Update on Fatty Acid Digestion and Metabolism and Impacts on Milk Production

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Introduction

Recently, the effects of individual fatty acid (**FA**) on digestibility, metabolism, and production responses of dairy cows has received renewed attention. The addition of supplemental FA sources to diets is a common practice in dairy nutrition to increase dietary energy density and to support milk production. The ability to understand and model FA, the effects of individual FA, and different FA supplements on production parameters has direct impact on dairy industry recommendations and the usefulness of FA supplementation strategies. We will briefly review the biological processes and quantitative changes during the metabolism of FA in the rumen and the effect this has on FA availability to the dairy cow, the digestibility of these FA, and their overall impact on performance. Our emphasis in the current paper is on recent research supplementing palmitic (C16:0), stearic (C18:0), and oleic (*cis*-9 C18:1) acids on feed intake, nutrient digestibility, milk production and milk composition, and energy partitioning.

Fatty Acid Metabolism in the Rumen

As well as being derived from specific supplements, FA in the dairy cow's diet are also present in forages and concentrates. Each feed/fat source is composed of a different mix of individual FA. The majority of FA in dairy cow diets contain 16- and 18-carbons. Generally, most cereal grains and seeds contain a high concentration of linoleic acid (C18:2 n-6), whereas linolenic acid (C18:3 n-3) is typically the predominant FA in forage sources. Unsaturated FA are toxic to many rumen bacteria, thus an extensive metabolism of dietary lipids occurs in the rumen, which has a major impact on the profile of FA available for absorption and tissue utilization (Palmquist et al., 2005). The 2 major processes that occur are hydrolysis of ester linkages in lipids found in feedstuffs and the biohydrogenation of unsaturated FA. It appears that the degree of toxicity of different unsaturated FA varies for individual ruminal bacteria species; all the main species that comprise the ruminal cellulolytic bacteria appear vulnerable to inhibition by unsaturated FA (Maia et al., 2007, 2010). Biohydrogenation of unsaturated FA results in the conversion of unsaturated FA to saturated FA, mainly C18:0, through a series of biohydrogenation intermediates (conjugated C18:2 and *trans* C18:1 FA). The major substrates are 18:2 n-6 and 18:3 n-3 and the rate of rumen biohydrogenation is in the range of 70 to 95% and 85 to 100%, respectively (Jenkins et al., 2008); thus, C18:0 is the predominant FA available for absorption by the dairy cow under typical feeding situations (Bauman and Lock, 2006).

FA supplements are often used as a means to increase the energy density of the diet and many of these are referred to as inert.

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In this case, inertness simply means that the FA supplement has minimal affects on rumen fermentation. Although deemed inert at the level used, they can still be hydrolyzed, if a triglyceride, or biohydrogenated, if unsaturated. Often, calcium-salts of palm FA or canola are referred to as 'protected'. However, these are not protected from rumen biohydrogenation but rather are considered to be ruminally inert with regard to their effects on the microbial population (Palmquist, 2006).

Fatty Acid Metabolism in the Intestine

The lipid material that reaches the intestine consists of approximately 80 to 90% free FA attached to feed particles. The remaining lipid components are microbial phospholipids plus small amounts of triglycerides and glycolipids from residual feed material. These esterified FA are hydrolyzed by intestinal and pancreatic lipases (Doreau and Ferlay, 1994). FA absorption occurs predominantly in the jejunum region of the small intestine. Prior to reaching the jejunum, 2 secretions, bile and pancreatic juice, are added to the digesta in the duodenum. Before FA absorption can occur, it is necessary for the lipid material absorbed onto the feed particles to be solubilized into the aqueous environment. Lysolecithin acts as an amphiphile (substance with both water and lipid-loving capacity) and further increases the solubility of saturated FA (Freeman, 1969). Lysolecithin together with bile salts desorb FA from feed particles and bacteria, allowing the formation of the micelles (Lock et al., 2005). In ruminants, micelle formation is the key to this process, and therefore, key to efficient FA absorption (Lock et al., 2005). Once micelles are formed, they facilitate transfer of water-insoluble FA across the unstirred water layer of intestinal epithelial cells, where the FA and lysolecithin are absorbed.

