methods. J. Anim. Sci. 81:3250-3254.

Perfield II, J.W., A.L. Lock, A. Sæbø, J.M. Griinari, D.A. Dwyer, and D.E. Bauman. 2007. Trans-9, cis-11 conjugated linoleic acid (CLA) reduces milk fat synthesis in lactating dairy cows. J. Dairy Sci. 90:2211-2218.

Rabiee, A.R., K. Breinhild, W. Scott, H.M. Golder, E. block, and I.J. Lean. 2012. Effect of fat additions to diets of dairy cattle on milk production and components: A meta-analysis and meta-regression. J. Dairy Sci. 95:3225-3247.

Rodney, R.M., P. Celi, W. Scott, K. Breinhild, and I.J. Lean. 2015. Effects of dietary fat on fertility of dairy cattle: A meta-analysis and meta-regression. J. Dairy Sci. 98:5601-5620.

Saebo, A., P.C. Saebo, J.M. Griinari, and K.J. Shingfield. 2005. Effect of abomasal infusions of geometric isomers of 10,12 conjugated linoleic acid on milk fat synthesis in dairy cows. Lipids 40:823-832.

Schneider, P., D. Sklan, W. Chalupa, and D.S. Kronfeld. 1988. Feeding calcium salts of fatty acids to lactating cows. J. Dairy Sci. 71:2143-2150.

Sklan, D., E. Bogin, Y. Avidar, and S. Gur Arie. 1989. Feeding calcium soaps of fatty acids to lactating cows: Effect on production, body condition and blood lipids. J. Dairy Res. 56:675-682.

Sklan, D., U. Moallem, and Y. Folman. 1991. Effect of feeding calcium soaps of fatty acids on production and reproduction responses in high producing lactating cows. J. Dairy Sci. 74:510-517.

Stoffel, C.M., P.M. Crump, and L.E. Armentano. 2015. Effect of dietary fatty acid supplements, varying in fatty acid composition, on milk fat secretion in dairy cattle fed diets supplemented to less than 3% total fatty acids. J. Dairy Sci. 98:431-442.

Thomas, M.G., B. Bao, and G.L. Williams. 1997. Dietary fats varying in their fatty acid composition differently influence follicular growth in cows fed isoenergetic diets. J. Anim. Sci. 75:2512-2519.

Wu, Z., O.A. Ohajuruka, and D.L. Palmquist. 1991. Ruminal synthesis, biohydrogenation, and digestibility of fatty acids by dairy cows. J. Dairy Sci. 74: 3025-3034.

Zhang, C.M., Y.Q. Guo, Z.P. Yuan, Y.M. Wu, J.K. Wang, J.X. Liu, and W.Y. Zhu. 2008. Effect of octadeca carbon fatty acids on microbial fermentation, methanogenesis and microbial flora in vitro. Anim. Feed Sci. Technol. 146:259-269.

Table 1. Representative fatty acid (FA) content and composition in grains, forages, and oilseeds included in livestock rations.

		% of Total FA				
Feedstuff	FA, % of DM	16:0	18:0	18:1	18:2	18:3
Barley	1.6	27.6	1.5	20.5	43.3	4.3
Corn	3.2	16.3	2.6	30.9	47.8	2.3
Dehydrated Alfalfa	1.4	28.5	3.8	6.5	18.4	39.0
Ryegrass	4 to 7	11.9	1.0	2.2	14.6	68.2
Cottonseed	18.6	25.3	2.8	17.1	53.2	0.1

Table 2. Added fatty acids (3.5%) on 24 h rumen in vitro from Zhang et al. (2008).

	Control	Stearic	Oleic	Linoleic	Linolenic
Ac/Pr	5.27[a]	4.87[a]	4.13[b]	2.90[c]	2.08[d]
F. succinogenes	2.04[c]	2.69[a]	2.26[b]	1.37[d]	1.13[e]
Methane, mmol	1.03[a]	0.99[ab]	0.94[b]	0.75[c]	0.56[d]
Protozoa	2.99[a]	2.26[b]	1.96[c]	1.80[c]	1.30[c]

[abcd]Means with different superscripts within a row differ ($P < 0.05$).

Table 3. Fractional digestibilties of individual fatty acids in ruminants as reported in several data summaries. Differences among summaries are shown according to sections of intestinal tract, species of ruminants, and fat sources omitted.[1]

	Moate et al. (2004)	Glasser et al. (2008)	Boerman et al. (2015)
6:0	0.725		0.771
18:0	0.728	0.63	0.728
18:1	0.669	0.86	0.802
18:2	0.776	0.80	0.735
18:3	0.775	0.74	0.805
Duodenum to feces	X (Intestinal BH NS)		
Duodenum to ileum		X	X
Species	Dairy	Dairy, beef, sheep (NS)	Lactating dairy
n (studies, obs)	8,36	77, 294	?, 10-18
Outliers deleted	HT, WS	HT	PHT

[1]Abbreviations: BH = biohydrogenation, HT = hydrogenated tallow, PHT = partially hydrogenated tallow, WS = whole soybeans, NS = not significant.

