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Effectiveness of short-term feeding strategies for altering conjugated linoleic acid content of beef^{1,2}

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ABSTRACT: A steer finishing trial was performed to determine the effect of short-term dietary regimens on conjugated linoleic acid (CLA) content of muscle tissues. The experimental design was an incomplete 3×2 factorial, with three levels of soybean oil (SBO; 0, 4, and 8% of diet DM) and two levels of forage (20 vs. 40% of diet DM). Forty Angus \times Hereford steers averaging 504 ± 29.0 kg were allotted randomly to one of four treatments for the last 6 wk of the finishing period. Treatments were: 80:20 concentrate:forage control diet (C); 80:20 concentrate:forage + 4% SBO (C4); 60:40 concentrate:forage + 4% SBO (F4); and 60:40 concentrate:forage + 8% SBO (F8). After 42 d on the experimental diets, steers were sacrificed and samples were collected from the chuck, loin, and round muscle groups. Fatty acid (FA; mg/100 mg of FA) composition was determined by gas-liquid chromatography. Data were statistically analyzed with mixed models procedures. The performance and carcass quality model included the effects of SBO and forage. The model for FA composition included the effects of SBO, forage, muscle group, and interactions. Orthogonal contrasts were used to deter-

mine linear effects of SBO. There were no differences in growth performance among treatments ($P > 0.05$). Increasing dietary SBO linearly decreased dressing percent ($P = 0.04$), and tended to linearly decrease marbling score ($P = 0.12$) and quality grade ($P = 0.08$). The only CLA isomer detected in tissue samples was *cis-9,trans-11*. Addition of SBO to diets linearly increased linoleic acid (18:2 $n-6$; $P = 0.04$) and tended to linearly increase linolenic acid (18:3 $n-3$; $P = 0.10$) in muscle tissues. The CLA in lean tissues was decreased ($P = 0.005$) with SBO-containing diets. These findings suggest that increased PUFA may limit ruminal production of CLA and *trans*-vaccenic acid (VA) and/or may depress stearyl-CoA desaturase expression or activity in lean tissues, which in turn limits CLA formation and accretion in tissues. Increasing dietary forage tended to increase 18:0, 18:2 $n-6$, CLA, and 18:3 $n-3$ ($P \leq 0.15$), suggesting that increased forage may mitigate toxic effects of PUFA on ruminal biohydrogenation, thereby increasing the pool of CLA and VA available for CLA formation and accretion in tissues. Short-term feeding of elevated SBO and forage levels can alter FA profiles in muscle tissues.

Key Words: Beef, Finishing, Forage, Hydrogenation, Linoleic Acid, Soybean Oil, Steers

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Introduction

Conjugated linoleic acid (CLA), a naturally occurring fatty acid (FA) found in ruminant products, has potentially beneficial health attributes (Pariza, 1999). Rit-

zenhaler et al. (2001) reported that humans must consume >400 mg of *cis-9,trans-11* (c9,t11) CLA per day to receive some of these health benefits, but average daily intake of c9,t11 CLA is <200 mg/d. Enhancement of CLA in meat and milk would promote greater daily consumption of CLA.

Ruminants produce CLA in two known manners. First, ruminal bacteria, thought to be primarily fiber-digesting bacteria, biohydrogenate dietary linoleic and linolenic acids to CLA (Grinari and Bauman, 1999).

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Secondly, *trans*-11 18:1 FA (*trans*-vaccenic acid, **VA**) can be converted to *c9,t11* CLA by Δ^9 -desaturase in body tissues (Griinari and Bauman, 1999). Vaccenic acid is also produced by ruminal biohydrogenation of linoleic acid (Harfoot and Hazelwood, 1997). Subsequent studies indicate that the majority of milk CLA is derived from the desaturation of VA by Δ^9 -desaturase (Griinari et al., 2000; Corl et al., 2001). Ruminal CLA and VA production is dependent on dietary factors including the source and levels of dietary lipid and forage (Griinari and Bauman, 1999), and ruminal production of these FA will therefore impact yields of CLA in meat or milk.