Effects of C16:0, C18:0, and *cis*-9 C18:1 on Fatty Acid Digestibility

Our recent FA digestibility research has utilized and focused on C16:0 and C18:0-enriched supplements. Of particular importance, Boerman et al. (2017) fed increasing levels of a C18:0-enriched supplement (85% C18:0) to dairy cows and observed no positive effect on production responses, which was likely associated with the pronounced decrease in total FA digestibility as FA intake increased (Figure 1A). Similarly, Rico et al. (2017) fed increasing levels of a C16:0-enriched supplement (87% C16:0) to dairy cows, and even though a positive effect was observed on production response up to 1.5% diet DM, a decrease in total FA digestibility as FA intake increased was observed (Figure 1B). However, considering that the range on FA intake was similar across both studies, the decrease in total FA digestibility was more pronounced when there was increased intake/rumen outflow of C18:0 rather than C16:0. This is supported by our meta-analysis, in which a negative relationship between the total flow and digestibility of FA was observed (Figure 2A), with the decrease in total FA digestibility driven by the digestibility of C18:0 (Figure 2B) because of the negative relationship between duodenal flow and digestibility of C18:0 (Boerman et al., 2015). The exact mechanisms for these differences in digestibility are not understood; however, potential causes include the lower solubility of C18:0 compared to C16:0, which would be more dependent of emulsification for absorption (Drackey, 2000). Additionally, results have shown that *cis*-9 C18:1 has greater digestibility than C18:0 and C16:0 (Boerman et al., 2015). Also, Freeman (1969) examined the amphiphilic properties of polar lipid solutes and found that *cis*-9 C18:1 had a positive effect on the micellar solubility of C18:0.

To further understand what factors influence FA digestibility, we recently utilized a random regression model to analyze available individual cow data from 5 studies that fed a C16:0-enriched supplement to dairy cows. We observed that total FA digestibility was negatively impacted by total FA intake but positively influenced by the intake of *cis*-9 C18:1 (unpublished results). This suggests that a combination of 16-carbon and unsaturated 18-carbon FA may improve FA digestibility, but reasons for this needs to be determined. This is supported by our recent results comparing combinations of C16:0, C18:0, and *cis*-9 C18:1 in supplemental fat (de Souza et al., 2016a); we observed that FA digestibility increased when a supplement containing more *cis*-9 C18:1 was fed compared with a control diet (Figure 3). Also, FA digestibility was markedly reduced when a supplement containing more C18:0 was fed compared with the other FA treatments due to decreases in both 16- and 18-carbon FA digestibility (Figure 3).

Effect of Fatty Acids on NDF Digestibility

The amount of FA that are included in the diet is relatively small for lactating dairy cattle, and changes in FA digestibility therefore may have minimal effects on overall DM digestibility and digestible energy intake. Changes in intake and digestibility of other nutrients, such as NDF, due to FA supplementation may affect positively or negatively the digestible energy value of the fat supplement.

Weld and Armentano (2017) performed a meta-analysis to evaluate the effects of fat supplementation on DMI and NDF digestibility of dairy cows. Supplementation of fat supplements high in medium chain FA (12 and 14-carbons) decreased both DMI and NDF digestibility. Addition of vegetable oil decreased NDF digestibility by 2.1 percentage units, but did not affect DMI. Also, feeding saturated prilled fat (combinations of C16:0 and C18:0) did not affect DMI, but increased NDF digestibility by 0.22 percentage units. Overall, the authors concluded that the addition of a fat supplement, in which the FA are 16-carbon or greater in length, has minimal effects on NDF digestibility.

We recently utilized a random regression model to analyze available individual cow data from 6 studies that fed a C16:0-enriched supplement to dairy cows (de Souza et al., 2016b). We observed that NDF digestibility was positively impacted by total C16:0 intake (Figure 4A) and DMI was not affected. This suggests that that the increase in NDF digestibility when C16:0-enriched supplements are fed to dairy cows is not explained through a decrease in DMI. Additionally, when comparing combinations of C16:0, C18:0, and *cis*-9 C18:1 in supplemental fat, we observed that feeding supplements containing C16:0 or C16:0 and *cis*-9 C18:1 increased NDF digestibility compared with a supplement containing C16:0 and C18:0 (de Souza et al., 2016a; Figure 4B).

Overall Impact of Fatty Acid Supplementation on Production Responses

There is a wide range of FA supplements available for lactating dairy cattle. For example, calcium-salts of free FA and prilled saturated free FA are 2 common types of supplements used in the dairy industry and they differ in FA content and profile. Calcium-salt supplements typically contain 80 to 85% FA, and these provide approximately 50% saturated and 50% unsaturated FA. By comparison, prilled saturated free FA contain approximately 99% FA, which are approximately 90% saturated, 10% unsaturated. A summary of the FA profile of some commonly used supplements is provided in Table 1. Although in general FA supplementation has been shown to increase milk yield, milk fat

yield, and the efficiency of milk production, great variation has been reported in production performance for different FA types, and indeed, the same supplement across different diets and studies. This is evident in a meta-analysis examining the effect of FA supplementation to diets of dairy cows (Rabiee et al., 2012). In general, milk production and milk fat content and yield increased, DMI and milk protein concentration decreased, and milk protein yield was not affected by FA supplementation. There was a wide range of responses (~5 standard deviations) for all variables, indicating varied and marked biological effects of the different FA supplements (Rabiee et al., 2012).

