Fatty Acid Digestibility and Impacts on Responses of Dairy Cows

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Introduction

The addition of supplemental fatty acid (**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. The emphasis of the current paper is on 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. We will focus on recent research supplementing palmitic acid (C16:0) and stearic acid (C18:0)-enriched supplements on feed intake, digestibility, milk production, and milk composition.

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. For example, corn, cottonseed, safflower, sunflower, and soybean oils are high in C18:2 n-6, whereas linseed is high in C18:3 n-3. Unsaturated FA are toxic to many rumen bacteria, thus an extensive metabolism of dietary lipids occurs in the rumen that has a major impact on the profile of FA available for absorption and tissue utilization (Palmquist et al., 2005). The two major processes that occur are hydrolysis of ester linkages in lipids found in feedstuffs and the biohydrogenation of unsaturated FA. A series of recent in vitro studies concluded that biohydrogenation occurs to enable rumen bacteria to survive the bacteriostatic effects of unsaturated FA, and that the toxicity of unsaturated FA is probably mediated via metabolic effects rather than disruption of membrane integrity. Furthermore, 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

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range of 70-95% and 85-100%, 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).

Fatty acid supplements are often used as a means to increase the energy density of the diet and many of these are referred to as inert. In this case inertness simply means that the FA supplement has minimal effects 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 80-90% 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, two 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. In ruminants, micelle formation is the key to this process and, therefore, key to efficient FA absorption (Lock et al., 2005).

During FA digestion in the small intestine, bile secretions supply bile salts and lecithin, and pancreatic secretions provide enzymes to convert lecithin to lysolecithin and bicarbonate to raise the pH. 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). 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.

Impact of Supplemental 16- and 18-Carbon Fatty Acid on Fatty Acid Digestibility

Under typical feeding situations, C18:0 is the predominant FA available for absorption by the dairy cow, regardless of the diet fed. As result, this FA has a critical impact on total FA digestibility as we observed in a recent meta-analysis and meta-regression examining the intestinal digestibility of long-chain FA in lactating dairy cows (Boerman et al., 2015). We observed similar digestibility values among 16- and 18-carbon FA in the control diets (non-fat supplemented diet), which suggests that at low levels of FA intake, the potential differences in FA digestibility frequently presented in the literature between saturated and unsaturated FA is minimal (Figure 1A). However, when we compared the digestibility of 16- and 18-carbon FA to the digestibility of C18:0

in diets supplemented with fat across the entire data set, we observed modest differences between C18:0 and unsaturated FA (Figure 1B). Implications for differences among FA was highlighted when we generated best-fit equations for the relationship between flow and digestibility of FA (Boerman et al., 2015). We observed a negative relationship between the total flow and digestibility of FA (Figure 2A). Furthermore, the decrease in total FA digestibility appears to be driven by the digestibility of C18:0 because a negative relationship between the duodenal flow and digestibility of C18:0 was observed (Figure 2B). The exact mechanisms for the reduction in digestibility are not understood; however, potential causes include limits in lysolecithin or competition for absorption sites (Drackey, 2000). Additional research to understand the observed reduction in C18:0 digestibility and how this may be overcome or improved is required.

Our recent FA digestibility research has utilized and focused on C16:0 and C18:0-enriched supplements. Of particular importance, Boerman and Lock (2014b) 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 3A). Similarly, de Souza et al. (2015) 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 dry matter, we observed a decrease in total FA digestibility as FA intake increased (Figure 3B). Considering the results presented in Figure 3, given that the range on FA intake is similar across both studies, the decrease in total FA digestibility is more pronounced when there is increased intake/rumen outflow of C18:0 rather than C16:0, similar to our observations in Figure 2. The exact mechanisms for these differences in digestibility are not understood; however, potential causes include the lower solubility C18:0 than C16:0, which would be more dependent of lysolecithin for absorption.

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 (unpublished results). We observed that total FA digestibility was negatively impacted by total FA intake, but positively influenced by the intake of *cis*-9 C18:1. This suggests that a combination between 16-carbon and unsaturated 18-carbon FA may improve FA digestibility, but reasons for this effect needs to be further determined.

