Abomasal Infusion of Butterfat Increases Milk Fat in Lactating Dairy Cows

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ABSTRACT

The objective of this study was to compare the effects of abomasal infusion of butterfat containing all fatty acids (FA) present in milk, including the short- and medium-chain FA, with infusion of only the long-chain FA (LCFA) present in milk, on the FA composition and milk fat yield in lactating dairy cows. Eight rumen-fistulated Holstein cows, in early lactation (49 ± 20 days in milk) were used in a replicated 4×4 Latin square design. Treatments were abomasal infusion of the following: 1) no infusion (control), 2) 400 g/d of butterfat (butterfat), 3) 245 g/d of LCFA (blend of 59% cocoa butter, 36% olive oil, and 5% palm oil) providing 50% of the 16:0 and equivalent amounts of C18 FA as found in 400 g of butterfat, and 4) 100 g/d of conjugated linoleic acid (CLA, negative control), providing 10 g of *trans*-10, *cis*-12 CLA. Fat supplements were infused in equal portions 3 times daily at 0800, 1400, and 1800 h during the last 2 wk of each 3-wk experimental period. Daily dry matter intake and milk production were unaffected by the infusion treatments. Butterfat infusion increased milk fat percentage by 14% to 4.26% and milk fat yield by 21% to 1,421 g/d compared with controls (3.74% and 1,178 g/d). Milk fat percentage and fat yield were decreased by 43% by CLA. Milk protein percentage was higher (3.70%) in CLA-infused cows than in control (3.30%), butterfat (3.28%), or LCFA (3.27%) treatments. Although LCFA had no effect on fat synthesis, abomasal infusion of butterfat increased milk fat percentage and yield, suggesting that the availability of short- and medium-chain FA may be a limiting factor for milk fat synthesis.

Key words: lactating dairy cow, milk fat synthesis, de novo fatty acid

INTRODUCTION

The current milk component pricing system was introduced by the Federal Milk Marketing Administra-

tion in 2000. Accordingly, there has been a shift in the producer payment from the historic system based on the volume of milk (adjusted for fat content) to one based primarily on the amounts of milk fat and protein produced. The milk component pricing system provides a powerful economic incentive for dairy producers to produce high value milk components, namely fat and protein. Milk component yields are driven by both milk volume and component concentration. The diet of the dairy cow has no effect on milk lactose and mineral content (Sutton, 1989). Compared with milk fat responses, only modest effects of diet have been reported on milk protein concentration (Sutton, 1989). Milk fat is the milk component most easily manipulated by diet (Sutton, 1989). Reports in the literature have shown that milk fat percentage and yield can be reduced up to 46% (Piperova et al., 2000; Peterson et al., 2003) by milk fat-depressing diets containing high levels of grain and polyunsaturated fatty acids (PUFA).

In contrast, very few studies have demonstrated consistent ways to increase milk fat concentration. Abomasal infusion of mostly saturated long-chain fatty acids (LCFA) tended to increase milk fat yield compared with infusion of mostly unsaturated fatty acids (FA) or mixtures of both (Drackley et al., 1992). Abomasal infusion of canola, soybean, or sunflower oil did not significantly affect milk fat percentage in lactating cows but changed milk FA profile reflecting the FA composition of the infused oils (Christensen et al., 1994). Inclusion of fats and oils in the diet of lactating cows usually decreases the proportion of de novo FA produced by the mammary gland (Clapperton and Banks, 1985; LaCount et al., 1994).

Short- and medium-chain FA (6:0 to 14:0, plus 50% of 16:0), constitute 50% of total milk FA and originate from de novo FA synthesis in the mammary gland (Palmquist and Jenkins, 1980). These FA are essential for the formation of milk triacylglycerols (Moore and Christie, 1979) and for maintaining the fluidity of milk fat (Barbano and Sherbon, 1980). With exception of oleic acid, which is produced from stearic acid by the Δ^9 -desaturase system in the mammary gland, the LCFA in milk are derived from dietary sources (Palmquist and

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Jenkins, 1980). Experiments with milk fat-depressing diets in lactating cows have demonstrated that yields of short- and medium-chain FA synthesized de novo were reduced to a greater extent than LCFA yields (Lor and Herbein, 1998; Chouinard et al., 1999; Baumgard et al., 2002). These observations suggest that provision of short- and medium-chain FA via dietary means might enhance milk fat content, reducing the need for de novo synthesis.

One could reason that a fat containing the FA composition identical to milk fat would provide the ideal fat supplement for milk fat production. Alternatively, if short- and medium-chain FA are not limiting, then a fat supplement containing only LCFA with a composition identical to that found in milk fat would be ideal for meeting the needs of FA that are typically absorbed from the diet. These conceptual approaches were used as means to potentially increase milk fat synthesis. The objective of this study was to compare the effects of abomasal infusion of butterfat containing all FA present in milk, including the short- and medium-chain FA, with infusion of only the long-chain FA present in milk, on the FA composition and milk fat yield in lactating dairy cows.

MATERIALS AND METHODS

Animals, Experimental Design, Treatment, and Sampling

All procedures for this experiment were conducted under a protocol approved by the University of Maryland Institutional Animal Care and Use Committee. Eight rumen-fistulated multiparous Holstein cows in early lactation (49 ± 20 DIM) were used in a replicated 4×4 Latin square design balanced for carryover effects. Treatments were abomasal infusion of the following: 1) no infusion (control); 2) 400 g/d of butterfat as a source of short- and long-chain FA (butterfat); 3) 245 g/d of a LCFA mixture providing 50% of the 16:0 and equivalent amounts of C18 FA as found in 400 g of butterfat (LCFA); and 4) 100 g/d of commercial conjugated linoleic acid (CLA) mixture providing 10 g of *trans*-10, *cis*-12 CLA/d, which served as a negative control.