Utilizing a larger data set than Rabiee et al. (2012), we recently performed a meta-analysis of production responses to commercially available FA supplements (Boerman and Lock, 2014). Overall, FA supplementation increased yield of milk and milk components and reduced DMI. However, type of supplement influenced response with prilled saturated FA supplements not reducing DMI, tallow having no effect on milk fat yield, and Ca-salts of palm FA having no effect on milk protein yield. It is important to note that most studies simply compared a single commercial FA supplement with a non-FA supplemented control diet. This makes direct comparisons between different FA supplements difficult to interpret, and importantly, to provide accurate answers to commonly asked questions (by farmers and nutritionists) as to which are the best FA supplements to use. There are limited reports in the published literature that have undertaken direct comparisons between different commercially available FA supplements. Results also suggest that responses to FA supplements interact with other dietary components, and this should be examined further.

Effects of C16:0, C18:0, and *cis*-9 C18:1 on Production Responses

We have recently carried out a series of studies examining the effect of individual saturated FA on production and metabolic responses of lactating cows (Lock et al., 2013, Piantoni et al., 2013, Rico et al., 2014, Piantoni et al., 2015). Piantoni et al. (2015) reported that C18:0 increased DMI and yields of milk and milk components, with increases more evident in cows with higher milk yields, but the response occurred only in 1 of the 2 periods of the crossover design. Reasons why only higher yielding cows responded more positively to C18:0 supplementation and only in one period remains to be determined. Also, our results indicate that C16:0 supplementation has the potential to increase yields of 3.5% FCM and milk fat, as well as the conversion of feed to milk, independent of production level when it was included in the diet for soyhulls or C18:0 (Table 2). Additionally, in a recent dose response study with mid lactation cows, feeding a C18:0-enriched supplement (85% C18:0) increased DMI but had no effect on the yields of milk or milk components when compared to a non-FA supplemented control diet, which was probably associated with the decrease in FA digestibility (Figure 1, Boerman et al., 2017).

Furthermore, we recently utilized a random regression model to analyze available individual cow data from 10 studies that fed a C16:0-enriched supplement to dairy cows (de Souza et al., 2016b). We observed that energy partitioning toward milk was increased linearly with C16:0 intake, as a result of a linear increase in milk fat yield and energy corrected milk (**ECM**) with increasing intake of C16:0. In a recent study (unpublished results), we evaluated the long-term effects of C16:0 supplementation and observed that C16:0 consistently increased DMI, milk yield, and ECM compared with a

non-fat control diet over the 10-wk period of supplementation (Figure 5). Also, in a study with fresh cows (1 to 70 DIM; unpublished data), we evaluated the effects of C16:0 supplementation on performance and observed that C16:0 consistently increased milk fat yield and ECM compared with a non-fat control diet throughout the feeding period (Figure 6).

When we compared combinations of C16:0, C18:0, and *cis*-9 C18:1 in a FA supplement, a supplement containing more C16:0 increased energy partitioning toward milk due to the greater milk fat yield response compared with the other treatments (de Souza et al., 2016a). In contrast, a FA supplement containing C16:0 and *cis*-9 C18:1 increased energy allocated to body reserves compared with other treatments. The FA supplement containing a combination of C16:0 and C18:0 reduced nutrient digestibility, which most likely explains the lower production responses observed compared with the other treatments. This may suggest that C16:0 and *cis*-9 C18:1 are able to alter energy partitioning between the mammary gland and adipose tissue, which may allow for different FA supplements to be fed in specific situations according to the metabolic priority and needs of dairy cows. Further research is needed to confirm these results in cows at different stages of lactation or other physiological conditions.

Conclusions

The addition of supplemental FA to diets is a common practice in dairy nutrition to increase dietary energy density and to support milk production. Although in general FA supplementation has been shown to increase milk yield, milk fat yield, and the efficiency of milk production, great variation has been reported in production performance for different FA supplements, and indeed, the same supplement across different diets and studies. Just as we recognize that not all protein sources are the same it is important to remember that not all FA supplements are the same. The key is to know what FA are present in the supplement, particularly FA chain length and their degree of unsaturation. The digestibility of the FA supplement, as well as potential interactions with other dietary factors, is important for determining the energetic value of a supplement. Once this information is known, it is important to consider the possible effects of these FA on DMI, rumen metabolism, small intestine digestibility, milk component synthesis in the mammary gland, energy partitioning between the mammary gland and other tissues, and body condition. The extent of these simultaneous changes, along with the goal of the nutritional strategy employed, will ultimately determine the overall effect of the supplemental FA and the associated decision regarding their inclusion in diets for lactating dairy cows.