Fatty Acid Metabolism in the Mammary Gland

Lipids in milk are primarily in the form of triglycerides (98%) with phospholipids and sterols accounting for 1.0 and 0.5 % of total lipids, respectively. Bovine milk is extremely complex and contains about 400 FA, a large proportion of which are derived from lipid metabolism in the rumen (Jensen, 2002). Milk FA are derived from 2 sources; <16 carbon FA from de novo synthesis in the mammary gland and >16 carbon FA originating from extraction from plasma. 16-carbon FA originate from either de novo or preformed sources. Substrates for de novo synthesis are derived from ruminal fiber digestion and dietary FA supply preformed FA for direct incorporation into milk fat

(Palmquist, 2006). Microbial synthesis of branched and odd-chained number FA in the rumen and absorption of biohydrogenation intermediates also contribute to the diversity of FA secreted in milk fat. Under typical conditions, about half of the FA in milk are synthesized de novo, 40 to 45 % originate from FA in the diet, and less than 10% are derived from mobilization of adipose tissue (Palmquist and Jenkins, 1980). However, nutrition can substantially alter the balance between mammary de novo FA synthesis and uptake of preformed FA. C16:0, C18:0 and *cis*-9 C18:1 are the major FA in milk fat. The relatively high melting point of C16:0 and C18:0 requires the production of de novo synthesized FA or the conversion of C16:0 and C18:0 to *cis*-9 C16:1 and *cis*-9 C18:1, respectively, in the mammary gland in order to maintain fluidity.

Effect of Fatty Acid Supplementation 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. Even significant reductions in individual FA digestibility estimates may have little effect on reducing total DM digestibility compared with reductions in digestibility of more abundant feed ingredients. Changes in intake and digestibility of other nutrients, such as NDF, due to fat supplementation may affect positively or negatively the digestible energy value of the fat supplement.

Weld and Armentano (2015) 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 (C12, C14) decreased both DMI and NDF digestibility. Addition of vegetable oil decreased NDF digestibility by 2.1 percentage units, but did not affect DMI. Although feeding calcium-salts of palm FA distillate decreased DMI by 1.45 kg/day, it increased NDF digestibility by 2.2 percentage units. Overall, the authors concluded that the addition of a fat supplement, in which the fatty acids are C16 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 (unpublished results). We observed that NDF digestibility was positively impacted by total C16:0 intake and DMI was not affected. This suggests that the increase in NDF digestibility when C16:0-enriched supplements are fed to dairy cows is not explained through a decrease in DMI. Reasons for this effect needs to be further determined.

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 two common types of supplements used in the dairy industry and they differ in FA content and FA profile. Calcium-salt supplements typically contain 80-85% 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, 2014a). Available data were collected from 133 peer-reviewed publications of which 88 met our selection criteria, comprising 159 treatment comparisons. Calcium-salts of palm FA distillate (PFAD; n=73), saturated prilled FA (PRILLS; n=37), and tallow (n=49) supplemented at ≤ 3% diet DM were compared to non FA supplemented diets used as controls. Treatment comparisons were obtained from either randomized design (n=99) or crossover/Latin square design experiments (n=60). Preliminary results from the meta-analysis are shown in Figure 4.

Overall, FA supplementation increased yield of milk and milk components and reduced DMI. However type of supplement influenced response with PRILLS not reducing DMI, tallow having no effect on milk fat yield, and PFAD having no effect on milk protein yield. It is important to note that the majority of the studies reported in Figure 4 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 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 from the meta-analysis also suggest that responses to FA supplements interact with other dietary components, and this should be examined further.

Impact of Supplemental C16:0 and C18:0 on Production Responses

In the 1960's Steele and co-workers performed a series of studies using relatively pure sources of C16:0 and C18:0 and and their findings suggested that C16:0 supplementation induces a higher milk fat response (concentration and yield) when compared to C18:0 supplementation. More recent work from Enjalbert et al (1998) suggests that the uptake efficiency of the mammary gland is higher for C16:0 than for C18:0 and *cis*-9 C18:1. 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). These results indicate that C16:0 supplementation has the potential to increase yields of

milk 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).

Rico et al. (2013) fed increasing levels of a C16:0-enriched supplement (87% C16:0) to dairy cows and observed a quadratic response with a positive effect on milk fat yield, 3.5% fat-corrected milk and feed efficiency up to 1.5% diet DM (Table 3). 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 (unpublished results). 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 3.5% fat-corrected milk with increasing intake of C16:0.

