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LANDCORP LECTURE

Regulating milk fat synthesis: potential on-farm applications of basic science

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ABSTRACT

This review covers results from numerous trials evaluating conjugated linoleic acid (CLA) effects on milk fat synthesis and its potential as an on-farm management tool to improve dairy cow performance. Supplemental CLA reduces milk fat synthesis in numerous animal models, and in grazing dairy cows can improve energy balance as well as increase milk and milk protein yield. Mammary lipid metabolism effects are thus far specific to *trans*-10, *cis*-12 CLA, and we demonstrated *trans*-10, *cis*-12 CLA reduces mRNA expression of enzymes required for *de novo* fatty acid synthesis, fatty acid uptake and intracellular transport, and triglyceride formation. The amount of CLA required to reduce milk fat synthesis in lactating cows has little or no effect on circulating basal bioenergetic metabolites and hormones or stimulated responses to homeostatic signals. We hypothesized CLA can be utilized to stimulate milk fat depression when milk synthesis and other physiological processes are limited by energy availability, as is the case in early lactation, during heat stress and occasionally in pasture based dairying. Our research focuses on identifying the mechanisms of action and potential use of CLA as an on-farm management tool to increase farm profit via increased milk production, improved reproduction and decreased metabolic disorders.

Keywords: conjugated linoleic acid; milk fat; energy balance; transition dairy cow.

INTRODUCTION

Conjugated linoleic acid (CLA) is a group of ruminant derived fatty acids that have been demonstrated to improve (in experimental animal models) or ameliorate a plethora of human diseases, ranging from cancer to lupus (Belury, 2002). As a consequence, there has been a global effort to increase the CLA content in ovine and bovine lipids in an attempt to increase the nutritional value and marketability of ruminant derived food products. While attempting to enhance the CLA content of milk fat it

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was serendipitously discovered that exogenous CLA caused severe (> 45%) milk fat depression (MFD) in dairy cows fed total mixed rations (TMR) or pasture (see reviews by Bauman *et al*., 2001; Baumgard *et al*., 2002c).

The supplements used in the above studies contained a mixture of CLA isomers, but based on the increase in milk fat content of *trans*-10 18:1 observed during diet-induced MFD, we hypothesized that CLA isomers containing a *trans*-10 double bond were responsible for reducing milk fat synthesis (Bauman *et al*., 2001). We subsequently confirmed this as cows receiving *trans*-10, *cis*-12 CLA had over a 40% reduction in milk fat content and milk fat yield whereas similar amounts of *cis*-9, *trans*-11 CLA, *trans*-8, *cis*-10 CLA and *cis*-11, *trans*-13 CLA have no effect (Baumgard *et al*., 2000; Perfield *et al*., 2004).

Cows abomasally infused with *trans*-10, *cis*-12 CLA also have substantial changes in milk fatty acid composition. In particular, the content of short and medium chain fatty acids (*de novo* synthesized fatty acids) are dramatically reduced. The reduction in yield of C4 to C16 fatty acids contributed almost 80% (on a molar basis) to the total decrease in milk fat yield (Baumgard *et al*., 2000). To examine the mechanism by which *trans*-10, *cis*-12 CLA decreases milk fat synthesis we biopsied mammary tissue from CLA treated cows and evaluated lipogenic capacity and gene expression for key enzymes involved in milk fat synthesis (Baumgard *et al*., 2002b). Lipogenic capacity was dramatically decreased (~80%) when cows received *trans*-10, *cis*-12 CLA. Likewise, gene expression of acetyl CoA carboxylase, fatty acid synthetase, Δ^9-desaturase, acylglycerol phosphate acyltransferase, glycerol phosphate acyltransferase, fatty acid binding protein and lipoprotein lipase were reduced 39 to 54%. These genes are involved in *de novo* fatty acid synthesis, fatty acid desaturation, triglyceride formation and mammary uptake and transport of fatty acids. Thus, treatment with *trans*-10, *cis*-12 CLA resulted in coordinated decreases in the expression of genes for key enzymes associated with most aspects of milk fat synthesis and it is thought that reduced SREBP-1 proteolytic activation regulates these effects (Peterson *et al*., 2004).