In the LCFA treatment, only 50% of the palmitic acid found in the butterfat was included, because 50% of palmitic acid is thought to be synthesized de novo (Palmquist and Jenkins, 1980). The LCFA mixture was a blend of 59% cocoa butter, 36% olive oil (Unilever, Englewood Cliffs, NJ), and 5% palm oil (GloryBee Foods Inc., Eugene, OR). In the butterfat treatment, butter oil was prepared from commercially available unsalted butter (Wellsley Farms, Natick, MA) melted at 37°C and separated from the protein coagulate by filtering. The CLA mixture was provided by Vitrus Nutrition

Figure 1. Fatty acid composition of postruminally infused butterfat and long-chain fatty acid (LCFA) mixture.

(Corcoran, CA). Amounts of postruminally infused individual FA in the LCFA mixture and butterfat are shown in Figure 1. The FA composition of the fat supplements is presented in Table 1.

Experimental periods were 3 wk. The first week of each period was without fat infusion to reduce carryover effects. This was followed by 2 wk of abomasal infusion. The fat was infused via tygon tubing (0.48-cm i.d., 0.64-cm o.d.; VWR Scientific, Bridgeport, NJ) that passed through the ruminal cannula, the rumen, the omasum, and into the abomasum, where the line was maintained using a 10-cm circular plastisol flange. The fat mixtures were liquified at 50°C in air oven and mixed well before infusion. The amount of each FA mixture was divided into equal portions and manually infused 3 times a day (133.33 g of butterfat, 81.6 g of LCFA, and 33.33 g of CLA at 0800, 1400, and 1900 h). Actual amounts of infused fat were recorded each day. Patency and location of the infusion line inside the cow were checked on alternate days.

Cows were housed in individual tie stalls and were fed a basal diet containing 55% forage and 45% concentrate (DM basis) to meet NRC (2001) nutrient specifications for a 650-kg cow producing 40 kg of milk containing 3.7% milk fat and 3.1% milk protein. Ingredient and chemical composition of the basal diet is given in Table 2. Diets were fed as TMR once daily at 0800 h. Forage and ingredient DM were measured weekly, and the TMR was adjusted accordingly to maintain a constant forage-to-concentrate ratio on a DM basis. Amounts of feed offered and refused were recorded once daily. Cows were milked twice a day at 0600 and 1600 h, and milk production was recorded electronically at each milking. Samples for milk composition and FA

Table 1. Fatty acid composition of the butterfat, long-chain fatty acid (LCFA), and conjugated linoleic acid (CLA) supplements

Fatty acid	Butterfat	LCFA	CLA
	g/100 g of FAME ¹		
4:0	3.34		
6:0	2.22		
8:0	1.06		
10:0	1.93		
12:0	3.00		
14:0	12.09	0.18	0.15
14:1	0.66		
15:0	0.89		
15:1	0.01		
16:0	26.73	24.41	5.79
16:1	1.17	0.55	0.12
16:1 <i>trans</i>	0.02		
17:0	0.61		
17:1	0.18		
18:0	11.45	21.17	2.54
18:1 <i>cis</i> -9	26.79	45.67	29.02
18:1 <i>cis</i> -11	0.54		0.72
18:1 <i>cis</i> -12	0.55		0.02
18:1 <i>cis</i> -13	0.09		0.06
18:1 <i>cis</i> -14 + 19:0	0.18		0.62
18:1 <i>trans</i> total	2.09		0.23
18:2n-6	2.80	6.37	0.88
18:3	0.39	0.44	0.29
22:0	0.04		0.14
Others	0.56	1.21	3.21
<i>Cis</i> -8, <i>trans</i> -10 18:2	0.00		0.68
<i>Trans</i> -8, <i>cis</i> -10 18:2	0.00		0.75
<i>Cis</i> -9, <i>trans</i> -11 18:2	0.55		14.59
<i>Cis</i> -9, <i>trans</i> -13 18:2	0.00		0.74
<i>Cis</i> -13, <i>trans</i> -12 18:2	0.00		1.09
<i>Cis</i> -11, <i>trans</i> -13 18:2	0.01		9.44
<i>Trans</i> -10, <i>cis</i> -12 18:2	0.01		9.66
<i>Trans</i> -11, <i>cis</i> -13 18:2	0.03		1.00
<i>Trans</i> -11, <i>trans</i> -13 18:2	0.00		1.17
<i>Trans/trans</i> 18:2	0.02		10.71
<i>Cis/cis</i> 18:2			6.21

¹Fatty acid methyl esters.

analysis were collected from the last 6 consecutive milkings of wk 3 of each experimental period. Milk fat, protein, and SCC were determined by infrared analysis (Foss Milk-O-Scan, Foss Food Technology Corp., Eden Prairie, MN) on fresh samples from individual milkings. A subset of samples from each milking was composited and frozen at -20°C for subsequent analysis of individual FA.