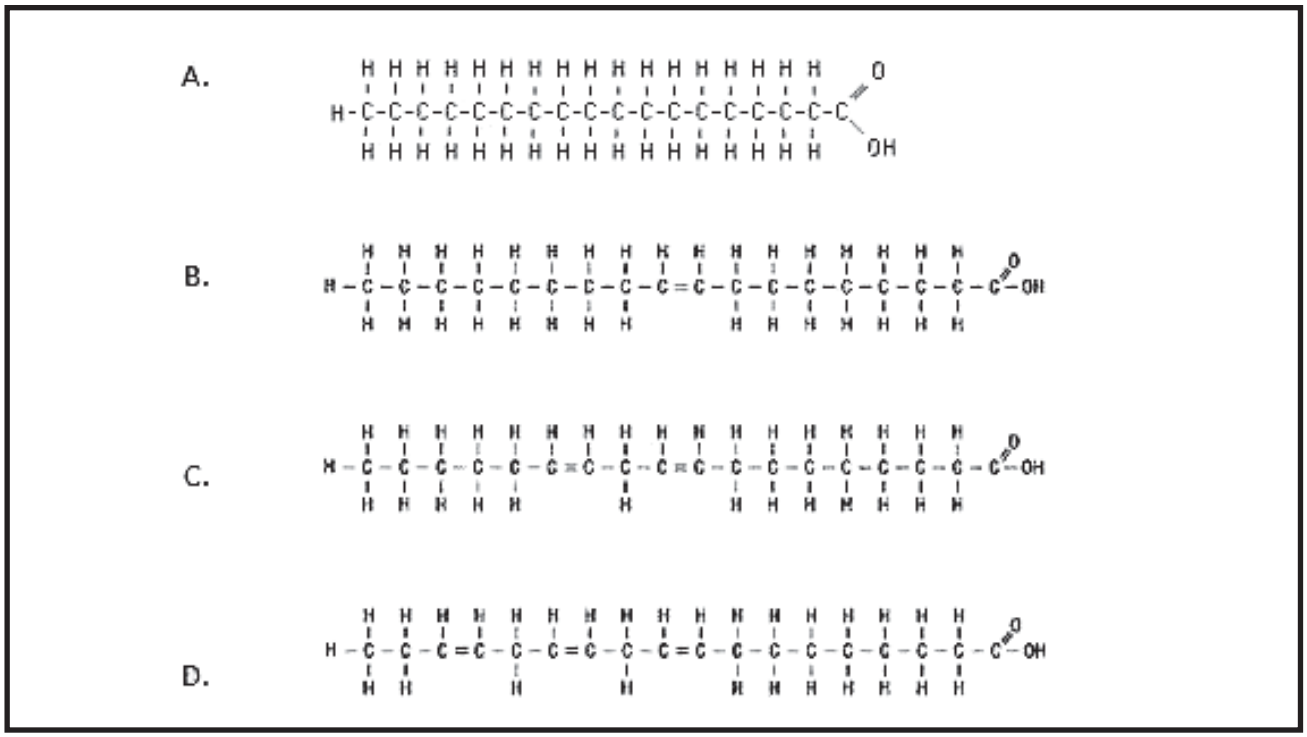

Figure 1. Structures of A) stearic acid, a saturated fatty acid, and the three primary unsaturated fatty acids consumed by cattle, B) oleic acid, C) linoleic acid, and D) linolenic acid.