The effects of CLA in dairy cows appear to be specific to the mammary gland as there are little or no effect on basal plasma concentrations of metabolites (glucose, NEFA, β-hydroxybutyrate) and hormones (leptin, insulin, IGF-I) associated with energy homeostasis (Baumgard *et al*., 2000, 2002a; Mackle *et al*., 2003). Furthermore, in contrast to observations in growing animals there appears to be little or no effect on response to homeostatic signals regulating lipolysis (adrenaline) and glucose disposal (insulin) and plasma variables associated with lipid metabolism and energy homeostasis (Baumgard *et al*., 2002a). Thus, it should be possible to use CLA to reduce milk fat synthesis at various stages of the lactation cycle while maintaining normal regulation of whole body energy homeostasis and lipid metabolism.

Transition period bioenergetics

The period immediately prior to and following calving is associated with large metabolic adaptations. Characteristically, cows in this stage of lactation have larger energy requirements (milk synthesis and maintenance costs) than they can obtain from feed (Drackley, 1999). As a consequence, animals enter into a severe negative energy balance (NEBAL), which is associated with an increased risk of metabolic disorders and health problems (Drackley, 1999), decreased milk yield and reduced reproductive performance (Beam & Butler, 1999; Lucy *et al*., 1992). Improving energy balance (EBAL) immediately after calving has been intensely studied, and traditional methods include increasing dietary concentrates and supplemental fat. However, the incidence and severity of NEBAL continues to be the primary issue surrounding transition period failures thus reduced economic return for producers (Drackley, 1999).

Milk fat is the major determinant of milk energy and thus has a large influence on calculated net EBAL. Reducing the nutrient demand for milk synthesis via decreasing milk fat production should therefore alleviate the severity and extent of NEBAL. Improving calculated net EBAL should theoretically reduce the demand for tissue (primarily adipose) mobilization, reduce condition loss, decrease the plasma metabolite levels responsible for fatty liver and ketosis (NEFA) and provide (probably via insulin and/or IGF-I) a signal to stimulate ovarian function and several dimensions of reproductive performance.

CLA and EBAL

Feeding rumen inert (RI)-CLA supplements (Bauman *et al*., 2001) decreases milk fat synthesis during established lactation, but similar amounts of RI-CLA supplements have little or no effect at decreasing milk fat immediately following parturition (Bernal-Santos *et al*., 2003; Selberg *et al*., 2004). In order for supplemental RI-CLA to be used as a management tool to improve EBAL parameters as we hypothesized, it must reduce milk fat synthesis immediately postpartum (i.e. 1-7 days in milk, DIM). We hypothesized that the early lactating mammary gland is less sensitive to CLA, and theorized that a larger CLA dose is required during this period to achieve milk fat reductions similar to those observed in established lactation.

Studies

Study 1

The objective of this TMR-based transition study was to determine the quantity of dietary RI-CLA supplement required to achieve MFD immediately postpartum, theoretically alleviating or reducing the severity and/or duration of NEBAL during the transition period. Experimental conditions have previously been described in detail (Moore *et al*., 2004), but briefly, multiparous Holstein cows (n = 19) were randomly assigned to one of four doses of RI-CLA supplements (0, 200, 400 and 600 g/day) with each dose providing equal amounts of fatty acids by replacing and balancing treatments with a RI supplement of palm fatty acid distillate. Doses provided a total of 468 g fatty acids/day and either 0, 62, 125 or 187 g of mixed (including *trans*-10, *cis*-12) CLA isomers/day, respectively. To capture most of the metabolic changes and large fluctuations in production variables we initiated RI-CLA feeding 10 day prior to anticipated parturition and continued until 21 DIM.

Data from this study demonstrated high doses of RI-CLA supplements (approximately 3-times that used during established lactation) reduced milk fat content and milk fat yield immediately postpartum. Effects were apparent at day 1 of lactation, significantly different by day 5, and became more pronounced as DIM increased. During the first 21 day of lactation, RI-CLA supplements decreased milk fat yield by as much as 33% (Figure 1).