FA Composition

Milk fat was extracted using a modified Folch procedure (Christie, 1982) from composited wk 3 samples. The FA methyl esters (**FAME**) were prepared by mild transesterification with 0.4 mol/L of H₂SO₄ in methanol (Christie, 1982) at room temperature, using trionadecenoic (Nu-Chek Prep Inc., Elysian, MN) as internal standard (Pipero et al., 2002). The FAME were analyzed using an Agilent 6890 GC (Agilent Technologies,

Table 2. Ingredient and chemical composition of the basal diet

Item	DM, %
Ingredient	
Corn silage	30.13
Alfalfa haylage	23.00
Corn grain, ground	21.71
Citrus pulp	8.05
Soybean meal	14.35
Limestone	0.26
Salt	0.48
Magnesium oxide	0.32
Sodium bicarbonate	1.04
Potassium magnesium sulfate	0.17
Dicalcium phosphate	0.39
Trace minerals and vitamins ¹	0.10
Chemical composition	
DM, %	66.71
CP	17.43
RUP ²	33.34
ADF	19.88
NDF	29.80
NE _L , ² Mcal/kg	1.75
Ca	0.69
P	0.38
Na	0.54
Mg	0.36
S	0.22
K	1.20
Cl	0.50

¹Trace mineral and vitamin mix combined (per kg of mix) 15 mg of Mn, 50 mg of Zn, 10 mg of Cu, 0.60 mg of I, 0.20 mg of Co, 0.30 mg of Se, 0.12 g of retinyl acetate, 0.40 g of cholecalciferol, and 0.05 mg of DL-tocopheryl acetate.

²Calculated value.

Santa Clara, CA) equipped with a Supelco 2560 capillary column (100 m × 0.25 mm, 0.2 mm, Supelco, Bellefonte, PA) and a flame ionization detector. The column was maintained at 173°C isothermal. Hydrogen was used as carrier gas with a linear velocity of 26 cm/s and split ratio of 1:100. The injection port and detector were maintained at 250°C. Detector airflow was 400 mL/min, and hydrogen flow was 30 mL/min. Helium make-up gas was used at 30 mL/min. Individual FA and 18:1 isomers were identified using GLC-463 standard mixture (Nu-Chek Prep Inc.).

Although GLC conditions can be adjusted to quantify FAME from 8:0 to 12:0 with some accuracy, the very short FAME are volatile, water soluble, and require correction factors (Kramer et al., 1997). To avoid these difficulties, short- and medium-chain FA were analyzed as FA butyl esters (**FABE**), which were mathematically converted to FAME and normalized to the FAME chromatogram. The original FABE procedure of Gander et al. (1962) was modified as previously described (Pipero et al., 2000). Milk samples (200 µL) in screw-capped glass tubes were heated at 100°C for 1 h in the presence of 1 mL of butyl alcohol and 200 µL of acetyl chloride. Aliquots of the upper layer, containing FABE, were analyzed on a short 25 m × 0.2 mm fused silica

capillary column coated with HP1 (Hewlett-Packard, Avondale, PA) using a Hewlett-Packard 5880 GLC equipped with a split injector and flame ionization detector. Helium was used as the carrier gas at a flow rate of 2 mL/min with a split ratio of 45:1. After 5 min at 90°C, the column temperature was raised (4°C/min) to 106°C and at 10 min, programmed at 5°C/min to a final temperature of 250°C. Standard mixtures, including GLC-60 (Nu-Chek Prep Inc.), were converted to FAME to aid in the identification and quantification of components.

Individual CLA were analyzed as methyl esters using a Waters 2690 HPLC (Waters Associates, Milford, MA) separations module, equipped with a Waters 2996 PDA detector, and 3 Chromspher 5 lipid (250 × 4.6 mm, 5 µM, Varian, Palo Alto, CA) HPLC columns in series. The mobile phase was 0.1% acetonitrile in hexane, at 1 mL/min, kept in a sealed bottle at -15°C. The PDA detector was operated between 190 and 300 nm, and HPLC chromatograms read at 233 nm were used for quantitative analysis. Columns were maintained at 20°C. Typical injection volume was 1 µL, containing 10 to 25 µg of FAME. A CLA standard mixture (Nu-Chek Prep Inc.) was used to identify individual isomers. Details on the identification and quantification of the CLA isomers by HPLC analysis have been reported elsewhere (Sehat et al., 1998; Eulitz et al., 1999).

Statistical Analysis

Milk production, milk components, and FA composition data were analyzed as a replicated 4 × 4 Latin square using the MIXED procedure in SAS (SAS Institute, 2000). The fixed effects were the treatments, whereas the random portion of the model included cow, square, and period. Probability of $P \leq 0.05$ was considered statistically significant. One cow was diagnosed with displaced abomasum and surgically repaired at the end of period 1. To allow for recovery from surgery, data from this cow were not included for experimental periods 1 and 2 (control and LCFA treatments, respectively). Because of missing data for this cow, the results are presented as least squares means. The largest standard error was reported in the treatments with unequal replication. Fisher's protected least significance differences were used for pairwise treatment mean comparisons.

RESULTS

The FA profile of the infused mixtures is presented in Table 1. Butterfat infusion provided short- and medium-chain FA ($C < 16$), in addition to palmitic acid and $C > 18$ LCFA. Also, the butterfat treatment con-

tained small amounts of CLA (0.63%) with *cis*-9, *trans*-11 CLA being the predominant isomer. The LCFA mixture was formulated to provide equivalent amounts of LCFA of dietary origin, as in the infused butterfat, assuming that 50% of 16:0 in milk fat is derived from the diet. The CLA supplement contained 55% of CLA with *cis*-9, *trans*-11 (14.59%); *cis*-11, *trans*-13 (9.44%); and *trans*-10, *cis*-12 (9.66%) being the major isomers.

Average daily DMI, milk production, and milk composition are presented in Table 3. The daily DMI and milk production was not affected by the infusions. However, butterfat infusion significantly ($P < 0.05$) increased FCM (3.5%) compared with the control. Milk production efficiency (FCM/NE_L intake) was lower with CLA infusions but did not differ due to butterfat or LCFA infusions from the control.