Soybean oil (**SBO**) has been used as a source of linoleic acid throughout the finishing period to promote greater CLA accretion in lean tissues with equivocal results (Engle et al., 2000; Beaulieu et al., 2002), and where CLA accretion was increased with SBO addition, growth performance was reduced (Engle et al., 2000). We hypothesized that short-term (i.e., 6-wk) feeding of diets varying in level of SBO and forage would alter deposition of CLA in lean tissues of beef cattle. Therefore, the objective of this study was to determine changes in CLA content of beef from steers fed diets with 4 or 8% SBO and 20 or 40% corn silage (**CS**) for the last 6 wk of the finishing period.

Materials and Methods

Animals and Diets

The current study was conducted in accordance with the principles and specific guidelines presented in Guidelines for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 1999). Forty Angus \times Hereford steers with average initial weights of 323 ± 18.0 kg were randomly allotted into eight pens with five steers per pen. Animals were implanted with Synovex Plus (Fort Dodge, Fort Dodge, IA) on d 13 and 117 after initial allotment. After a 30-d receiving period, steers were fed a finishing diet balanced to meet NRC requirements (NRC, 1996) for 1.4 kg of gain/d for 70 d. Animals were fed once daily at 1000. Upon reaching target weight (approximately 500 kg), animals were blocked by weight and randomly allotted to one of four treatments with five steers per pen, two pens per treatment. Treatments were as follows: 80:20 concentrate:forage control finishing diet (**C**), C + 4% SBO (**C4**), 60:40 concentrate:forage finishing diet + 4% SBO (**F4**), 60:40 concentrate:forage finishing diet + 8% SBO (**F8**). Experimental diets were formulated to meet NRC requirements (NRC, 1996) for 1.4 kg gain/d and to be isonitrogenous and isocaloric. To make the diets isonitrogenous with the C and C4 treatment diets, 44% soybean meal was added to the F4 and F8 treatment diets, and a bypass fat, Sweet 80, was added to the C and F4 treatment diets to make the diets isocaloric to the C4 and F8 treatments diets. Composition and nutrient analysis of experimental diets

Table 1. Composition of experimental diets on DM basis

Ingredient	Treatment ^a			
	C	C4	F4	F8
	Diet DM, %			
Corn	74.1	72.3	45.9	48.2
Corn silage	20.0	20.0	40.0	40.0
Soybean meal, 44%	1.30	1.50	3.60	3.00
Bypass fat ^b	3.60	—	4.60	—
Soybean oil ^c	—	4.00	4.00	8.00
Limestone	0.80	2.00	1.80	0.60
Trace mineral salt	0.10	0.10	0.10	0.10
Vitamins A, D, and E mix	0.10	0.10	0.10	0.10

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bSweet 80, Morgan Manufacturing Co., Paris, IL. Fatty acid composition (mg of FA/100 mg of fat) was: C12:0 = 0.72, C14:0 = 4.70, C15:0 = 0.62, C16:0 = 29.8, C17:0 = 2.55, C18:0 = 58.3, C18:1*trans* = 1.01, C18:1*n-9cis* = 1.07, C18:1*n-7cis* = 0.10, C18:2*n-6trans* = 0.29, C18:2*n-6cis* = 0.06, C20:0 = 0.65, C22:0 = 0.09, C24:0 = 0.04.

^cCentral Soya Corp, Gibson City, IL.

are shown in Tables 1 and 2. Animals were fed the experimental diets until reaching an end weight of 569 ± 30 kg (42 d). Animals were killed (Fruitland Dressed Meat, Fruitland, MO), and tissue samples were collected for FA analyses.

The study was designed on the premise that the increasing levels of SBO and forage would provide more substrate and promote the fiber-degrading bacterial population responsible for biohydrogenation leading to higher yields of CLA and VA in the rumen, which would in turn increase the accretion of CLA in lean tissues. However, the potential effect of forage was likely limited by sorting of diets by the steers. Sorting is defined as selectively eating certain components or ingredients of a mixed ration and refusal of other components or

Table 2. Nutrient analysis of experimental diets

Nutrient	Treatment ^a			
	C	C4	F4	F8
DM	74.3	72.4	46.0	48.3
	% of DM			
OM	96.2	95.0	94.3	95.5
CP	8.80	9.04	8.85	8.78
ADF	9.30	13.5	14.7	12.4
NDF	21.0	19.0	26.6	24.4
NFC ^b	58.3	58.6	48.9	52.7
Fat	8.19	8.33	10.0	9.63
Ash	3.76	5.05	5.69	4.47

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bNFC = nonfibrous carbohydrate, determined by formula: $NFC = 100 - (Ash + CP + NDF + Fat)$.

ingredients. Based on proximate analysis of diet and ort samples during the experimental period, the calculated average daily NDF intake per steer was 1.7, 1.5, 2.0, and 1.7 kg for C, C4, F4, and F8 diets, respectively. Therefore, the actual difference in NDF intake between pens fed the control and forage diets was less than anticipated (0.25 vs. 0.5 kg·animal⁻¹·d⁻¹). Because the actual NDF intake levels were closer than anticipated, the true forage effect on CLA concentrations in lean tissues may have been masked.