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Table 1. Fatty acid (**FA**) composition of common fat supplements (data from our laboratory).

FA, g/100 g	Tallow	Ca-salt palm FA	Saturated free FA	C16:0-enriched
C14:0	3.0	2.0	2.7	1.6
C16:0	24.4	51.0	36.9	89.7
C18:0	17.9	4.0	45.8	1.0
C18:1	41.6	36.0	4.2	5.9
C18:2	1.1	7.0	0.4	1.3

Table 2. Summary of DMI, milk production and composition, body weight, and body condition score (**BCS**) for cows supplemented with C16:0 and C18:0 supplements. The C16:0 supplement contained ~ 99% C16:0 and the C18:0 supplement contained ~ 98% C18:0.

	Piantoni et al. (2013)[1]			Piantoni et al. (2015)[2]			Rico et al. (2014)[3]		
Variable	Control	C16:0	SEM	Control	C18:0	SEM	C16:0	C18:0	SEM
DMI, kg/day	27.8	27.8	0.54	25.2^{n}	26.1^{m}	0.42	32.1	32.3	0.44
Milk yield, kg/day	44.9^{b}	46.0^{a}	1.7	38.5^{n}	40.2^{m}	0.71	46.6	45.8	2.02
Fat yield, kg/day	1.45^{b}	1.53^{a}	0.05	1.35^{n}	1.42^{m}	0.03	1.68^{y}	1.59^{z}	0.05
Milk fat, %	3.29^{b}	3.40^{a}	0.11	3.60	3.59	0.12	3.66^{y}	3.55^{z}	0.09
Protein yield, kg/day	1.38	1.41	0.04	1.14^{n}	1.19^{m}	0.02	1.50	1.49	0.05
Milk protein %	3.11	3.09	0.05	3.00	2.99	0.05	3.24	3.29	0.05
3.5% FCM, kg/day	42.9^{b}	44.6^{a}	1.35	38.6^{n}	40.5^{m}	0.76	47.5^{y}	45.6^{z}	1.64
3.5% FCM/DMI	1.54^{b}	1.60^{a}	0.03	1.53	1.55	0.04	1.48^{y}	1.40^{z}	0.05
Body weight, kg	722	723	14.7	727	730	12.8	720	723	13.6
BCS	2.99	2.93	0.15	2.67	2.67	0.11	2.93^{z}	2.99^{y}	0.11

[1]Treatments were either a control diet (with 2% of diet DM as added soyhulls) or a C16:0-supplemented diet (with 2% of diet DM as C16:0). Means within a row with different superscripts (a, b) differ ($P < 0.05$).

[2]Treatments were either a control diet (with 2% of diet DM as added soyhulls) or a C18:0-supplemented diet (with 2% of diet DM as C18:0). Means within a row with different superscripts (m, n) differ ($P < 0.05$).

[3]Treatments were either a C16:0-supplemented diet (with 2% of diet DM as C16:0) or a C18:0-supplemented diet (with 2% of diet DM as C18:0). Means within a row with different superscripts (y, z) differ ($P < 0.05$).