Butterfat infusion increased milk fat percentage by 14% ($P < 0.03$) to 4.26% and milk fat yield by 21% ($P < 0.02$) to 1,421 g/d compared with controls (3.74% and 1,178 g/d). Infusion of LCFA had no effect on either milk fat percentage or milk fat yield, although milk fat yield was numerically (8.5%) higher compared with controls. Infusion of CLA decreased milk fat percentage and fat yield by 43% ($P < 0.001$), whereas milk protein percentage was 0.40 to 0.43 percentage units greater (3.70%; $P < 0.01$) compared with the other treatments.

Concentrations (g/100 g of FAME) and yield (g/d) of individual FA in milk are shown in Tables 4 and 5, respectively. Fatty acid concentrations of individual short- and medium-chain FA that are synthesized *de novo* in the mammary gland did not differ between control and butterfat- or LCFA-infused cows. Compared with the controls, concentrations of $C < 16:0$ (total short and medium chain) FA, palmitic acid, or $C > 16:0$ FA were not altered due to butterfat infusion, whereas LCFA infusion decreased $C < 16:0$ and palmitic acid but increased $C > 16:0$ FA. Concentrations of the total monounsaturated FA (MUFA) were significantly greater ($P < 0.05$) in cows infused with butterfat and LCFA compared with the controls (Table 4). The yield of short- and medium-chain FA was increased by 21% with butterfat ($P < 0.05$). Cows infused with butterfat produced milk with numerically the highest yield of 16:0 and significantly greater yields of 14:0, 15:0, and 17:0 (Table 5, $P < 0.02$, 0.01, and 0.02, respectively). Milk of cows infused with butterfat was enriched with 14:1, 16:1, 17:1, and 18:1 *cis*, causing a 37% ($P < 0.001$) increase in the yield of total MUFA. Similar changes were observed in the yield of PUFA (18:2n-3, $P < 0.004$; 18:2i, $P < 0.001$; and 18:3n-3, $P < 0.001$) with the butterfat treatment. Yields of 18:1 *cis*-9 (26% increase; $P < 0.005$) and 18:2n-6 (43% increase; $P < 0.002$) FA were most affected by the LCFA infusion. Total saturated

Table 3. Least squares means for DMI, milk production, and milk composition from cows fed the control diet or the control diet plus abomasal infusion of conjugated linoleic acid (CLA), butterfat, or long-chain fatty acid (LCFA) supplements

Item	Treatment				SEM
	Control	CLA	Butterfat	LCFA	
DMI, kg/d	23.7	24.1	24.2	25.7	1.1
Milk					
kg/d	31.8 ^{ab}	29.9 ^b	33.7 ^a	33.1 ^{ab}	2.5
FCM, 3.5%	32.87 ^b	23.65 ^c	37.72 ^a	35.04 ^{ab}	2.71
Efficiency, FCM/NE _L	0.78 ^a	0.55 ^b	0.83 ^a	0.77 ^a	0.44
Efficiency, FCM/DM	1.37 ^b	0.98 ^c	1.51 ^a	1.38 ^b	0.07
Milk NE/NE intake	0.53 ^a	0.41 ^b	0.56 ^a	0.52 ^a	0.02
Fat, %	3.74 ^b	2.16 ^c	4.26 ^a	3.79 ^{ab}	0.19
Fat yield, g/d	1,178 ^b	661 ^c	1,421 ^a	1,279 ^{ab}	107.7
Protein, %	3.30 ^b	3.70 ^a	3.28 ^b	3.27 ^b	0.12
Protein, g/d	1,033	1,086	1,061	1,085	62.6
Lactose, %	4.63 ^a	4.45 ^b	4.59 ^{ab}	4.70 ^a	0.08
SCC, 10 ³ /mL	102	174	205	97	82.8

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

FA were marginally increased with butterfat and LCFA infusion.

Except for 4:0 concentrations, CLA infusion reduced concentrations (20%, $P < 0.001$) and yield (56%, $P < 0.0001$) of all short- and medium-chain FA and 16:0. Conjugated linoleic acid had similar effect on the yield of FA C > 16:0 (38% decrease; $P < 0.001$) and proportionally decreased all saturated FA (Table 5). Compared with the controls, the concentration (489%, $P < 0.001$; Table 6) and yield (336%, $P < 0.001$; Table 7) of total CLA increased in cows infused with CLA. This reflected the increase in the percentage and yield of individual CLA isomers (Table 6 and 7). The *cis*-9, *trans*-11 CLA isomer was the predominant CLA isomer in the milk fat of cows receiving all treatments. Milk fat percentage of *trans*18:1 was increased in cows infused either with butterfat or CLA (Table 6), compared with the control or LCFA-infused cows. However, the yield of *trans* 18:1 was lowest in cows receiving CLA due to the reduction of milk fat (Table 7). *Trans* 11-18:1 was the predominant isomer in milk of cows receiving all treatments. The *trans* 18:1 and CLA isomer profile in cows infused with LCFA was similar to that in the control.

DISCUSSION

This is the first study to examine the effects of post-ruminal infusion of de novo (short- and medium-chain FA) vs. dietary-derived (LCFA) FA on milk fat synthesis in lactating cows. Because our LCFA treatment contained nearly identical amounts of LCFA (C18 plus 50% of 16:0) as in butterfat, inferences about the role of short- and medium-chain FA on milk fat synthesis can be made by comparing the butterfat and LCFA treatments. In contrast, CLA infusion was used as a

negative control to demonstrate responsiveness of cows to changes in FA infusion. The CLA mixture provided 10 g/d of *trans*-10, *cis*-12 CLA and decreased milk fat yield by 43%. Consistent with other CLA infusion experiments (Chouinard et al., 1999; Baumgard et al., 2000), de novo FA synthesis and FA desaturation were predominantly inhibited.