Measurements and Sampling

Body weights were determined on a weekly basis. Diet and ort samples were collected daily and stored at 4°C. On a weekly basis, diet and ort samples were composited and stored at -20°C until analyzed. Corn silage and diet DM were determined on a weekly basis. Daily DMI was determined per pen using weekly diet and ort DM values. Dietary and ort analyses were performed on well-mixed subsamples of weekly composites previously described.

Immediately following sacrifice, carcasses were hot weighed and then stored at 4°C. After 48 h, carcass quality was determined by a certified USDA meat grader using the following measurements: backfat; rib-eye area; kidney, heart, and pelvic (**KHP**) fat percentage; maturity; marbling; and quality grade. Tissue samples (approximately 100 g) were removed at the 12th rib of the loin and the upper quadrants of the chuck and the round on the left half of each carcass. Excised tissues were placed in individual plastic storage bags and then stored at -20°C for later analysis.

Analyses

Diets, corn silage, and ort samples were analyzed for the following: DM, OM, CP, NDF, ADF, fat, and ash. Dry matter was determined by drying at 100°C for 24 h. Fiber fractions, ADF, and NDF were determined by the methods of Goering and Van Soest (1970), with modifications by Van Soest (1990). Dietary CP was determined by Kjeldahl method (AOAC, 1990) using automated equipment (Foss Tecator, Höganäs, Sweden). Ash and OM were determined by standard AOAC methods (AOAC, 1990). Dietary fat was estimated by the following formula (Sukhija and Palmquist, 1988):

$$\text{Fat} = \text{Long chain fatty acids (LCFA)} / 0.9$$

Long chain fatty acids used for the estimation of dietary fat were defined as C14 or greater. Dietary nonfibrous carbohydrates (**NFC**) was calculated using the following formula:

$$\text{NFC} = 100 - (\text{CP} + \text{NDF} + \text{Fat} + \text{Ash})$$

Nutrient intake per animal was calculated by subtracting the amount (kg) of nutrient in orts recovered

per day from the amount (kg) of nutrient fed per day in the diet, and then dividing by the number of animals in each pen.

Lipid from tissue, diet, and ort samples was extracted using the methods described by Hara and Radin (1978) with slight modification. Briefly, for tissue extraction, samples were thawed at room temperature and sliced into thin strips using an individual 3-in scalpel for each sample. Two grams of sliced tissue was weighed in a 50-mL screw-cap test tube and 36 mL of a 3:2 mixture of hexane and isopropanol (**HIP**) was added. Sealed tubes were then placed on a shaker table (Fisher Scientific, St. Louis, MO) for 24 h at maximal speed. Samples were filtered under vacuum through Whatman #4 filter paper, and filtrate was collected into clean 50-mL screw-cap test tubes. A 2-mL rinse of the original tube was also filtered and collected. The total filtrate was transferred to a previously weighed 100-mL beaker, and the tube was rinsed with 2 mL of HIP, which was added to the beaker. Beakers were placed in a fume hood under continual N₂ gassing overnight to evaporate away the solvent. After evaporation, beakers were placed in a desiccator for 10 min, and then weighed to determine grams of lipid extracted/grams of tissue. Toluene was added to yield 0.05 g of lipid/mL of solution. Once the lipid was entirely dissolved, the solution was transferred to a 4-mL vial, which was flooded with N₂, sealed, and stored at -20°C.

Lipids were esterified according to the procedures of Christie (1989). Briefly, 1 mL of extracted lipid in toluene was transferred to a test tube containing 6.17 mg of trionadecanoin, which was used as an internal standard. Two milliliters of 0.5 M sodium methoxide in anhydrous methanol was added, and the solution was mixed and blanketed with N₂. Tubes were sealed, incubated at 50°C for 10 min, and then cooled to room temperature. Next, 0.1 mL of glacial acetic acid was added to each sample, followed by 5 mL of dH₂O. Five milliliters of hexane was added, tubes were vortexed, and then centrifuged (900 × g, 3 min). The hexane layer was transferred by pipette to a test tube containing anhydrous sodium sulfate; tubes were sealed and stored at -20°C for later analysis.

