

Recent Advances in Our Understanding of Fatty Acid Digestion and Metabolism in Lactating Dairy Cows

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■ Take Home Messages

- ▶ Identify what you are trying to achieve, then design your nutritional program (including fatty acid [FA] supplementation) around those objectives. Evaluate the effects of individual FA and commercial FA supplements on production performance and tangible factors not measured daily in the tank.
- ▶ Important to consider the possible effects of FA in the rumen, in the small intestine, in the mammary gland, and energy partitioning between tissues.
- ▶ Not all FA or fat sources are the same. Know what FA are in the supplement you are using. The profile of supplemental FA is key in determining production responses and energy partitioning.
- ▶ Digestibility appears to be a good indicator of inclusion or not of a FA in the diet, assuming that this source of FA does not markedly affect DMI.
- ▶ Use of supplemental FA in the fresh period should be considered; new research suggests that FA supplementation increases performance in fresh cows.

■ Introduction

Recently, the effects of individual fatty acids (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. In fresh cows, the high metabolic demand of lactation and reduced DMI during the immediate postpartum period result in a state of negative

energy balance. Approaches to increase the energy intake of postpartum cows include increasing starch content of the diet and supplementing FA to increase the energy density of the diet. However, feeding high starch diets that promote greater ruminal propionate production during early lactation could be hypophagic and therefore further reduce DMI and increase the risk of ruminal acidosis and displaced abomasum (Allen and Piantoni, 2013). Regarding supplemental FA, some authors suggest that caution should be exercised when using dietary FA to increase the caloric density of diets in early lactation dairy cows since a high lipid load may affect the endocrine system, feed intake, and increase the risk for metabolic disorders (Kuhla et al., 2016). However, just as we recognize that not all protein sources are the same, it is important to remember that not all FA or FA supplements are the same. We will briefly review the biological processes and quantitative changes during the metabolism of FA, 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), oleic (*cis*-9 C18:1), omega-3, and omega-6 acids on feed intake, nutrient digestibility, milk production and milk composition, health, and reproduction.

■ **C16:0, C18:0, and *Cis*-9 C18:1 Effects on FA Digestibility**

Our recent FA digestibility research utilized and focused on C16:0, C18:0, and *cis*-9 C18:1. Of particular importance, Boerman et al. (2017) fed increasing levels of a C18:0-enriched supplement (93% C18:0) to mid-lactation 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 mid-lactation 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 with increasing FA intake was observed (Figure 1B). However, considering that the range in 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, with the decrease in total FA digestibility driven by the digestibility of C18:0 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 on emulsification for absorption (Drackey, 2000). Additionally, results have shown that *cis*-9 C18:1 has greater digestibility than C16:0 and C18:0 (Boerman et al., 2015).

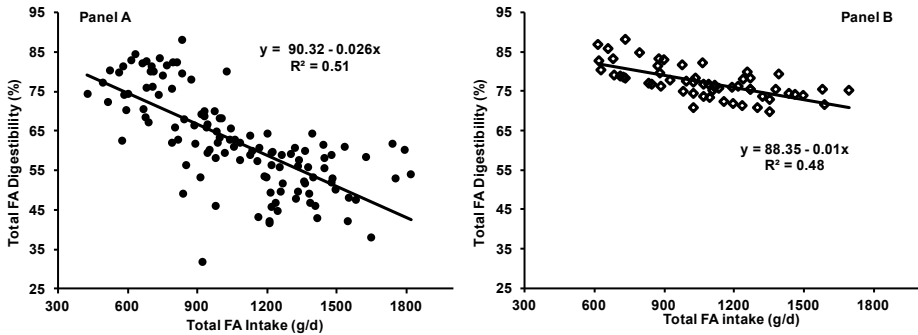


Figure 1. Relationship between total FA intake and apparent total-tract FA digestibility of dairy cows supplemented with either a C18:0-enriched supplement (Panel A) or a C16:0-enriched supplement (Panel B). Results in Panel A utilized 32 mid-lactation cows receiving diets with increasing levels (0 to 2.3% dry matter) of a C18:0-enriched supplement (93% C18:0) in a 4 X 4 Latin square design with 21-d periods (Boerman et al., 2017). 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 (Rico et al., 2017).