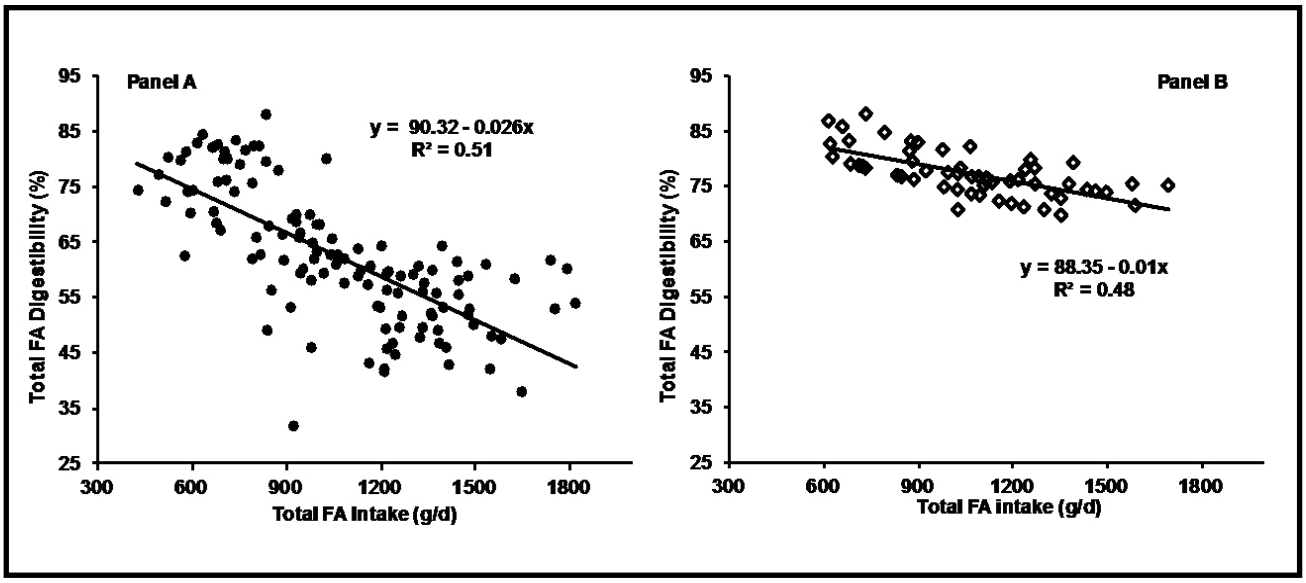

Figure 1. Relationship between total fatty (**FA**) intake and apparent total-tract FA digestibility of dairy cows supplemented with either a C18:0-enriched supplement (Panel A) or a C16:0-enriched supplement (Panel B). Results in Panel A utilized 32 mid-lactation cows receiving diets with increasing levels (0 to 2.3% of dry matter) of a C18:0-enriched supplement (85% C18:0) in a 4 X 4 Latin square design with 21-day periods (Boerman et al., 2017). Results in Panel B utilized 16 mid-lactation cows receiving diets with increasing levels (0 to 2.25% of dry matter) of a C16:0-enriched supplement (87% C16:0) in a 4 X 4 Latin square design with 14-day periods (Rico et al., 2017).

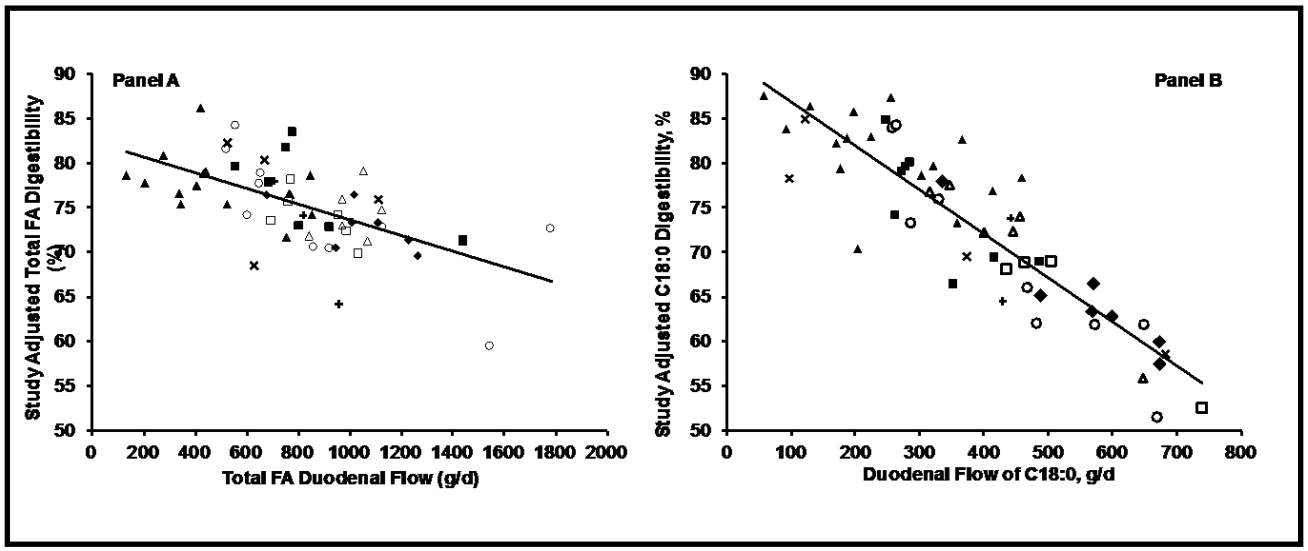

Figure 2. Relationship between study adjusted apparent total fatty acid (**FA**) intestinal digestibility and total FA duodenal flow (Panel A) and study adjusted C18:0 apparent intestinal digestibility and duodenal flow of C18:0 (Panel B). Results from a meta-analysis using 15 published studies that measured duodenal flow and intestinal digestibility of FA in dairy cows (Boerman et al., 2015). Control treatments represented by black triangles; animal-vegetable fat treatments represented by black diamonds; calcium salt treatments represented by black squares; tallow treatments represented by open circles; vegetable oil treatments represented by open triangles; seed meal treatments represented by open squares; whole seed treatments represented by black addition sign; and other treatments represented by black multiplication sign.