Fatty acid methyl esters (**FAME**) were quantified by GLC with a Hewlett Packard 5890 chromatograph equipped with a flame-ionization detector and a Hewlett Packard 3390 A integrator (Agilent Technologies, Palo Alto, CA). The sample (0.035 μL) was introduced by direct injection onto a Stabilwax fused-silica capillary column (30 m × 0.32 mm i.d., 0.25 μm film thickness; Restek Corp., Bellefonte, PA). Helium was used as the carrier gas at 8 mL/min and as the make-up gas at 25 mL/min. The injector and detector were set at 250°C and 240°C, respectively. Column temperature was programmed at 185°C for 4.5 min, raised 10°C/min to 245°C, and held there for 1 min. All FA were identified by comparing retention times with those of known FAME standards (Matreya, Inc., Pleasant Gap, PA; Nu-

Table 3. Fatty acid methyl esters (FAME) standards used to identify fatty acids using gas-liquid chromatography

Company ^a	Catalog No.	Fatty acid	Purity (%)
Sigma	M3378	14:0	99
	M3650	14:1 n -5	99
	P6250	15:0	99
	P5177	16:0	99
	P9667	16:1 n -7	99
	H4515	17:0	99
	S5376	18:0	99
	O4754	18:1 n -9	99
	L1876	18:2 n -6	99
	L2626	18:3 n -3	99
	A3881	20:0	99
	E3511	20:3 n -6	99
	E2012	20:5 n -3	99
	D3534	22:4 n -6	99
Nu-Chek-Prep, Inc.	U42M	17:1 n -7	99
	U66M	20:1 n -9	99
	U68M	20:2 n -6	99
	U71M	20:4 n -6	99
	U84M	22:6 n -3	99
Matreya, Inc.	1244	22:5 n -3	99
	1245	<i>cis</i> -9, <i>trans</i> -11 CLA	98
	1249	<i>trans</i> -10, <i>cis</i> -12 CLA	98
	1181	<i>trans</i> -9, <i>trans</i> -11 CLA	98

^aSee text for company locations.

Chek-Prep, Inc., Elysian, MN; Sigma, St. Louis, MO; Table 3).

CLA isomers of *c9,t11*; *trans*-10,*cis*-12 (**t10,c12**); and *trans*-9,*trans*-11 (**t9,t11**) configuration were obtained as FA (Matreya) and methylated with 1.5*N* HCl in methanol at 60°C for 30 min. (Dionisi et al., 1999). Our analysis achieved baseline resolution of these CLA isomers; however, no GLC system can resolve all known CLA FAME (Kramer et al., 2001). Perhaps most significant in this regard is the known coelution of *trans*-7,*cis*-9 with *c9,t*-11. Based on analyses of beef fat with silver-ion HPLC conducted by Yurawecz et al. (1998) and Fritsche et al. (2000), we estimate that 9 to 17% of our reported *c9,t11* CLA concentrations may actually have been the *trans*-7,*cis*-9 isomer. We were also unable to resolve 20:1 n 9 from *t9,t11* CLA, which we consider a marker for all *trans,trans* CLA isomers. Based on the previously cited investigations, we calculate that all *trans,trans* CLA isomers combined might comprise 7 to 24% of this very small peak.

Fatty acid data were reported as mg/100 mg of FA. The percentage composition (mg/100 mg of FA) of CLA was calculated by multiplying the peak area of CLA by the milligrams of internal standard divided by the area of internal standard, divided by the total FA (mg), and then multiplying by 100.

Experimental Design and Statistical Analyses

The experimental design was an incomplete 3 × 2 factorial with SBO and forage as main factors. All data were analyzed using PROC MIXED procedures of SAS

(SAS Inst., Inc., Cary, NC.). The statistical model for performance and carcass quality included the effects of SBO and forage. The statistical model for FA composition included the effects of SBO, forage, muscle group, and the interactions of forage × muscle group and oil × muscle group. Orthogonal contrast statements were utilized in both models to determine linear effects of oil. Pen was the experimental unit for animal performance, carcass quality, and FA data. Significance was determined at $P \leq 0.05$. Differences of $P > 0.05$ to $P \leq 0.15$ are discussed as trends.