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 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). Finally, we recently evaluated the effects of varying the ratio of dietary C16:0, C18:0, and *cis*-9 C18:1 in basal diets containing soyhulls or whole cottonseed on FA digestibility. We observed that feeding a supplement containing C16:0 and *cis*-9 C18:1 increased FA digestibility compared with a supplement containing C16:0, a mixture C16:0 and C18:0, and a non-fat control diet. The supplement containing a mixture C16:0 and C18:0 reduced 16-, 18-carbon, and total FA digestibility compared with the other treatments (de Souza et al., 2018). This is displayed in Figure 2 by using a Lucas test to estimate the apparent digestibility of the supplemental FA blends. The slopes (i.e., digestibility of the supplemental FA blends) in soyhulls based diets were 0.64, 0.55 and 0.75 and in cottonseed diets were 0.70, 0.56 and 0.81 for supplements containing C16:0, a mixture C16:0 and C18:0, and a mixture of C16:0 and *cis*-9 C18:1, respectively. This supports the concept that a combination of 16-carbon and unsaturated 18-carbon FA may improve FA digestibility, but reasons for this need to be determined.

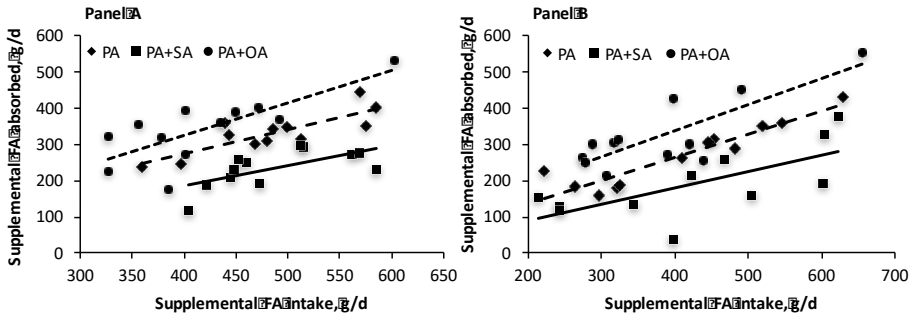


Figure 2. Lucas test to estimate total FA digestibility of supplemental FA treatments when cows received either a soyhulls basal diet (Panel A) or a cottonseed basal diet (Panel B). PA (Palmitic Acid; C16:0) long-dashed line (1.5% of FA supplement blend to provide ~ 80% of C16:0); PA+SA (Stearic Acid; C18:0) solid line (1.5% of FA supplement blend to provide ~ 40% of C16:0 + 40% of C18:0); and PA+OA short-dashed line (1.5% of FA supplement blend to provide ~ 45% of C16:0 + 35% of C18:1 cis-9). Digestibility of supplemental FA was estimated by regressing intake of supplemental FA on intake of digestible supplemental FA. The mean intakes of FA and digestible FA when cows were fed the control diet were subtracted from the actual intakes of total FA and digestible FA for each observation. From de Souza et al. (2018).

In fresh cows, there is scarce information about the effects of supplemental FA on FA digestibility. We recently conducted a study to evaluate the effects of timing of C16:0 supplementation on performance of early lactation dairy cows (de Souza and Lock, 2017b). We observed a treatment by time interaction for C16:0 supplementation during the fresh period (1 – 24 DIM); although C16:0 reduced total FA digestibility compared with control, the magnitude of difference reduced over time (Figure 3). Interestingly, we also observed an interaction between time of supplementation and C16:0 supplementation during the peak period (25 – 67 DIM), due to C16:0 only reducing FA digestibility in cows that received the control diet in the fresh period. This may suggest an adaptive mechanism in the intestine when C16:0 is fed long-term. Understanding the mechanisms responsible for this effect deserves future attention, as does the impact of other supplemental FA during early post-partum on FA digestibility and nutrient digestibility.