We hypothesized that reducing milk fat synthesis in early lactation, a time when nutrient availability may limit production, may allow for energy partitioning to support increased protein and/or milk synthesis (Bauman *et al*., 2001; Baumgard *et al*., 2002c) as has been observed from cows on pasture in established lactation (Medeiros *et al*., 2000; Mackle *et al*., 2003). However, yield and content of milk components other than milk fat were unaltered in this trial, which is similar to results reported in TMR-based CLA studies during established lactation (see review by Baumgard *et al*., 2002c). Although milk fat synthesis was markedly decreased in the early stages of lactation and there was a numerical improvement (≥ 4 Mcal/day) in EBAL during the 2nd and 3rd wk, overall net EBAL and plasma NEFA levels were unaffected by CLA dose. Although overall EBAL was not statistically different, RI-CLA did decrease days to EBAL nadir compared with controls by 4.7 days for the highest dose (Figure 2). This is relevant as recovery of EBAL from its nadir in early lactation provides an important signal for initiating ovarian activity (Lucy *et al*., 1992; Beam & Butler, 1999) and days to nadir is highly correlated with days to first ovulation (Beam & Butler, 1999). This provides evidence suggesting that feeding RI-CLA supplements during the transition period may positively impact reproduction.

The present study demonstrates that dietary RI-CLA supplements reduce milk fat synthesis at the onset of lactation, but the CLA dose required is much greater (i.e. 3-times) than is necessary to cause a similar reduction in milk fat synthesis during established lactation.

FIGURE 1: Temporal pattern of milk fat yield from cows fed increasing doses of a rumen inert conjugated linoleic acid (CLA) supplement during early lactation. Values are least squares means, n = 4 for the 0 g/day CLA dose and n = 5 for the remaining CLA doses; SEM averaged 123 and ranged from 119 to 134 g/day.

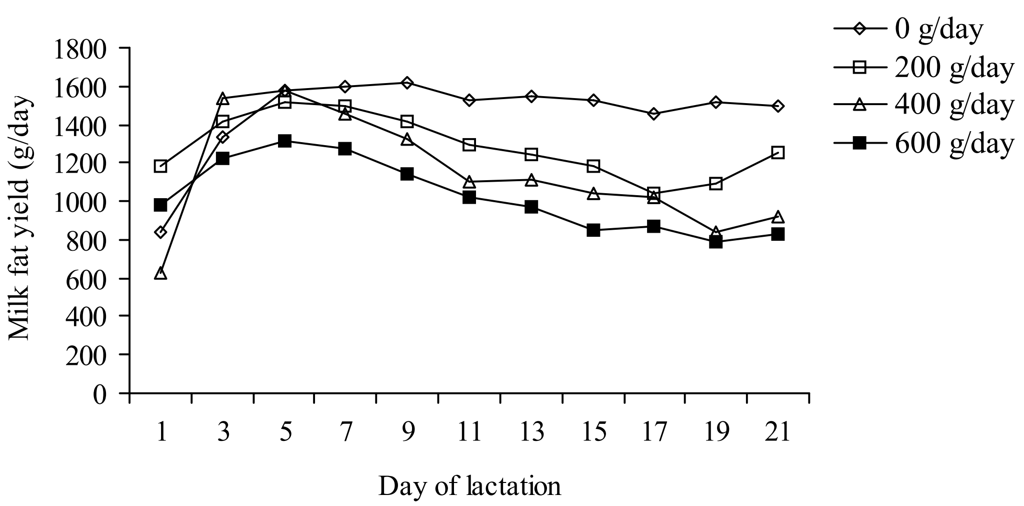

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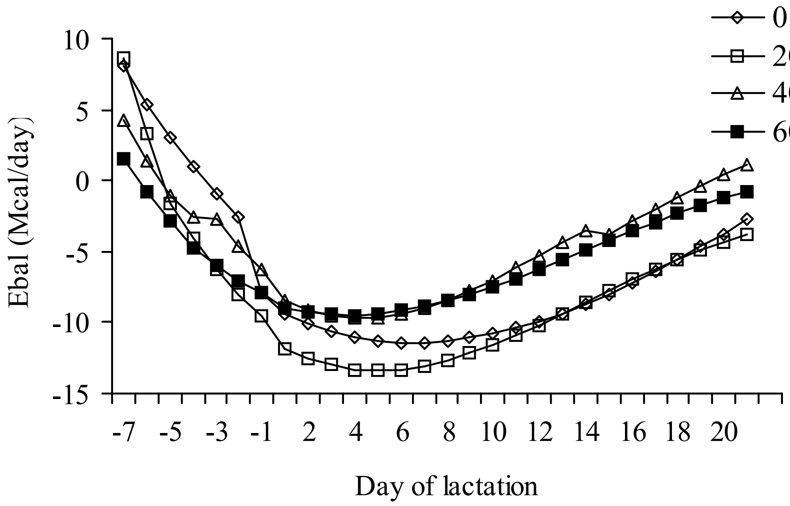
FIGURE 2: Temporal pattern of calculated net energy balance for cows fed increasing doses of a rumen inert conjugated linoleic acid (CLA) supplement during early lactation. Values are least squares means, n = 4 for the CLA 0 g/day dose and n = 5 for the remaining CLA doses; SEM averaged 2.6 and ranged from 2.5 to 2.8 Mcal/day.