Generally, DMI is affected by abomasal infusion of highly unsaturated FA (Bremmer et al., 1998; Benson et al., 2001) and to a lesser degree of saturated LCFA (Bremmer et al., 1998). The infusion mixtures in this study contained both saturated and unsaturated FA (Table 1), and the maximum amount of FA infused was limited to 400 g/d to avoid possible adverse effects on DMI (Drackley et al., 1992).

Infusion of FA did not affect DMI and resulted in a marginal increase in milk production in cows infused with butterfat and LCFA treatments. Milk fat percentage and yield were significantly increased with the butterfat but not with LCFA infusion treatments. The increase in total milk fat was more apparent when yields of individual FA were compared. The differences in the effects of butterfat and LCFA were associated with the short- and medium-chain FA provided by the butterfat. Earlier experiments (Storry et al., 1969) did not show changes in milk fat yield when synthetic tripropionin, tributyrin, tricaproin, tricaprylin, and tricaprins containing short-chain FA (3:0, 4:0, 6:0, 8:0, and 10:0) were intravenously infused for 2 d in lactating dairy cows. However, milk fat yield was increased by 16% during intravenous infusion of trilaurin (12:0) and trimyristin (14:0; Storry et al., 1969). Similarly, a 12% increase in milk fat yield was reported in lactating cows fed diets supplemented with coconut oil, containing predominantly 12:0 and 14:0 FA (Storry et al.,

Table 4. Least squares means for fatty acid composition of milk from cows fed the control diet or the control diet plus abomasal infusion of conjugated linoleic acid (CLA), butterfat, or long-chain fatty acid (LCFA) supplements

Fatty acid	Treatment				SEM
	Control	CLA	Butterfat	LCFA	
	g/100 g of FAME ¹				
4:0	3.45	3.04	3.52	3.47	0.36
6:0	1.81 ^a	0.83 ^b	1.54 ^a	1.71 ^a	0.10
8:0	1.24 ^a	0.55 ^b	1.06 ^a	1.17 ^a	0.08
10:0	3.22 ^a	1.55 ^b	2.83 ^a	2.96 ^a	0.19
12:0	4.01 ^a	2.41 ^b	3.91 ^a	3.73 ^a	0.25
14:0	12.31 ^a	10.96 ^b	12.65 ^a	11.78 ^{ab}	0.37
14:1	1.14 ^{ab}	1.19 ^{ab}	1.38 ^a	1.05 ^b	0.08
15:0 (iso)	0.23 ^a	0.19 ^b	0.22 ^a	0.23 ^a	0.02
15:0 (anteiso)	0.51	0.47	0.51	0.50	0.03
15:0	1.22	1.25	1.27	1.13	0.04
15:1	0.07	0.03	0.02	0.01	0.02
16:0	35.08 ^a	35.41 ^a	33.10 ^{ab}	31.53 ^b	1.33
16:0 (iso)	0.36	0.31	0.35	0.33	0.03
16:1	1.63	1.98	1.76	1.22	0.16
16:1 <i>trans</i>	0.04	0.03	0.03	0.03	0.01
17:0	0.79 ^a	0.71 ^b	0.78 ^a	0.74 ^{ab}	0.03
17:0 (iso)	0.06	0.06	0.06	0.06	0.00
17:1 (iso)	0.15 ^b	0.18 ^a	0.19 ^a	0.20 ^a	0.01
17:1 (anteiso)	0.43	0.39	0.41	0.38	0.03
17:1	0.21 ^a	0.23 ^a	0.21 ^a	0.18 ^b	0.01
18:0	8.08 ^{ab}	8.91 ^a	7.31 ^b	8.47 ^{ab}	0.42
18:1 <i>cis</i> -9	16.50 ^b	18.01 ^b	18.13 ^b	20.84 ^a	0.84
18:2 ²	0.47 ^b	0.58 ^a	0.60 ^a	0.44 ^b	0.03
18:2n-6	2.40 ^b	2.89 ^a	2.52 ^b	2.93 ^a	0.14
18:3 ³	0.14 ^b	0.09 ^c	0.11 ^c	0.17 ^a	0.01
18:3n-3	0.40 ^b	0.46 ^a	0.40 ^b	0.43 ^{ab}	0.03
20:0	0.10 ^{ab}	0.11 ^a	0.09 ^b	0.12 ^a	0.01
GLA ⁴	0.03	0.03	0.03	0.03	0.00
Other	0.55 ^{ab}	0.73 ^a	0.59 ^{ab}	0.49 ^b	0.07
Summations					
<16:0	29.21 ^a	22.47 ^b	28.91 ^a	27.74 ^a	0.89
>16:0	31.40 ^b	34.63 ^{ab}	32.60 ^b	36.21 ^a	1.35
>20:0	0.16 ^b	0.20 ^a	0.20 ^a	0.20 ^a	0.01
MUFA ⁵	20.17 ^b	22.04 ^{ab}	22.13 ^a	23.91 ^a	1.19
SFA ⁶	72.47 ^a	66.76 ^c	69.20 ^{ab}	67.93 ^{bc}	1.38
PUFA ⁷	3.04 ^c	3.59 ^a	3.26 ^{bc}	3.57 ^{ab}	0.16

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Fatty acid methyl esters.

²Nonconjugated 18:2 isomers.

³Nonconjugated 18:3 isomers.

⁴Gamma linoleic acid.

⁵Monounsaturated fatty acids.

⁶Saturated fatty acids.