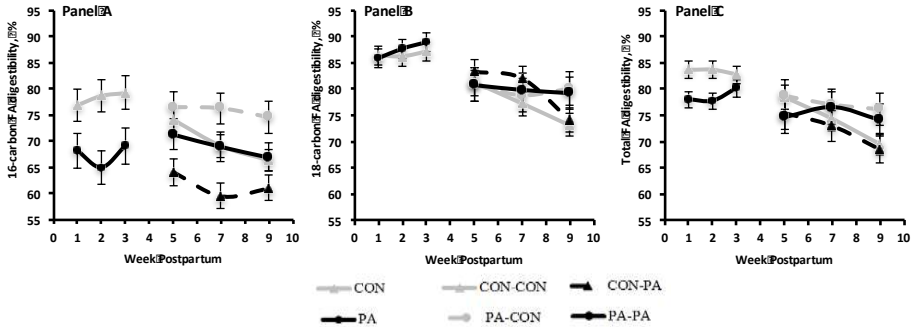


Figure 3. The effects of C16:0-enriched supplementation for early lactation cows on digestibility of 16-carbon (Panel A), 18-carbon (Panel B), and total FA (Panel C). Results utilized 52 early-lactation cows receiving the following diets: no supplemental fat (CON) or a C16:0 supplemented diet (PA) that was fed either from calving (1 to 24 DIM; fresh period FR) or from 25 to 67 DIM (peak period). From de Souza and Lock (2017b).

■ Effect of Fatty Acids on NDF Digestibility

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 any FA supplement. Weld and Armentano (2017) performed a meta-analysis to evaluate the effects of FA supplementation on DMI and NDF digestibility of dairy cows. Supplementation of 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 supplements (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, but the effect of C16:0-enriched supplements were not evaluated.

We recently utilized a random regression model to analyze available individual cow data from 6 studies that fed C16:0-enriched supplements to dairy cows (de Souza et al., 2016). We observed that NDF digestibility was positively impacted by total C16:0 intake (Figure 4A) 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. 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., 2018).

With early lactation cows, Piantoni et al. (2015b) fed a saturated fat supplement (~ 40% C16:0 and 40% C18:0) and observed that fat supplementation increased NDF digestibility by 3.9% units in the low forage diet (20% fNDF), but had no effect in the high forage diet (26% fNDF). In our recent study that evaluated the effects of timing of C16:0 supplementation (PA) on performance of early lactation dairy cows (de Souza and Lock, 2017b), we observed that C16:0 supplementation consistently increased NDF digestibility ~ 5% units over the 10 weeks of treatment compared with control (Figure 4B).

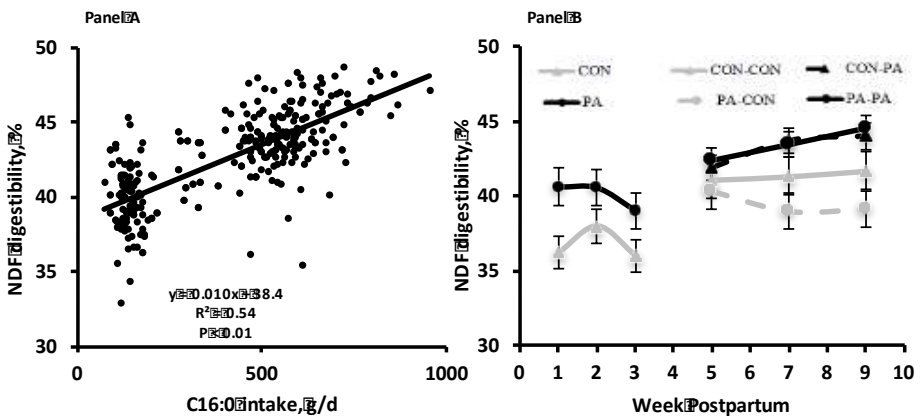


Figure 4. Panel A: Relationship between C16:0 intake and NDF digestibility of dairy cows fed C16:0-enriched FA supplements. Panel B: The effects of C16:0-enriched supplementation in early lactation cows on NDF digestibility. Results in Panel A represent a combined data set evaluated using a random regression model from 6 studies feeding C16:0-enriched supplements on NDF digestibility of post-peak cows (de Souza et al., 2016). Results in Panel B utilized 52 early-lactation cows receiving the following diets: no supplemental fat (CON) or a C16:0 supplemented diet (PA) that was fed either from calving (1 to 24 DIM; fresh period) or from 25 to 67 DIM (peak period). From de Souza and Lock (2017b).