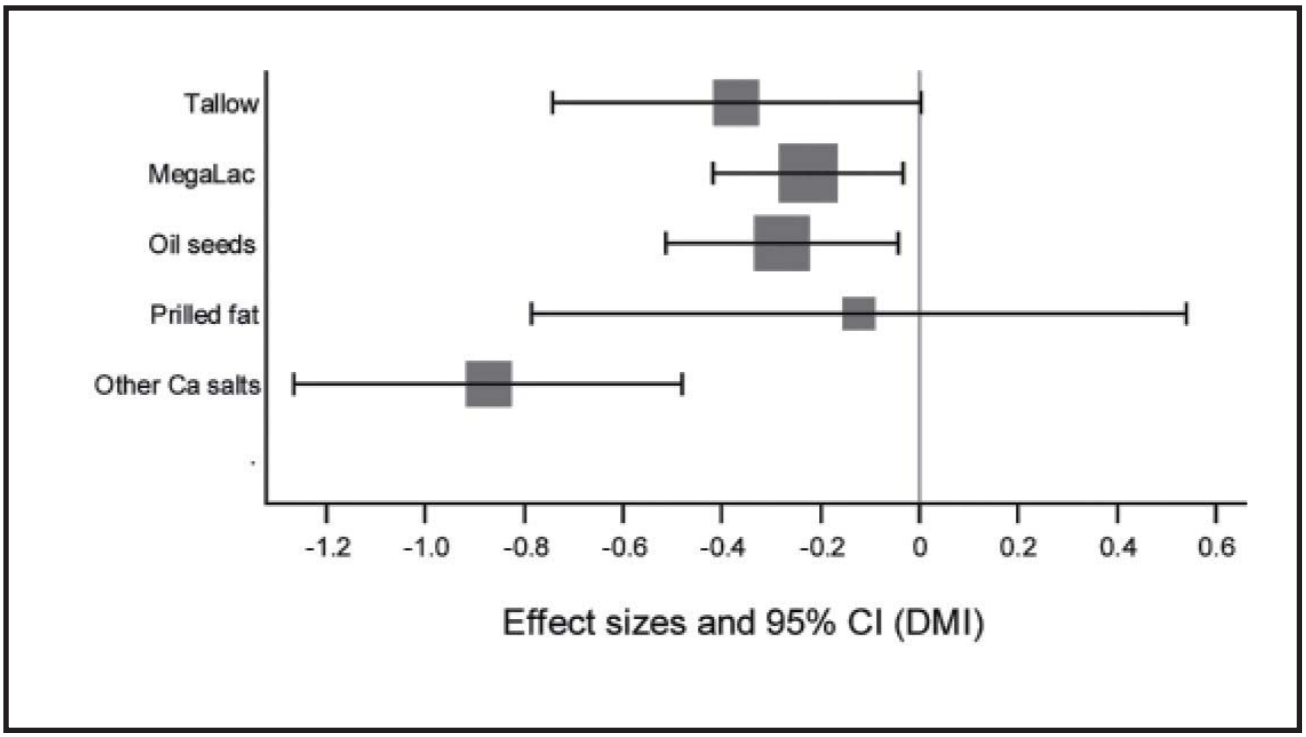

Figure 2. Forest plots taken from the meta-analysis of Rabiee et al. (2012) showing the variability in dry matter intake responses when fat was added to dairy diets. Box sizes are proportional to the inverse variance of the estimates. The upper and lower limit of the line connected to the square represents the upper and lower 95% CI for the effect size.