Results and Discussion

Effect of Soybean Oil and Forage on Performance and Carcass Quality of Steers

Increasing SBO and forage content of diets did not alter DMI, ADG, or gain:feed ratios ($P > 0.15$) among pens of steers in this study (Table 4). Addition of lipid to finishing diets has been shown to decrease DMI (Andrae et al., 2000; Engle et al., 2000) and ADG (Engle et al., 2000) in beef steers. However, feed efficiency was not affected in those studies. Beaulieu et al. (2002) found no changes in DMI, ADG, or gain:feed ratio when Angus-Waygu heifers were fed finishing diets supplemented with 5% SBO. The lack of changes in DMI in the current study may have been partly due to increased forage level in the F4 and F8 treatments and the shorter duration of the experimental period: 42 d compared to 84 to 112 d in normal finishing periods. Engle et al. (2000) suggested depressed rumen function from unsat-

Table 4. Effect of dietary soybean oil (SBO) and forage level on performance data of Angus × Hereford finishing steers during the 6-wk experimental period

Item	Treatment ^a				SEM	Significance (<i>P</i> -value)		
	C	C4	F4	F8		SBO	Forage	SBO linear
Animals	10	10	10	10	—	—	—	—
Initial BW, kg	508	501	503	505	9.4	0.82	0.70	0.67
Final BW, kg	572	569	570	565	9.9	0.86	0.93	0.61
ADG, kg/d	1.45	1.40	1.56	1.38	0.22	0.73	0.52	0.51
DM intake, kg/d	11.8	11.5	11.4	10.8	0.32	0.81	0.31	0.63
Feed efficiency ^b	0.12	0.12	0.14	0.13	0.01	0.64	0.51	0.38

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bKilograms of weight gained during experimental period divided by kilograms of DMI during experimental period.

urated FA caused the depression in DMI, and speculated that ruminal microorganisms would only tolerate added fat to 5% of the diet. Elevated dietary fiber, however, would lessen the inhibitory effects of unsaturated FA on ruminal fermentation. In the current study, total dietary fat ranged from 8.1 to 10.0% of DM, which was greater than dietary fat content of the diets used by Andrae et al. (2000) or Engle et al. (2000). Depressions in DMI from addition of plant oils (i.e., unsaturated FA sources) to finishing diets become larger as days on diet increase (Andrae et al., 2000; Engle et al., 2000).

Although addition of plant oils to ruminant diets can provide linoleic acid and linolenic acid for conversion to CLA, they can also produce undesirable effects. Dressing percentage decreased linearly as SBO in the diet increased ($P = 0.04$), and there was a trend for a linear decrease in quality grade when SBO increased in diets ($P = 0.07$; Table 5). Engle et al. (2000) found significant decreases in hot carcass weight, KHP fat percentage, yield grade and quality grade, and trends for decreases in dressing percentage, backfat, and marbling score when 4% SBO was added to beef finishing diets. These effects were attributed to the concomitant

decrease in steer growth performance with these diets. Beaulieu et al. (2002) reported a trend for dressing percentage to decrease, but no other changes in carcass quality traits when Angus-Waygu heifers were fed finishing diets supplemented with 5% SBO. Addition of extruded full-fat soybeans to steer finishing diets caused no changes in carcass quality traits (Madron et al., 2002) and substitution of high-oil corn for typical corn in isocaloric steer finishing diets has been shown to increase marbling score and quality grade of carcasses (Andrae et al., 2001). The slow release of oils from seeds in the rumen may mitigate the toxic effects of unsaturated fatty acids on microbial growth and therefore offset potential reductions in growth performance and carcass quality (Madron et al., 2002).