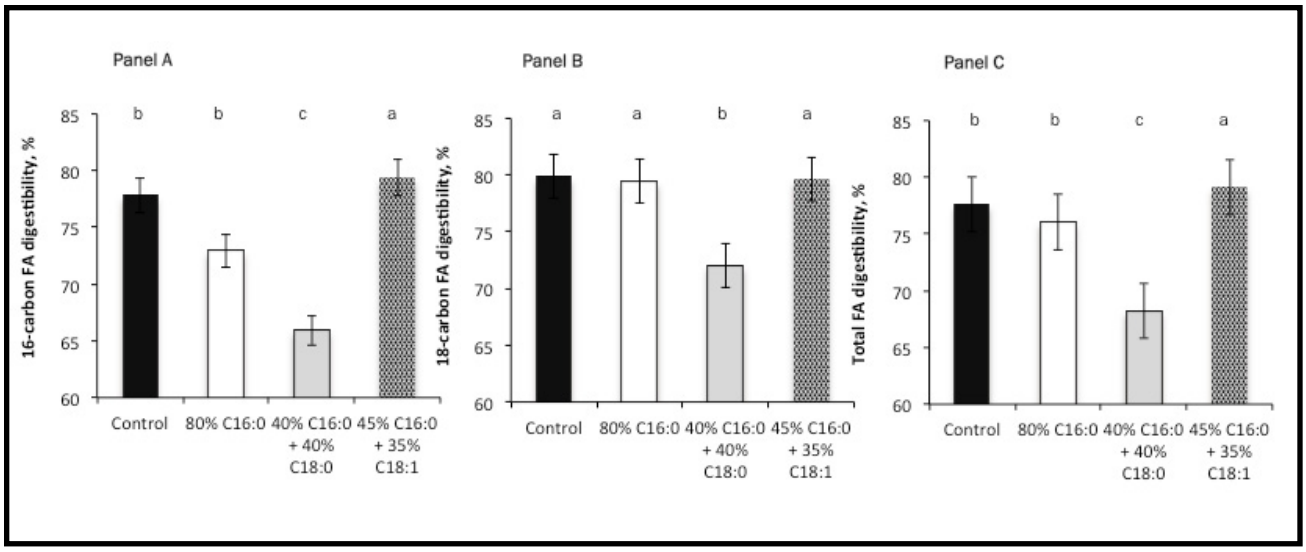

Figure 3. The effects of different dietary ratios of fatty acid (**FA**) on digestibility of 16-carbon (Panel A), 18-carbon (Panel B), and total FA (Panel C). Results utilized 24 mid-lactation cows receiving the following diets: CON (Control diet); PA (1.5% of FA supplement blend to provide ~ 80% of C16:0); PA+SA (1.5% of FA supplement blend to provide ~ 40% of C16:0 + 40% of C18:0); and PA+OA (1.5% of FA supplement blend to provide ~ 45% of C16:0 + 35% of C18:1 cis-9). in a 4 X 4 Latin square design with 21-day periods (de Souza et al., 2016a).