Study 2

A second transition CLA study was conducted utilizing cows in a pasture based dairying system (Kay *et al*., 2004). Objectives of the pasture-based transition trial were to determine if a high dietary RI-CLA dose (600 g/cow/day) could induce MFD immediately postpartum in grazing dairy cows and determine if CLA induced MFD would alleviate calculated NEBAL and associated variables (i.e. NEFA, etc.) and improve production parameters (milk and milk component synthesis).

Multiparous Holstein cows (n = 39) grazing pasture were randomly assigned to one of three treatments: 1) pasture (PAS), 2) PAS + 540 g/day Hyprofat (HYPRO; a palm fatty acid distillate; Bonimex BV., Rotterdam, The Netherlands) and 3) PAS + 600 g/day RI-CLA. HYPRO and RI-CLA supplements were isoenergetic, fed 2x/day in the milking parlor at 0700 and 1500 h and provided 0 and 197 g CLA/day, respectively. Treatments began 27 ± 10 days pre-partum and continued until 36 ± 1 DIM.

Data indicate RI-CLA supplementation decreased overall milk fat content and milk fat yield with RI-CLA-induced MFD becoming significant by day 3 when compared with PAS and by day 6 when compared with HYPRO. There was little or no overall RI-CLA effect on content or yield of protein and lactose and alkane data collected during week 4 of lactation indicated no difference in calculated pasture DMI. As a consequence of the similar pasture DMI, consuming additional energy via lipid supplement and severely decreasing milk fat yield, RI-CLA treated cows had a much higher (> 7.5 Mcal/day) calculated/predicted EBAL compared with PAS cows. Compared to HYPRO, CLA supplemented cows tended to increase (> 4.0 Mcal/day) EBAL which can be directly attributed to MFD as these cows were producing similar volumes of milk and consuming similar quantities of feed during this portion of the trial (21-28 day). The improved calculated EBAL compared to PAS was corroborated by the reduction (26%) in circulating NEFA levels, which are thought to reflect calculated EBAL. We also anticipated RI-CLA supplemented cows would have decreased NEFA concentration compared to HYPRO, but this was not the case. This result agrees with the TMR-based transition period study, but a reason for the lack of effect on NEFA is not clear as reducing energy output without altering other components of the EBAL equation should theoretically reduce the demand to mobilize adipose reserves.

As expected due to additional energy intake, both lipid-supplemented treatments produced more overall milk compared with PAS. Although there was no overall milk yield difference between HYPRO and RI-CLA treatments, a quadratic relationship existed between severity of MFD and positive milk yield response (Figure 3).

RI-CLA cows tended to produce more milk (1.8 kg/day) during the first 20 days postpartum when MFD was moderate (< 35%), however as MFD became more severe (> 35%, ~ 21 DIM) the positive response was eliminated and RI-CLA cows tended to produce less milk (2.5 kg/day) during the remainder of the trial (Figure 4). This suggests that during a time of energy deficiency (i.e. the transition period), moderate inhibition of milk fat synthesis may spare energy to be partitioned to increased milk yield, however severe MFD may adversely affect cellular mechanisms involved in milk synthesis and/or secretion. The quadratic response in milk yield is similar to a CLA dose response trial which demonstrated an increase in milk yield with moderate CLA-induced MFD, but no milk yield response with a high CLA dose, an amount that caused severe MFD in pasture-fed dairy cows in established lactation (Mackle *et al*., 2003). Similarly, in a CLA dose trial using TMR-fed cows, high CLA doses that resulted in severe MFD, reduced milk yield by almost 3 kg/day (Chouinard *et al*., 1999). Furthermore, Bell & Kennelly (2003) reduced milk yield by almost 40% when they abomasally infused a CLA dose 4-fold higher than necessary to evoke 40% MFD (Baumgard *et al*., 2000). Therefore although the CLA dose did not change during the present study, the milk yield response followed a similar pattern to the aforementioned trials with increasing MFD severity probably due to the increasing sensitivity of the mammary gland to CLA as lactation progressed. The present study demonstrates that a high dietary RI-CLA dose reduces milk fat synthesis immediately postpartum and may be useful as a management tool to alleviate NEBAL in pasture-fed dairy cows. Moderate MFD appears to have caused a positive response in milk yield, however as lactation progressed and MFD became more severe, the positive milk yield response diminished.