Effect of Soybean Oil and Forage Level on Fatty Acid Composition of Muscle Tissues

Our hypothesis was that short-term (i.e., 6-wk) feeding of diets varying in level of SBO and forage would elicit measurable responses in FA composition of muscle tissues in finishing steers. Mandell et al. (1997) fed

Table 5. Effect of dietary soybean oil (SBO) and forage level on carcass quality of Angus × Hereford finishing steers

Item	Treatment ^a				SEM	Significance (<i>P</i> -value)		
	C	C4	F4	F8		SBO	Forage	SBO linear
Dressing %	58.6	58.0	58.3	57.1	0.43	0.11	0.67	0.04
Hot carcass weight, kg	341	334	337	329	6.60	0.58	0.82	0.30
Backfat, cm	1.53	1.28	1.14	1.09	0.13	0.37	0.58	0.24
Longissimus muscle area, cm ²	78.1	76.1	84.5	80.0	2.77	0.72	0.04	0.42
KHP fat ^b , %	1.41	1.30	1.05	0.85	0.13	0.49	0.20	0.26
Yield grade	3.29	3.00	2.52	2.52	0.26	0.74	0.20	0.58
Marbling score ^c	4.66	4.40	4.71	4.32	0.20	0.28	0.29	0.12
Quality grade ^d	4.70	4.00	3.90	3.50	0.31	0.19	0.82	0.08

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bKidney, heart, and pelvic fat.

^cMarbling score: Slight = 4.0.

^dQuality grade: Low Select = 3, High Select = 4, Low Choice = 5, Choice = 6, High Choice = 7.

Table 6. Effect of dietary soybean oil (SBO) and forage level on long chain fatty acid (LCFA) concentrations in muscle tissues from Angus × Hereford finishing steers

Fatty acid isomer	Treatment ^a				SEM	Significance (<i>P</i> -value)		
	C	C4	F4	F8		SBO	Forage	SBO linear
	mg/100 mg of FA							
14:0	3.92	4.03	4.13	3.85	0.15	0.52	0.70	0.65
14:1 n -5	1.01	1.16	1.08	1.15	0.07	0.45	0.55	0.24
15:0	0.48	0.43	0.44	0.44	0.02	0.30	0.63	0.21
16:0	27.7	32.9	29.4	27.2	2.13	0.19	0.25	0.47
16:1 n -7	4.02	3.73	3.68	3.51	0.24	0.43	0.84	0.22
17:0	0.90	0.89	0.89	0.88	0.03	0.84	0.84	0.56
17:1	1.01	0.81	1.50	0.80	0.37	0.42	0.22	0.25
18:0	12.3	11.5	12.4	13.1	0.36	0.06	0.07	0.98
18:1	35.6	34.7	34.1	34.2	0.62	0.46	0.40	0.45
18:2 n -6	5.38	5.66	6.49	8.04	0.36	0.05	0.15	0.04
CLA <i>cis</i> -9, <i>trans</i> -11	0.31	0.25	0.28	0.31	0.01	0.005	0.08	0.16
18:3 n -3	0.20	0.21	0.25	0.28	0.01	0.22	0.06	0.10
20:0	0.09	0.05	0.06	0.06	0.01	0.25	0.93	0.29
20:1 n -9	0.21	0.19	0.18	0.18	0.01	0.44	0.78	0.44
20:2 n -6	0.48	0.49	0.37	0.43	0.07	0.80	0.21	0.57
20:5 n -3	0.15	0.17	0.17	0.19	0.01	0.15	0.77	0.06
22:5 n -3	0.25	0.24	0.32	0.31	0.03	0.99	0.11	0.97
22:6 n -3	0.08	0.09	0.17	0.10	0.03	0.44	0.15	0.43
Others	5.91	2.50	4.09	4.97	2.25	0.62	0.94	0.76
SFA ^b	45.4	49.8	47.3	45.5	2.17	0.30	0.40	0.53
MUFA ^b	41.9	40.6	40.5	39.9	0.80	0.41	0.95	0.21
PUFA ^b	8.35	8.46	9.58	11.5	0.55	0.12	0.21	0.11
<i>n</i> -6 Fatty acids	7.36	7.50	8.41	10.3	0.52	0.10	0.28	0.10
<i>n</i> -3 Fatty acids	0.67	0.72	0.90	0.89	0.07	0.91	0.11	0.83
PUFA:SFA	0.19	0.19	0.20	0.26	0.02	0.13	0.42	0.22
Desaturase index, % ^c	48.2	46.2	45.8	46.8	0.82	0.08	0.63	0.47

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bSFA = total saturated fatty acids, MUFA = monounsaturated fatty acids.