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, indicating that there was significant variation in response. Reasons why only higher yielding cows responded more positively to C18:0 supplementation than lower yielding cows remains to be determined. However, when we directly compared C16:0 and C18:0 supplementation the yield of milk fat and 3.5% FCM increased with C16:0 regardless of level of milk production (Table 2, Rico et al., 2014). 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 cows fed a non-FA supplemented control diet (Table 4), which is probably associated with the decrease in FA digestibility (Figure 3A, Boerman and Lock, 2014b).

There is mechanistic data to support the concept that individual FA can impact milk fat synthesis differently. Hansen and Knudsen (1987) utilized an in vitro system and reported that C16:0 stimulated de novo FA synthesis and incorporation into triglycerides whereas other FA were either neutral or inhibitory. In addition, there were only minor differences in the esterification efficiency into triglycerides of various FA, except for C16:0, which was a better substrate than the other FA tested. These results, in association with the digestibility results, suggest that C16:0-enriched supplements improve performance of dairy cows, while understanding factors that affect the digestibility of C18:0 with increasing intake/duodenal flow may allow the development of strategies to overcome this possible limitation.

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 its potential

interaction with other dietary factors is important to determine the energetic value of the 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 composition of common fat supplements (Data from our laboratory)

Fatty Acid, g/100 g	Tallow	Ca-salt PFAD	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 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/d	27.8	27.8	0.54	25.2^{n}	26.1^{m}	0.42	32.1	32.3	0.44
Milk yield, kg/d	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/d	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/d	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	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 ($P < 0.05$).

Table 3. Dry matter intake, milk production and composition, body weight, and BCS for cows supplemented with increasing levels of a C16:0-enriched supplement (Rico et al., 2013). The C16:0 supplement contained 87% C16:0

	C16:0 supplementation, % diet DM					
Variable	0%	0.75%	1.50%	2.25%	SEM	*P*-value
DMI, kg/d	28.8	28.8	28.6	27.4	0.83	0.05
Milk yield, kg/d	43.7	43.5	44.5	42.5	1.73	0.06
Fat yield, kg/d	1.63	1.69	1.78	1.70	0.09	0.01
Milk Fat, %	3.78	3.88	4.01	4.03	0.17	0.01
Protein yield, kg/d	1.36	1.36	1.40	1.32	0.06	0.08
Milk Protein, %	3.17	3.15	3.18	3.16	0.07	0.32
3.5% FCM, kg/d	45.3	46.1	48.0	45.9	1.91	0.02
3.5% FCM/DMI	1.57	1.60	1.68	1.68	0.07	0.21
Body weight, kg	703	705	701	701	25.7	0.76
BCS	2.66	2.48	2.71	2.84	0.05	0.94

Table 4. Dry matter intake, milk production and composition, body weight, and BCS for cows supplemented with increasing levels of a C18:0-enriched supplement (Boerman and Lock, 2014b). The C18:0 supplement contained 85% C18:0.

	C18:0 supplementation, % diet DM				SEM	*P*-value
Variable	0%	0.80%	1.50%	2.30%		
DMI, kg/d	28.5	29.1	29.6	30.0	0.61	0.13
Milk Yield, kg/d	38.3	38.6	38.2	37.8	1.65	0.51
Fat Yield, kg/d	1.43	1.40	1.40	1.42	0.04	0.61
Fat, %	3.79	3.72	3.74	3.82	0.08	0.29
Protein Yield, kg/d	1.33	1.33	1.32	1.30	0.05	0.49
Protein, %	3.49	3.50	3.48	3.49	0.05	0.91
3.5% FCM/DMI	39.8	39.4	39.3	39.3	1.40	0.77
FCM/DMI	1.43	1.39	1.35	1.33	0.04	0.03
Body weight, kg	738	739	735	737	12.0	0.58
BCS	3.44	3.40	3.39	3.42	0.08	0.37