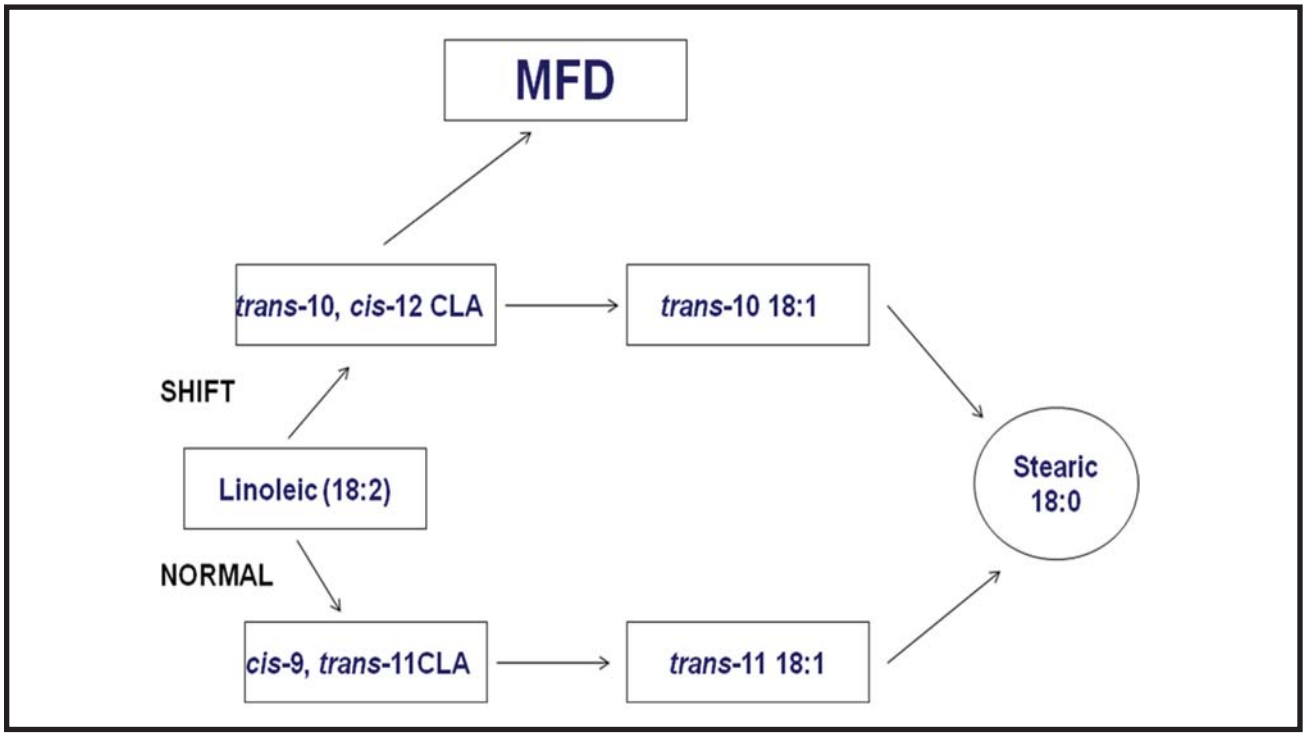

Figure 3. The shift in intermediates produced from biohydrogenation of linoleic acid in ruminal contents as a result of a diet-induced microbial shift (CLA = conjugated linoleic acid; MFD = milk fat depression.

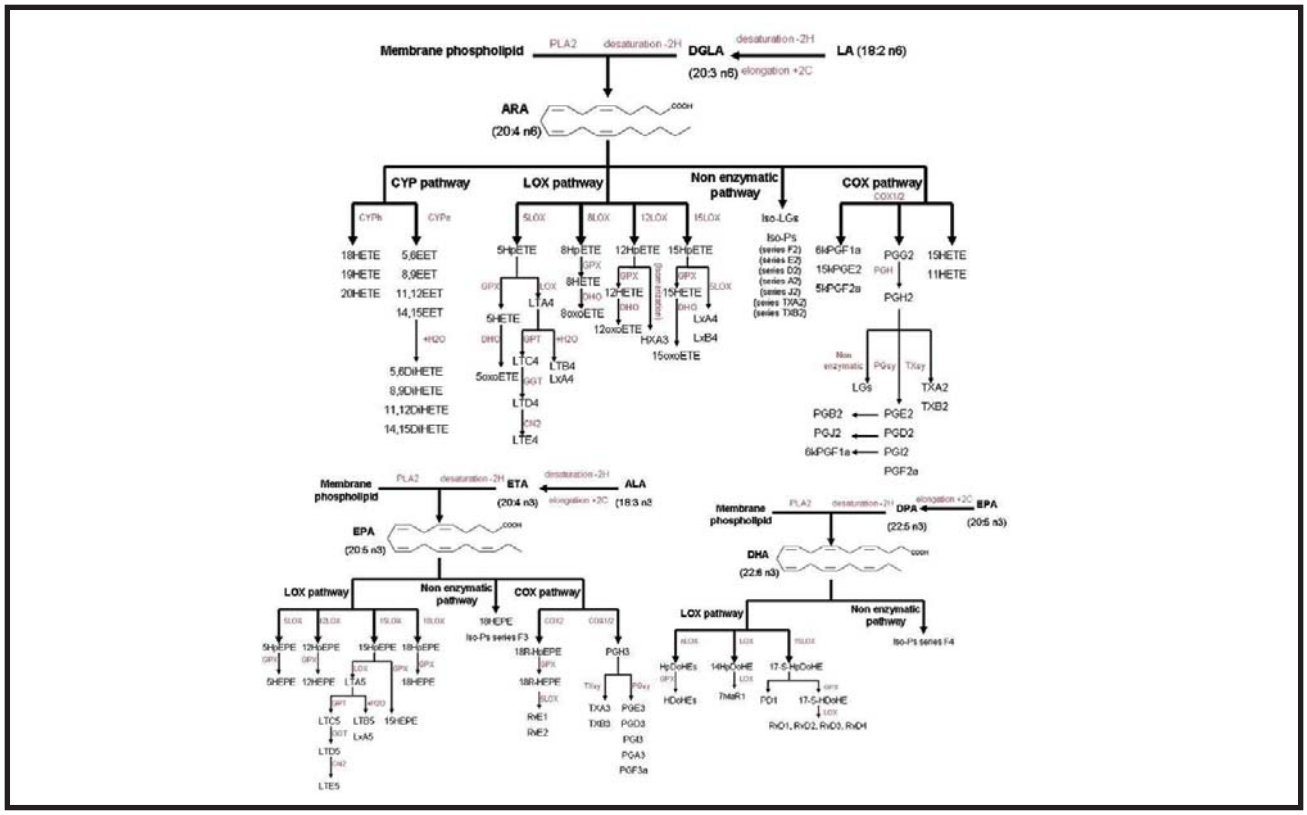

Figure 4. Parent fatty acids and major metabolites within each of the three omega fatty acid families (Dasilva et al., 2015).