^cEstimate of Δ^9 -desaturase activity.

fishmeal at 0, 5, and 10% of diet DM to steers for 0, 56, 112, and 168 d from the end of the finishing period, and found that addition of fishmeal to diets altered concentrations of FA containing 18 carbons or less, but time on experimental feed beyond 56 d from the end of the finishing period did not, supporting our hypothesis that short-term feeding of diets at the end of the finishing period could alter FA composition. The alterations in FA composition in muscle tissue for the current study (Table 6) were comparable to changes reported for cattle fed experimental diets for longer periods of time (Mandell et al., 1997; Beaulieu et al., 2002; Madron et al., 2002). Although the responses of muscle tissue FA composition to changes in dietary lipid and forage are often small (Mandell et al., 1998; Beaulieu et al., 2002; Madron et al., 2002), these changes do not necessarily require diets to be fed for a full finishing period. Additionally, Duckett et al. (1993) showed that although changes in tissue 18:0, 18:1, 18:2, and 18:3 concentrations became larger in steers fed the same diet for increasing periods of time, the time period for the greatest intramuscular fat deposition was between 84 and 112 d on feed (Duckett et al., 1993), which corresponds to the last 28 d of the finishing period. Therefore, diets designed to alter FA composition of lean tissues can

be fed when intramuscular fat deposition should be greatest to produce a discernible effect.

Linolenic acid (18:3), stearic acid (18:0), and linoleic acid (18:2) showed trends to increase ($P \leq 0.15$) when forage level increased from 20 to 40% of the diet DM (Table 6). Mandell et al. (1998) reported increases in 18:0 and 18:3 concentrations in loin tissues but no change in 18:2 when Limousin cross steers were fed high (95% of diet DM) vs. low (15% of diet DM) forage diets. Marmer et al. (1984) found greater 18:0 and 18:3 and lesser 18:2 muscle tissue concentrations in forage-fed steers compared with grain-fed steers. Similar differences in 18:0, 18:2, and 18:3 concentrations have been reported for grazed steers compared with concentrate-fed steers (Brown et al., 1979; Melton et al., 1982). French et al. (2000) attributed these changes in FA profile to differences in energy density between dietary treatments, which altered carcass quality and FA deposition. Controlling for rate of gain among treatments, French et al. (2000) showed that tissue linolenic acid increased, but stearic acid was unaltered as steers consumed increasing amounts of grazed forage in their diets. In the current study, diets were formulated to be isocaloric and ADG was equal across treatments (Table 4), so changes in FA from increased forage could not

have been confounded by energy intakes. Marmer et al. (1984) noted that forage-fed beef has consistently higher concentrations of 18:3 compared with concentrate-fed beef due to the greater amount of 18:3 found in forage grasses. Our observations support this finding.

Inclusion of SBO in diets increased linoleic acid concentration ($P = 0.05$), and the effect was linear ($P = 0.04$; Table 6). In contrast, Engle et al. (2000) and Beaulieu et al. (2002) both reported that addition of SBO to finishing steer diets did not alter linoleic acid concentrations in muscle tissue. Similarly, addition of 5% rapeseed oil to finishing diets did not alter linoleic acid concentrations in loin muscle tissue (Stasiniewicz et al., 2000). However, the diets fed in the studies of Engle et al. (2000), Beaulieu et al. (2002), and Stasiniewicz et al. (2000) were not isocaloric. Feeding isocaloric diets containing extruded full-fat soybeans as a source of linoleic acid at 0, 12.7, and 25.6% of diet DM to finishing steers, Madron et al. (2002) found that linoleic acid only increased at the highest level of soybean feeding. Substitution of high-oil corn for typical corn in isocaloric diets has been shown to increase 18:2 concentrations in loin tissues from feedlot steers (Andrae et al., 2001). However, the increases in linoleic acid reported by Andrae et al. (2001) and Madron et al. (2002) were smaller than the increase seen in the current study (15 and 19 vs. 49%, respectively).

There was a trend for SBO to increase linolenic acid concentration in a linear manner ($P = 0.10$; Table 6). Beaulieu et al. (2002) and Madron et al. (2002) both found increases in 18:3 when soybean sources of linoleic acid were fed to finishing steers. Engle et al. (2000) reported no changes in loin tissue 18:3 concentrations when 4% SBO was added to finishing steer diets. Increasing dietary linolenic acid using linseed has been shown to increase muscle tissue 18:3 concentrations (Enser et al., 1999, Stasiniewicz et al., 2000). Intakes of n-3 FA in the current study were elevated by the addition of SBO (Table 7), which may have contributed to the increase in 18:3 in muscle tissue.