■ 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. Piantoni et al. (2015a) 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 one of the two 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. Additionally, in a recent dose response study with mid lactation cows, feeding a C18:0-enriched supplement (93% 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 1A, Boerman et al., 2017). Our results, and those of others, indicate that C16:0 supplementation has the potential to increase yields of ECM 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 (Piantoni et al., 2013; Rico et al., 2014). We recently utilized a random regression model to analyze available individual cow data from 10 studies that fed C16:0-enriched supplements to post peak dairy cows (de Souza et al., 2016). 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 ECM with increasing intake of C16:0.

When we compared combinations of C16:0, C18:0, and *cis-9* C18:1 in FA supplements, 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., 2018). 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. Interestingly, in a follow up study we compared different ratios of C16:0 and *cis-9* C18:1 in FA supplements fed to post-peak cows and observed that supplements with more C16:0 favored energy partitioning to milk in cows producing less than 45 kg/d, while supplements with more *cis-9* C18:1 favored energy partitioning to milk in cows producing great than 60 kg/d (de Souza and Lock, 2017a). Also, regardless of production level, supplements with more *cis-9* C18:1 increased BW change. 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.

In early lactation cows, Beam and Butler (1998) fed a saturated FA supplement (~ 40% C16:0 and 40% C18:0) and observed that FA supplementation decreased DMI and did not affect yields of milk and ECM in the first 4 weeks after calving. Piantoni et al. (2015b) fed a similar saturated FA supplement (~ 40% C16:0 and 40% C18:0) and observed that FA supplementation during the immediate postpartum (1-29 DIM) favored energy partitioning to body reserves rather than milk yield, especially in the lower forage diet. The high forage diet with supplemental FA increased DMI and tended to decrease BCS loss compared with the same diet without FA supplementation. Also, regardless of forage level, feeding supplemental FA increased DMI, decreased BCS loss, but tended to decrease milk yield. When cows were fed a common diet during the carryover period, the low forage diet with FA supplementation fed during the immediate postpartum continued to decrease milk yield and maintained higher BCS compared with the other treatments. On the other hand, Weiss and Pinos-Rodriguez (2009) fed a similar saturated FA supplement (~ 40% C16:0 and 40% C18:0) to early-lactation cows (21 to 126 DIM) and observed that when high-forage diets were supplemented with FA, the increased NE_L intake went toward body energy reserves as measured by higher BCS with no change in milk yield. However, when low-forage diets were supplemented with FA, milk yield increased (2.6 kg/d) with no change in BCS.

In a recent study, we evaluated the effects of timing of C16:0 supplementation on the performance of early lactation dairy cows (de Souza and Lock, 2017b). During the fresh period (1-24 DIM), we did not observe treatment differences for DMI or milk yield (Figure 5A), but compared with control, C16:0 increased the yield of ECM by 4.70 kg/d consistently over time (Figure 5B). However, C16:0 reduced body weight by 21 kg (Figure 6), and body condition score by 0.09 units, and tended to increase body weight loss by 0.76 kg/d compared with CON. Feeding C16:0 during the peak period (25 to 67 DIM) increased the yield of milk by 3.45 kg/d, ECM yield by 4.60 kg/d, and tended to reduce body weight by 10 kg compared with control (Figure 6).

Interestingly, Greco et al. (2015) observed that decreasing the ratio of omega-6 to omega-3 FA in the diet of lactating dairy cows while maintaining similar dietary concentrations of total FA improved productive performance in early lactation. A dietary omega-6 to omega-3 ratio of approximately 4:1 increased DMI and production of milk and milk components compared with a 6:1 ratio. Approximately 1.3 kg of milk response could not be accounted for by differences in nutrient intake, which suggests that reducing the dietary FA ratio from 6:1 to 4:1 can influence nutrient partitioning to favor an increased proportion of the total net energy consumed being allocated to milk synthesis.