⁷Polyunsaturated fatty acids.

1971; Astrup et al., 1974). Pure saturated FA (12:0, 14:0, 16:0, or 18:0) fed to lactating cows (Steele and Moore, 1968b) produced variable changes in milk fat content but increased these FA in milk, suggesting that the proportions of FA from treatment supplements were increased in blood triacylglycerols. Comparable results were reported (Enjalbert et al., 2000) in lactating cows receiving duodenal infusion of palmitic, stearic, or oleic acids.

In this study, infusion of butterfat significantly increased the yield of FA with C ≤ 16:0, raising the over-

all milk fat yield compared with the other treatments. The increase was predominantly due to greater yield of 12:0 to 14:0 medium-chain FA. Short- and medium-chain FA are better absorbed than LCFA and are transported via the portal venous blood system (Grummer and Socha, 1989). Nevertheless, their transfer to milk fat may be reduced due to extensive metabolism by the extramammary tissues (Grummer and Socha, 1989).

The apparent transfer efficiency of the abomasally infused FA was calculated (amount of FA excreted in

Table 5. Least squares means for yield of fatty acids in milk from cows fed the control diet or the control diet plus abomasal infusion of conjugated linoleic acid (CLA), butterfat, or long-chain fatty acid (LCFA) supplements

Fatty acid	Treatment				SEM
	Control	CLA	Butterfat	LCFA	
	g of FAME ¹ /d				
4:0	39.19 ^a	18.48 ^b	49.30 ^a	45.43 ^a	5.75
6:0	21.02 ^a	5.98 ^b	21.02 ^a	26.76 ^a	2.50
8:0	14.13 ^a	3.93 ^b	14.56 ^a	15.53 ^a	1.59
10:0	36.52 ^a	10.96 ^b	39.12 ^a	31.40 ^a	3.78
12:0	46.07 ^a	16.07 ^b	54.58 ^a	48.99 ^a	4.75
14:0	144.31 ^b	73.24 ^c	179.34 ^a	149.56 ^{ab}	14.51
14:1	13.30 ^b	7.59 ^c	19.70 ^a	13.75 ^b	1.65
15:0 (iso)	2.76 ^a	1.31 ^b	3.14 ^a	2.81 ^a	0.26
15:0 (anteiso)	6.08 ^a	3.30 ^b	6.96 ^a	6.29 ^a	0.61
15:0	14.24 ^b	8.27 ^c	18.33 ^a	14.45 ^b	1.60
15:1	0.69	0.05	0.15	0.12	0.29
16:0	417.36 ^a	234.29 ^b	476.21 ^a	415.79 ^a	46.61
16:0 (iso)	3.47 ^a	2.14 ^b	4.67 ^a	4.24 ^a	0.55
16:1	18.87 ^b	11.32 ^c	25.10 ^a	14.80 ^{bc}	2.11
16:1 <i>trans</i>	0.31 ^{ab}	0.14 ^b	0.42 ^a	0.24 ^{ab}	0.10
17:0	9.24 ^b	4.78 ^c	11.21 ^a	9.42 ^b	0.90
17:0 (iso)	0.75 ^a	0.41 ^b	0.80 ^a	0.72 ^a	0.08
17:1 (iso)	1.44 ^b	1.18 ^b	2.58 ^a	2.56 ^a	0.28
17:1 (anteiso)	5.16 ^{ab}	2.76 ^c	5.72 ^a	4.53 ^b	0.54
17:1	2.41 ^b	1.45 ^c	3.08 ^a	2.29 ^b	0.42
18:0	90.10 ^a	60.54 ^b	102.17 ^a	105.14 ^a	8.85
18:1 <i>cis</i> -9	193.42 ^b	117.59 ^c	256.41 ^a	258.40 ^a	15.77
18:2 ²	5.68 ^b	3.84 ^c	8.34 ^a	5.68 ^b	0.58
18:2n-6	28.26 ^b	18.59 ^c	35.62 ^a	36.49 ^a	2.23
18:3 ³	1.12 ^{bc}	0.62 ^c	1.40 ^a	1.23 ^{ab}	0.17
18:3n-3	4.73 ^a	3.07 ^b	5.55 ^a	5.31 ^a	0.45
20:0	0.94 ^{bc}	0.77 ^c	1.26 ^{ab}	1.52 ^a	0.15
GLA ⁴	0.37 ^a	0.15 ^b	0.34 ^a	0.38 ^a	0.06
Other	6.46 ^b	4.73 ^c	8.29 ^a	5.97 ^{bc}	0.68
Summations					
<16:0	338.31 ^b	149.18 ^c	406.20 ^a	355.09 ^{ab}	30.42
>16:0	361.86 ^b	226.44 ^c	458.74 ^a	447.19 ^a	33.11
>20:0	1.78 ^{bc}	1.32 ^c	2.45 ^{ab}	2.49 ^a	0.13
MUFA ⁵	235.60 ^b	142.08 ^c	313.16 ^a	296.36 ^a	20.13
SFA ⁶	849.97 ^a	446.77 ^b	986.96 ^a	881.84 ^a	78.03
PUFA ⁷	36.37 ^b	23.97 ^c	46.96 ^a	45.30 ^a	3.27

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Fatty acid methyl esters.

²Nonconjugated 18:2 isomers.

³Nonconjugated 18:3 isomers.

⁴Gamma linoleic acid.

⁵Monounsaturated fatty acids.

⁶Saturated fatty acids.