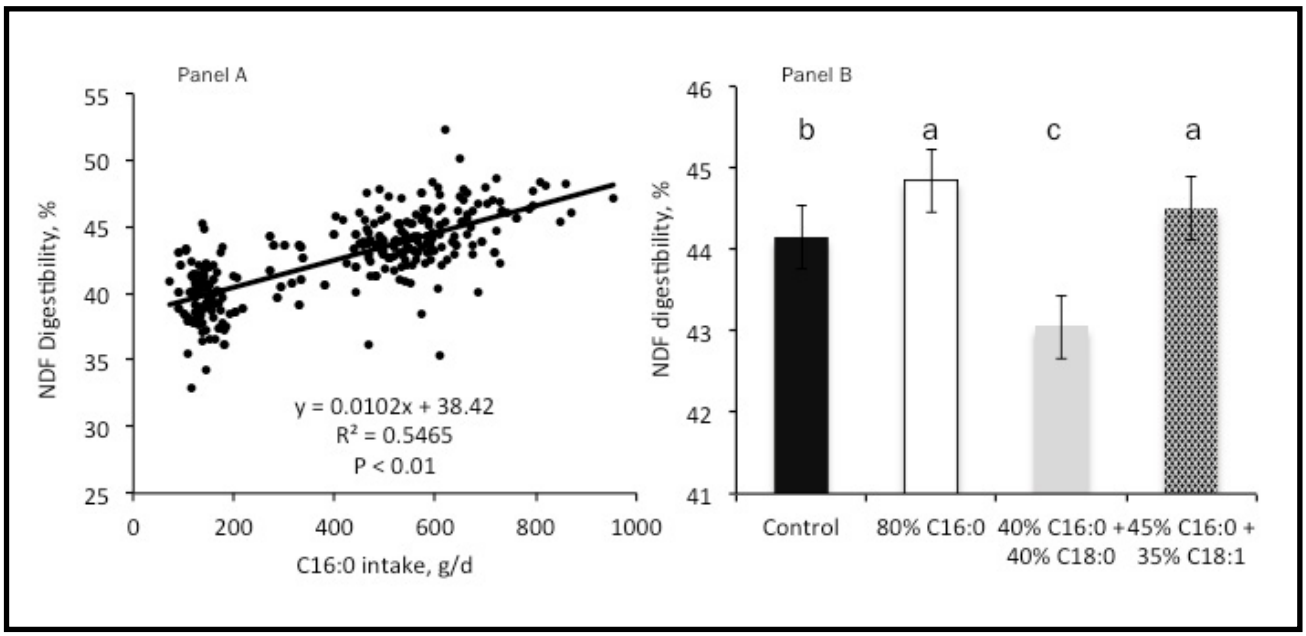

Figure 4. Panel A: Relationship between C16:0 intake and NDF digestibility of dairy cows fed C16:0-enriched fatty acid (**FA**) supplements. Panel B: The effects of different dietary ratios of FA on NDF digestibility. Results in Panel A represent a combined data set evaluated using a random regression model from 6 studies feeding C16:0-enriched supplements on NDF digestibility of dairy cows (de Souza et al., 2016b). Results in Panel B utilized 24 mid-lactation cows receiving the following diets: CON (Control diet); PA (1.5% of FA supplement blend to provide ~ 80% of C16:0); PA+SA (1.5% of FA supplement blend to provide ~ 40% of C16:0 + 40% of C18:0); and PA+OA (1.5% of FA supplement blend to provide ~ 45% of C16:0 + 35% of C18:1 cis-9). in a 4 X 4 Latin square design with 21-day periods (de Souza et al., 2016a).