Further studies focusing on altering the ratio of dietary FA are warranted, especially in early lactation cows.

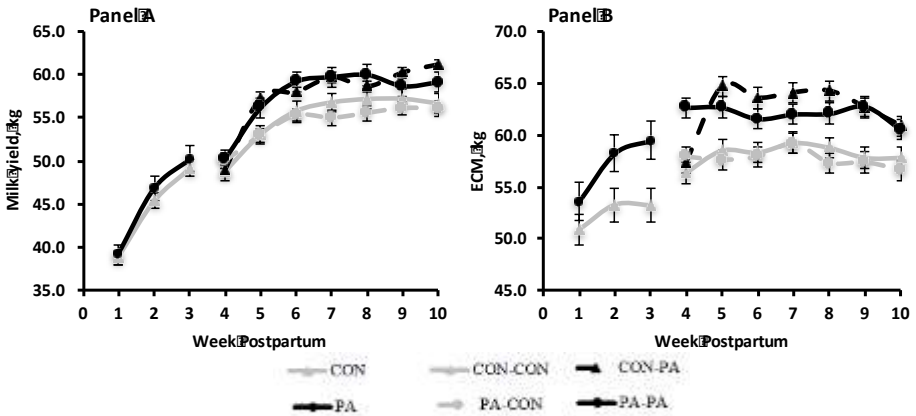


Figure 5. The effects of C16:0-enriched supplementation in early lactation cows on the yield of milk (Panel A) and ECM (Panel B). Results from 52 early-lactation cows receiving the following diets: no supplemental fat (CON) or a C16:0 supplemented diet (PA) that was fed either from calving (1 to 24 DIM; fresh period FR) or from 25 to 67 DIM (peak period). From de Souza and Lock (2017b).

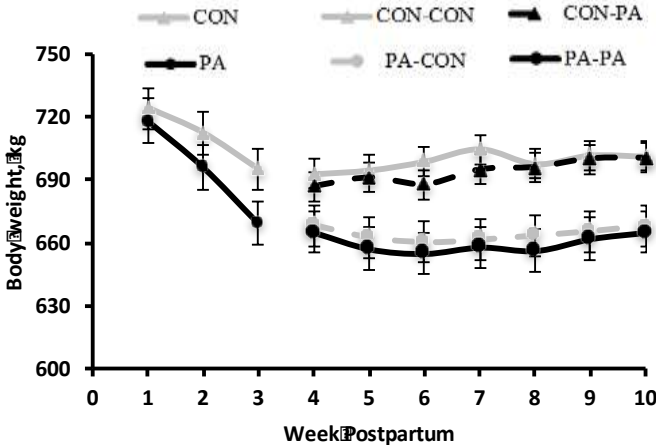


Figure 6. The effects of C16:0-enriched supplementation in early lactation cows on body weight. Results from 52 early-lactation cows receiving the following diets: no supplemental fat (CON) or a C16:0 supplemented diet (PA) that was fed either from calving (1 to 24 DIM; fresh period) or from 25 to 67 DIM (peak period). From de Souza and Lock (2017b).

■ Conclusion

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 improve reproduction performance, great variation has been reported in production performance for different FA supplements, and indeed the same supplement across different diets and studies. Results are contradictory about the benefits of FA supplementation to early lactation dairy cows. We propose that this is a result of differences in FA profile of supplements used and the time at which FA supplementation starts. Further work is required to characterize the sources of variation in response to FA supplementation. Just as we recognize that not all protein sources are the same it is important to remember that not all FA sources and 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. 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, body condition, and their effects on immune and reproductive function. The extent of these simultaneous changes along with the goal of the nutritional strategy employed will ultimately determine the overall effect of the FA supplementation and the associated decision regarding their inclusion in diets for lactating dairy cows.

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