⁷Polyunsaturated fatty acids.

milk fat as a % of the amount infused) by subtracting the FA yield in the control treatment. It should be recognized that these apparent values reflect changes not only in uptake but also in the net synthesis of FA. The overall transfer efficiency for C ≤ 16:0 in milk of cows infused with butterfat was 63% with transfer efficiencies of 44% (4:0), 0% (6:0), 0% (8:0), 33% (10:0), 67% (12:0), 83% (14:0), and 58% (16:0), respectively. Although 6:0 and 8:0 were most likely metabolized by other tissues, the transfer efficiencies of 10:0, 12:0, and 14:0 FA increased with the increase in chain length.

Storry et al. (1974) reported a net transfer of 42 and 48% for 12:0 and 14:0, respectively, to milk when protected coconut oil was fed to lactating cows. Compared with the control or LCFA-infused cows, yields of 10:0 and 12:0 tended to be higher, and yield of 14:0 was significantly greater in milk of cows infused with butterfat. The potential of 12:0 and 14:0 to increase is greater than that of shorter chain length FA, probably because the ratio of lymphatic to hepatic portal vein uptake (greater lymphatic absorption) is positively correlated to FA chain length (Leveille et al., 1967). These

Table 6. Least squares means for conjugated linoleic acid (CLA), *trans* 18:1, and *cis* 18:1 isomers in milk fat of cows fed the control diet or the control diet plus abomasal infusion of CLA, butterfat, or long-chain fatty acid (LCFA) supplements

Fatty acid	Treatment				SEM
	Control	CLA	Butterfat	LCFA	
	g/100 g of FAME ¹				
CLA					
<i>Cis</i> -8, <i>trans</i> -10	Trace	0.04 ^a	Trace	Trace	0.01
<i>Cis</i> -9, <i>trans</i> -11	0.40 ^b	0.83 ^a	0.51 ^b	0.38 ^b	0.07
<i>Trans</i> -8, <i>cis</i> -10	Trace	0.28 ^a	Trace	Trace	0.03
<i>Cis</i> -10, <i>trans</i> -12	Trace	0.02 ^a	Trace	Trace	0.00
<i>Trans</i> -9, <i>cis</i> -11	Trace	0.06 ^a	Trace	Trace	0.01
<i>Cis</i> -11, <i>trans</i> -13	Trace	0.44 ^a	0.01 ^b	0.02 ^b	0.12
<i>Trans</i> -10, <i>cis</i> -12	Trace	0.24 ^a	Trace	0.01 ^b	0.06
<i>Trans</i> -11, <i>cis</i> -13 + 21:0	0.04 ^b	0.05 ^a	0.03 ^b	0.03 ^b	0.01
<i>Cis/cis</i> CLA	Trace	0.28 ^a	Trace	Trace	0.03
<i>Trans/trans</i> CLA	0.09 ^b	0.35 ^a	Trace	Trace	0.04
Total CLA	0.53 ^b	2.59 ^a	0.55 ^b	0.44 ^b	0.21
<i>Trans</i> 18:1					
4	0.01	0.01	0.01	0.01	0.00
5	0.01	0.01	0.01	0.01	0.00
6 + 7 + 8	0.17 ^c	0.22 ^a	0.20 ^{ab}	0.17 ^{bc}	0.04
9	0.20 ^b	0.25 ^a	0.24 ^a	0.21 ^b	0.01
10	0.27 ^c	0.40 ^a	0.36 ^{ab}	0.28 ^{bc}	0.10
11	0.80	0.84	0.84	0.81	0.07
12	0.21 ^b	0.26 ^a	0.26 ^a	0.22 ^b	0.02
13 + 14	0.47 ^c	0.56 ^a	0.52 ^b	0.41 ^d	0.02
16	0.20 ^b	0.26 ^a	0.23 ^b	0.20 ^b	0.01
Total <i>trans</i> 18:1	2.34 ^b	2.81 ^a	2.67 ^a	2.32 ^b	0.10
<i>Cis</i> 18:1					
11	0.47 ^b	0.64 ^a	0.50 ^{ab}	0.52 ^{ab}	0.04
12	0.27 ^b	0.29 ^{ab}	0.32 ^a	0.27 ^b	0.01
13	0.05 ^c	0.08 ^a	0.07 ^b	0.04 ^d	0.00
<i>cis</i> 14 + 19:0	0.13 ^b	0.15 ^a	0.14 ^{ab}	0.13 ^b	0.01

^{a-d}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Fatty acid methyl esters.

FA might be expected to be metabolized to a lesser degree by the liver and be more available for the mammary gland (Grummer and Socha, 1989).

About 60% of 16:0 present in the butterfat was transferred in milk, and yield of 16:0 tended to be higher compared with the control or LCFA-infused cows. Feeding studies (Steele and Moore, 1968c) have shown that dietary addition of pure palmitic acid caused the greatest increase in milk fat yield in dairy cows, compared with addition of myristic or stearic acid. Addition of palmitic acid increased percentages and yields of 16:0 and 16:1 FA in milk fat and decreased 10:0, 12:0, and 14:0 as well as 18:0 and 18:1. Similarly, yield of 16:0 was increased, and total FA in milk were significantly higher during duodenal infusion of palmitic acid (Enjalbert et al., 2000).

Palmitic acid is an important FA for the synthesis of triacylglycerol in the mammary gland (Hansen and Knudsen, 1987). Initiation of acylation of the sn-1 position is a prerequisite for triacylglycerol synthesis, and palmitic acid is the most preferred substrate for the initial acylation of L- α glycerolphosphate by acyltrans-

ferase to form sn-1-lysophosphatidic acid (Kinsella and Gross, 1973). It has been shown (Kinsella and Gross, 1973) that myristyl, stearyl, and oleyl coenzyme A were rapidly acylated when sn-1-lysophosphatidic acid was used as substrate but were poorly acylated without the latter indicating that these FA are taken up mostly in the second step of triacylglycerol synthesis.