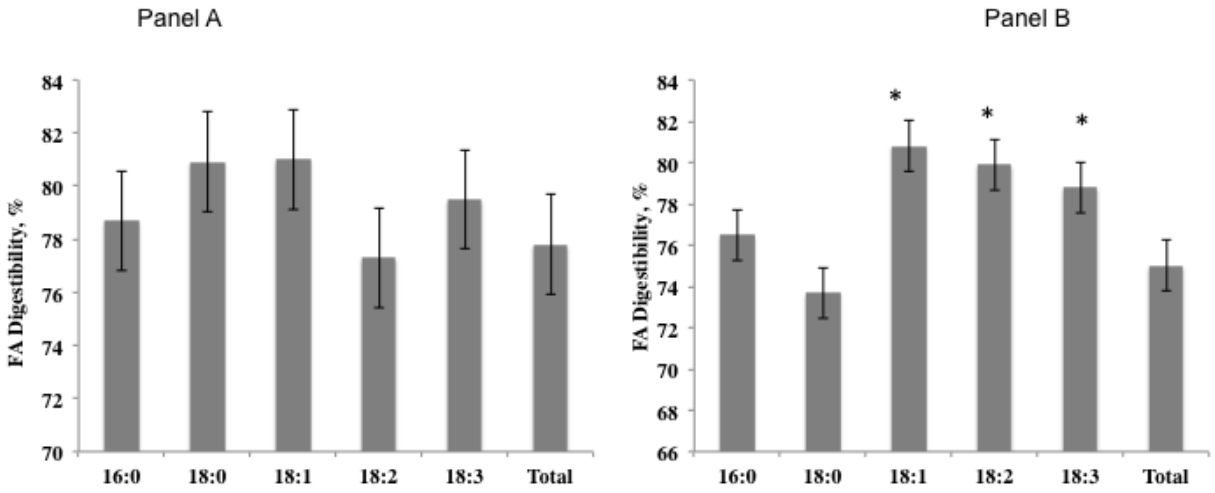

Figure 1. Meta-analysis of intestinal digestibility of FA in lactating dairy cows (Boerman et al., 2015). Apparent intestinal digestibility estimates from nonfat supplemented (control) treatments (Panel A; n = 16) and from control and fat supplemented treatments (Panel B; n = 43). Results are from 15 published studies that measured duodenal flow and intestinal digestibility of FA in dairy cows. * Refers to comparing individual FA digestibility against C18:0 ($P < 0.05$).

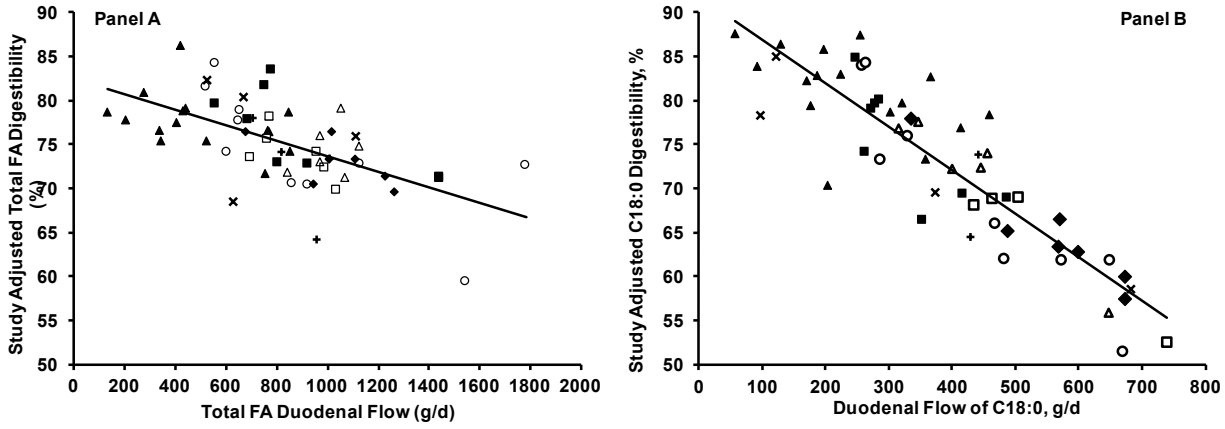

Figure 2. Relationship between study adjusted total FA intestinal digestibility and total FA duodenal flow (Panel A) and study adjusted C18:0 intestinal digestibility and duodenal flow of C18:0 (Panel B). Results from a meta-analysis using 15 published studies that measured duodenal flow and intestinal 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.