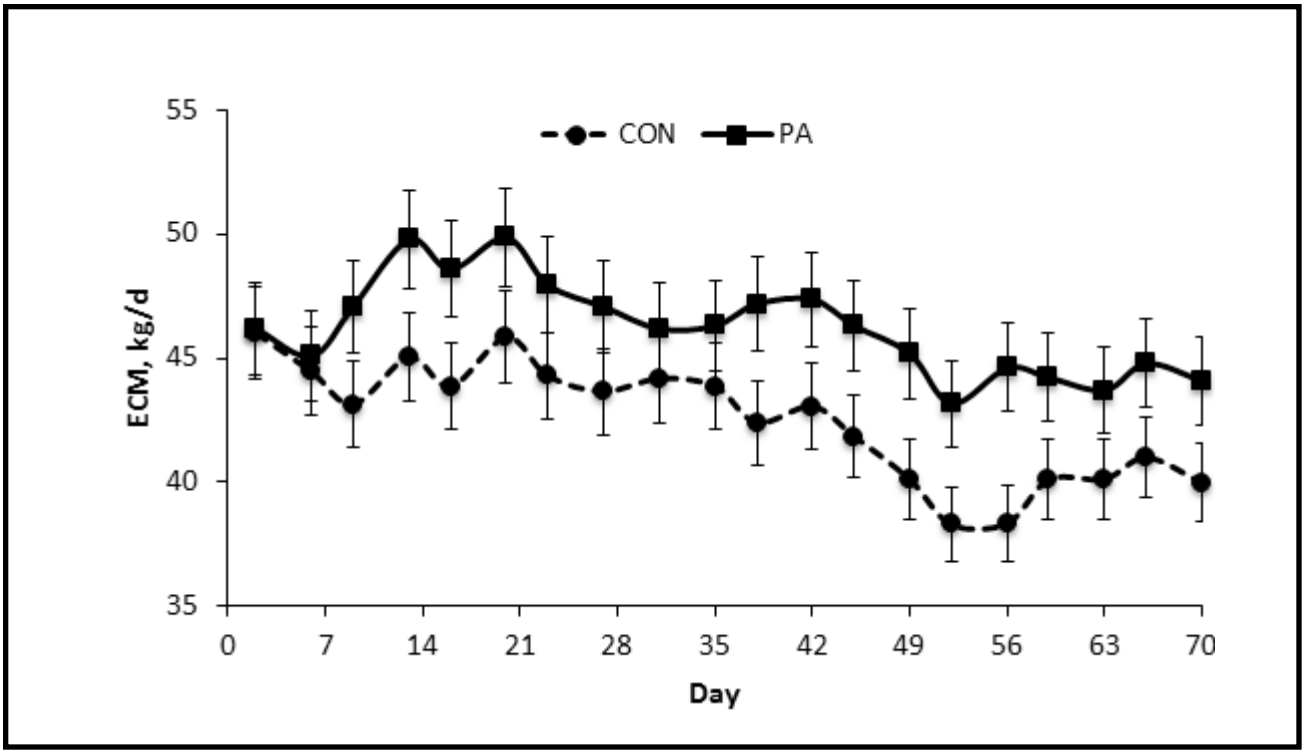

Figure 5. Effects of C16:0 supplementation on the yield of energy corrected milk in mid-lactation cows. The study utilized 40 mid-lactation cows in a block design receiving either a control diet containing no supplemental fat (**CON**) or a C16:0-enriched supplemented diet (**PA**; 1.5% diet DM) fed for 10 wks (unpublished results).

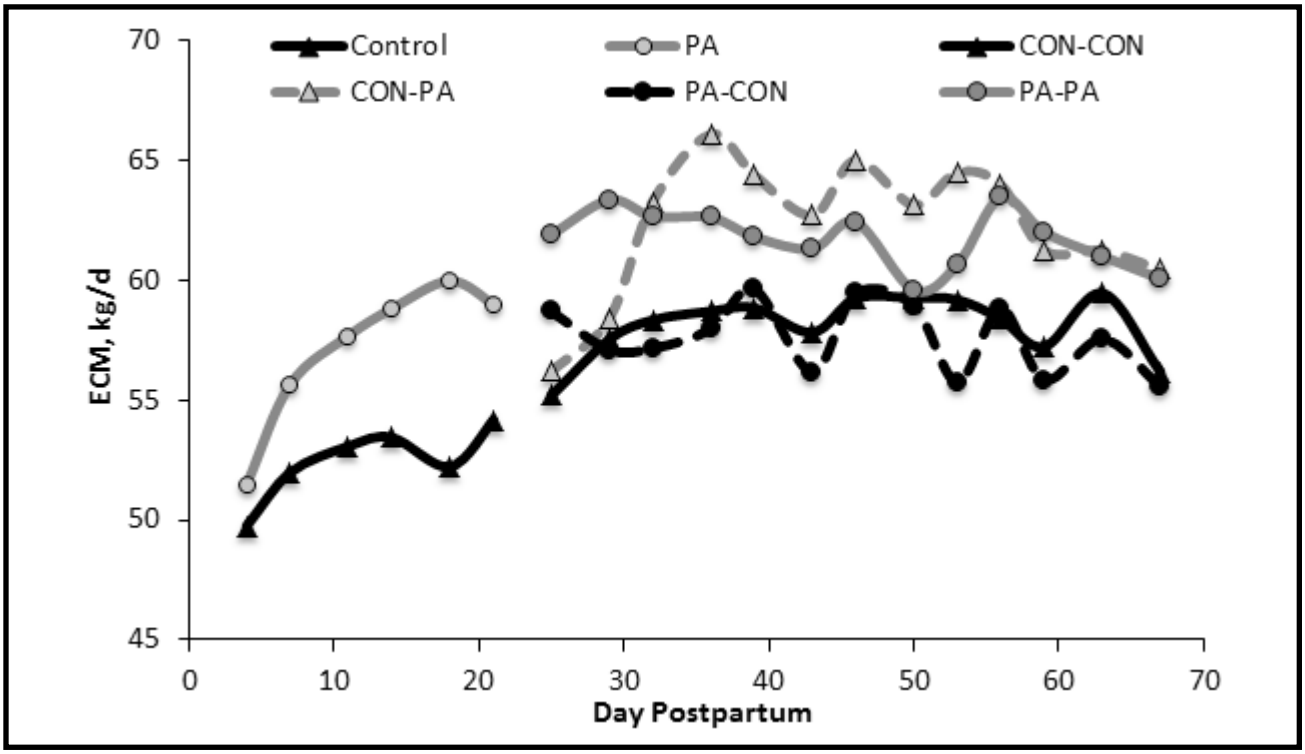

Figure 6. Effects of C16:0 supplementation on the yield of energy corrected milk in early lactation cows. The study utilized 52 early-lactation cows in a block design receiving either a control diet containing no supplemental fat (**CON**) or a C16:0-enriched supplemented diet (**PA**; 1.5% diet DM) that was fed either from calving (1 to 24 days; Fresh period) or after 3 weeks from calving (25 to 67 days; Lactation period). (Unpublished results).