FIGURE 3: Relationship between the percent change in milk yield and extent of milk fat depression (percent decrease in milk fat content) in RI-CLA cows compared with HYPRO cows

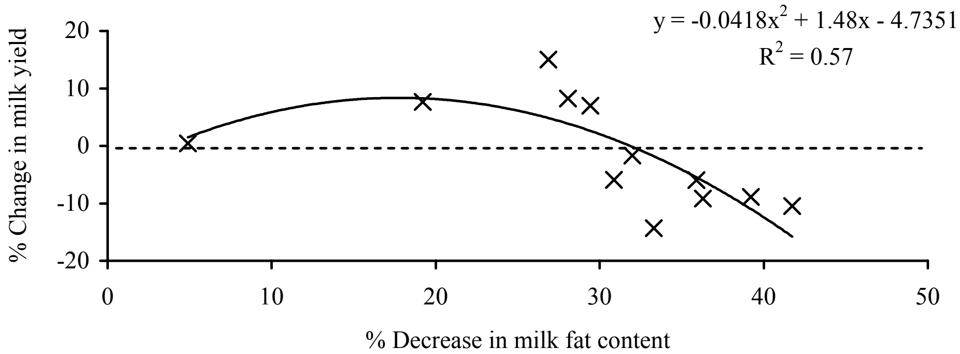
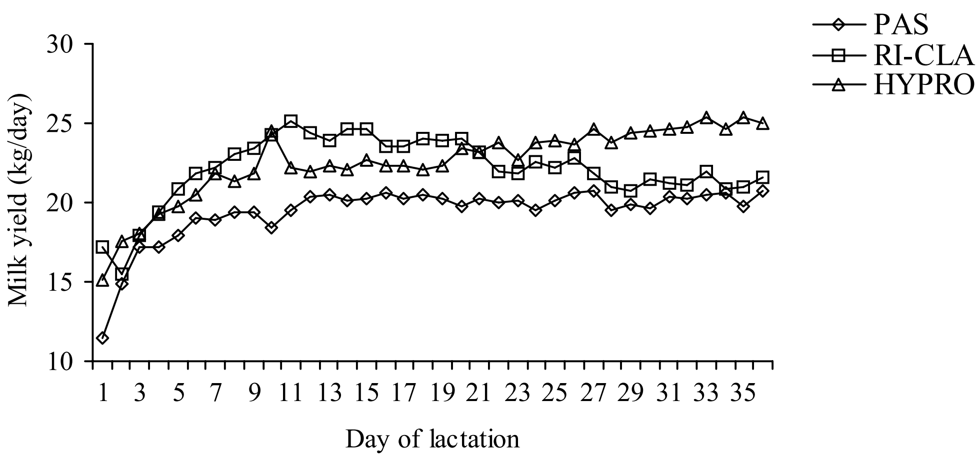


FIGURE 4: Effects of RP-CLA and HYPRO supplementation on temporal pattern of milk yield during first 36 days postpartum. Values represent least squares means (n = 13); SEM averaged 1.31 and ranged from 1.31 to 1.41



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The biological mechanism behind this remains unclear and further research is required to determine why the mammary gland demonstrates decreased sensitivity to *trans*-10 *cis*-12 CLA immediately postpartum and why severe MFD adversely affects milk yield.