Infusion of LCFA did not significantly alter milk fat yield. In contrast with other reports (Grummer, 1991; LaCount et al., 1994), yield of FA C < 16:0, including de novo FA, was not significantly reduced by LCFA infusion, but rather it was maintained as in the controls. Butterfat and LCFA infusion mixtures contained equal amounts of LCFA (except for 16:0) resulting in a similar increase in milk FA C > 16:0. However, compared with the butterfat treatment, the proportion of C18 FA was considerably greater than the proportion of palmitic acid in the LCFA infusion mixture. Steele and Moore (1968a) reported that addition of cottonseed oil (containing 21% palmitic acid and 76% total C18 FA) or tallow (containing 30% palmitic acid and 60% total C18 FA) to the diet of lactating cows increased

Table 7. Least squares means for yields of conjugated linoleic acid (CLA), *trans* 18:1, and *cis* 18:1 isomers in milk of cows fed the control diet or the control diet plus abomasal infusion of CLA, butterfat, or long-chain fatty acid (LCFA) supplements

Fatty acid	Treatment				SEM
	Control	CLA	Butterfat	LCFA	
	g of FAME ¹ /d				
CLA					
<i>Cis</i> -8, <i>trans</i> -10		0.25			
<i>Cis</i> -9, <i>trans</i> -11	4.72 ^b	5.24 ^b	7.28 ^a	4.83 ^b	0.63
<i>Trans</i> -8, <i>cis</i> -10	0.05 ^b	1.27 ^a	0.02 ^b		0.24
<i>Cis</i> -10, <i>trans</i> -12		0.06			
<i>Trans</i> -9, <i>cis</i> -11	0.01 ^b	0.32 ^a			0.09
<i>Cis</i> -11, <i>trans</i> -13	0.04 ^b	2.34 ^a	0.04 ^b	0.04 ^b	0.29
<i>Trans</i> -10, <i>cis</i> -12	0.02 ^b	1.50 ^a	0.01 ^b	0.02 ^b	0.13
<i>Trans</i> -11, <i>cis</i> -13 + 21:0	0.35	0.31	0.30	0.35	0.05
<i>Cis/cis</i> CLA	0.02 ^b	1.81 ^a	0.01 ^b	0.00 ^b	0.17
<i>Trans/trans</i> CLA	0.15 ^b	1.65 ^a	0.09 ^b	0.08 ^b	0.22
Total CLA	5.63 ^b	16.77 ^a	7.87 ^b	5.40 ^b	1.51
<i>Trans</i> 18:1					
4	0.14	0.08	0.12	0.14	0.03
5	0.13	0.09	0.13	0.13	0.03
6 + 7 + 8	2.03 ^{bc}	1.50 ^c	2.82 ^a	2.17 ^b	0.23
9	2.42 ^b	1.63 ^c	3.44 ^a	2.61 ^b	0.25
10	3.22 ^{bc}	2.63 ^c	5.08 ^a	3.55 ^b	0.40
11	9.50 ^b	5.72 ^c	11.76 ^a	10.31 ^{ab}	1.17
12	2.34 ^b	1.73 ^b	3.38 ^a	2.39 ^b	0.36
13 + 14	5.58 ^b	3.77 ^c	7.31 ^a	5.16 ^b	0.67
16	2.42 ^b	1.72 ^c	3.14 ^a	2.53 ^b	0.24
Total <i>trans</i> 18:1	27.78 ^b	18.87 ^c	37.18 ^a	28.99 ^b	2.82
<i>Cis</i> 18:1					
11	5.42 ^{bc}	4.07 ^c	7.31 ^a	6.57 ^{ab}	0.68
12	3.19 ^b	1.97 ^c	4.47 ^a	3.54 ^b	0.39
13	0.64 ^b	0.48 ^c	0.93 ^a	0.57 ^b	0.06
<i>Cis</i> 14 + 19:0	1.60 ^b	1.02 ^c	2.03 ^a	1.61 ^b	0.16

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Fatty acid methyl esters.

stearic and oleic acids in milk fat but did not alter yield of 16:0. In contrast, yields of 16:0 and 18:1 were increased when a mixture of 64% palmitic acid and 34% total C18 FA was added to the diet of lactating cows (Steele and Moore, 1968b). In our study, yield of 16:0 in cows infused with LCFA was maintained at a level similar to that observed in the controls, whereas the yield of 16:0 was increased with butterfat treatment. The difference between these treatments may have been influenced by the C18 to 16:0 ratios in the infusion mixtures. It has been suggested (Steele and Moore, 1968a; Grummer, 1991) that if de novo synthesis of 16:0 is inhibited by increased uptake of LCFA from the blood, the net yield of 16:0 in milk fat will depend on whether dietary transfer of 16:0 to milk fat is sufficient to compensate for the decrease in de novo synthesis.

In conclusion, the abomasal infusion of butterfat compared with LCFA demonstrated that milk fat synthesis could be regulated by the supply of short- and medium-chain FA in lactating cows. In addition, the increased availability of palmitic acid, the preferred substrate for the initial acylation of L- α -glycerophos-

phate, may have also stimulated triacylglycerol synthesis in the mammary gland. Compared with the controls, cows infused with butterfat produced milk fat with greater amounts of 12:0 and 14:0, MUFA, and PUFA. An increase in the proportions of unsaturated FA in milk fat is desirable because of the potential health benefits when included in human diet. However, further studies are needed to test and refine the role of short- and medium-chain FA on milk fat synthesis.

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