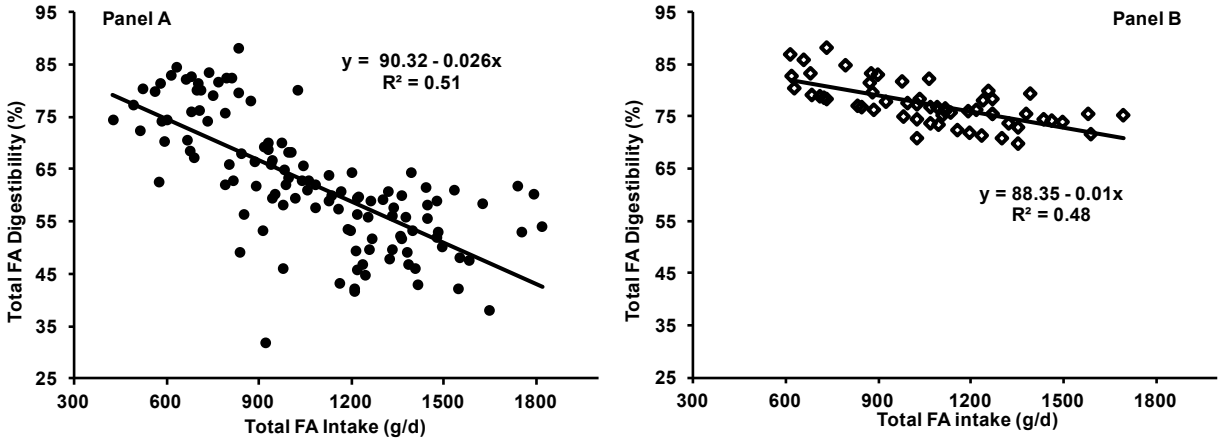

Figure 3. Relationship between total FA intake and total FA digestibility of dairy cows supplemented with either a C18:0-enriched supplement (Panel A) or a C16:0-enriched supplement (Panel B). Results in Panel A utilized 32 mid-lactation cows receiving diets with increasing levels (0 to 2.3% dry matter) of a C18:0-enriched supplement (85% C18:0) in a 4 X 4 Latin square design with 21-d periods (Boerman and Lock, 2014b). Results in Panel B utilized 16 mid-lactation cows receiving diets with increasing levels (0 to 2.25% dry matter) of a C16:0-enriched supplement (87% C16:0) in a 4 X 4 Latin square design with 14-d periods (de Souza et al., 2015).

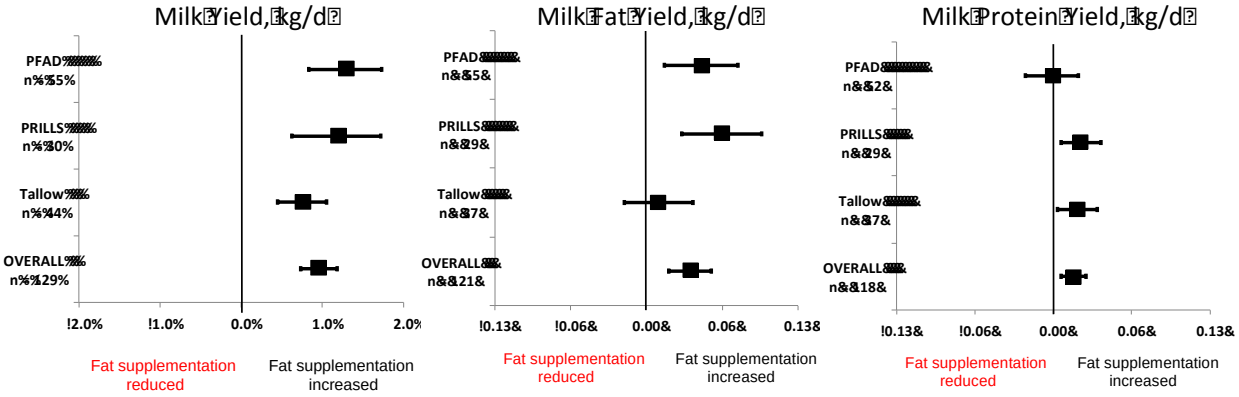

Figure 4. Effect of commercially available FA supplements on yield of milk, milk fat, and milk protein (Boerman and Lock, 2014a). All data reported in peer-reviewed journals in which FA supplements were included at ≤ 3% diet DM compared to control with no added FA supplement. All studies had to have measurements of variance reported. **PFAD** – calcium salts of palm FA distillate (~ 50% 16:0, ~ 50% unsaturated 18-carbon FA); **PRILLS** – saturated FA prills (> 80% saturated FA [16:0 and/or 18:0]); **Tallow** – animal fat labeled as tallow (~ 50% 16:0 and 18:0, ~ 45% 18:1). Data analyzed using Comprehensive Meta-Analysis (CMA) version 2.0 (Biostat, Englewood, NJ), calculating difference between FA supplemented and control diets using a random effects model.

SESSION NOTES