Study 3

Heat stress negatively impacts milk synthesis and impairs reproductive performance (Collier *et al*., 2004). As a consequence, heat stress is a significant financial burden in many dairy-producing areas of the world. The bioenergetic mechanism by which heat stress impacts production and reproduction is partly explained by reduced feed intake, but also includes an altered endocrine status, a reduction in rumination and nutrient absorption and increased maintenance requirements (Collier *et al*., 2004) resulting in a net decrease in nutrient/energy availability for production. This decrease in energy results in a reduction in EBAL, and explains why cows lose significant amounts of body weight when heat-stressed. As with pasture-fed cows (Medeiros *et al*., 2000; Mackle *et al*., 2003), we hypothesized that reducing milk fat synthesis during heat stress, a time when nutrient availability may limit production, may allow for energy to be partitioned to support increased protein and/or milk synthesis (Bauman *et al*., 2001; Baumgard *et al*., 2002c, Collier *et al*., 2004). In addition to enhancing milk yield, inhibiting milk fat synthesis, and thus improving energy availability, may improve animal well-being and reproductive success during periods of heat stress

Study objectives were to evaluate whether CLA-induced MFD during heat stress would allow for increased milk and milk component synthesis. Experimental procedures have been described in detail (Moore *et al*., 2005) but briefly, multiparous cows (n = 12) averaging 97 ± 17 DIM were used in a crossover design during the summer (mean temperature humidity index (THI) = 75.7). Treatment periods were 21 days with a 7 day adaptation period prior to and between periods. During adaptation periods all cows received a supplement of palm fatty acid distillate. Dietary treatment consisted of either 250 g/day of CLA supplement (78.9 g/day CLA, mixed isomers including *trans*-10, *cis*-12; RI-CLA) or 242 g/day of palm fatty acid distillate (control) to provide equal amounts of fatty acids.

In agreement with other trials feeding RI-CLA to mid and late lactating cows (see review by Baumgard *et al*., 2002c), milk fat content and yield were decreased (26 and 30%, respectively). However, even though the CLA-induced MFD increased available energy (approximately 3.5 Mcal/day) neither protein nor total milk synthesis increased as hypothesized. Even though this trial was not designed to determine the effects of CLA on reproduction, it is conceivable that improving EBAL could alleviate some of the poor reproductive performance associated with heat stress.

Although cows in this study were experiencing significant heat stress as indicated by THI, respiration rates and skin temperatures, the magnitude of heat stress did not appear extensive enough to induce severe NEBAL (i.e. –10 to –15 Mcal/day). Controls in this experiment had an estimated EBAL of 3.7 Mcal/day and therefore milk and milk component synthesis may not have been limited by energy availability, or limited enough to detect/measure production improvements. However, we must keep in mind, a proportionate decrease in milk yield during heat stress causes calculated EBAL to remain slightly positive and thus appears adequate because of this adjusted production level. However, despite the calculated positive EBAL, irrespective of treatment, cows lost approximately 18 kg of BW during this trial. In agreement, cows in established lactation from semi arid environments (i.e. Arizona, Middle East, etc.) typically lose 20 kg of body weight during the course of a summer (Dennis Armstrong, personal communication). In contradiction to the calculated EBAL, the loss of body weight indicates cows in this trial were in NEBAL and illustrates the difficulty in accurately calculating EBAL in heat stress cows. Furthermore, cows were already heat stressed at trial initiation and it is possible the deleterious effects of heat stress were too severe for 21 days of RI-CLA treatment to overcome. It is of interest to determine if CLA-induced MFD could prevent (in contrast to remedying) the negative effects of heat stress, if provided to thermal neutral animals prior to heat stress initiation.

CONCLUSION and FUTURE DIRECTION

Our group is generating evidence suggesting exogenous dietary RI-CLA can improve EBAL parameters during the transition period and when nutrient availability (i.e. heat stress and/or reduced pasture growth) may limit milk synthesis or reproductive variables. Whether or not the improved calculated net EBAL results in increased milk synthesis, reduced metabolic disorders and increased reproductive success remains to be observed. We are currently conducting larger and longer-term trials to answer these unknowns.

Additionally, we are actively investigating the mechanism why the mammary gland is less sensitive to CLA (specifically *trans*-10, *cis*-12 CLA) immediately postpartum. We have ruled out a number of hypotheses (lack of CLA incorporation, NEFA competition, and differences in fatty acid origin), and are currently utilizing Real Time-PCR to compare the effects of purified *trans*-10, *cis*-12 CLA on mammary gene expression in transitioning vs. established lactation cows.

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