Effect of Soybean Oil and Forage Level on CLA Concentration in Muscle Tissues

The concentration of CLA in muscle tissues was depressed by addition of SBO to diets ($P = 0.005$), but tended to increase when forage was increased from 20 to 40% of the diet DM ($P = 0.08$; Table 6). Alterations in CLA deposition in tissues or milk are attributed to both diet-mitigated changes in ruminal biohydrogenation, which alter the flow of CLA isomers and VA to the small intestine for absorption and utilization, and the activity of Δ^9 -desaturase on VA in tissues to produce CLA (Griinari and Bauman, 1999; Griinari et al., 2000; Corl et al., 2001). The t10,c12 CLA isomer has been shown to inhibit tissue Δ^9 -desaturase activity (Bretillon et al., 1999). Beaulieu et al. (2002) measured ruminal CLA isomer and *trans*-18:1 FA concentrations in steers fed diets containing 0, 2.5, 5.0, or 7.5% SBO, and

Table 7. Calculated average daily intake of individual fatty acids

Fatty acid isomer	Treatment ^a			
	C	C4	F4	F8
	g/d			
14:0	23.5	1.61	19.4	2.38
15:0	3.18	0.46	2.62	0.54
15:1n-5	1.30	2.30	1.71	2.27
16:0	271	197	239	183
16:1n-7	1.18	1.61	1.14	1.62
17:0	11.0	1.84	8.89	1.94
18:0	399	53.1	326	61.0
18:1	145	290	165	253
18:2n-6	240	452	266	409
18:3n-3	8.37	30.5	22.5	36.1
20:0	6.72	7.48	7.75	7.13
20:1n-9	1.18	2.88	1.60	2.59
20:2n-6	3.07	6.21	4.22	17.6
21:0	1.30	2.42	1.82	2.48
22:0	10.1	10.6	7.98	7.34
23:0	0.35	0.92	0.68	0.76
24:0	4.36	7.59	4.56	6.91
Total	1,137	1,083	1,090	1,010
SFA ^b	731	283	618	274
MUFA ^b	148	297	169	260
PUFA ^b	251	489	283	463
n-6 Fatty acids	243	458	270	427
n-3 Fatty acids	8.37	30.5	22.5	36.1
PUFA:SFA ratio	0.34	1.73	0.46	1.69

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bSFA = total saturated fatty acids, MUFA = total monounsaturated fatty acids.

found that t10,c12 CLA and *trans*-18:1 FA increased in a linear manner while c9,t11 CLA was unaffected. The findings of Beaulieu et al. (2002) would suggest that t10,c12 CLA produced in the rumen with SBO diets would be available to cause inhibition of tissue Δ^9 -desaturase. Tissue CLA isomers are predominantly c9,t11, with little to no t10,c12 being detectable (Beaulieu et al., 2002; Madron et al., 2002), which is consistent with our findings (Table 6). However, the t10,c12 CLA isomer could metabolically affect lipogenic pathways even if it were not detectable in tissue samples. Due to the limitations of our FA analysis methodology, any effect on Δ^9 -desaturase activity by altered t10,c12 CLA concentrations would be speculative at best.

Madron et al. (2002) suggested that the completeness of ruminal biohydrogenation in steers might limit CLA and VA concentrations while increasing stearic acid flow and thereby limiting potential CLA formation in tissues. The ruminal biohydrogenation pathways of linoleic acid and linolenic acid to stearic acid both consist of an initial isomerization reaction followed by hydrogenation reactions (Harfoot and Hazlewood, 1997). The last hydrogenation reaction converting VA to stearic acid is considered rate limiting in both pathways (Griinari and Bauman, 1999). In the current study, SBO

addition decreased CLA concentrations while linearly increasing linoleic and linolenic acid concentrations in muscle tissues (Table 6). Diets high in unsaturated fat are toxic to ruminal fiber-digesting bacteria, which are considered the primary biohydrogenating microorganisms in the rumen, and are involved in the initial isomerization of both linoleic and linolenic acid (Harfoot and Hazlewood, 1997). Therefore, the elevated unsaturated FA content of the SBO diets may have inhibited the fiber-digesting bacteria, limiting ruminal biohydrogenation, and causing the pool of CLA and VA available for utilization in CLA formation and accretion in muscle tissues to decrease.

The expression and activity of tissue Δ^9 -desaturase or stearoyl-CoA desaturase (SCD) has been shown to be inhibited by PUFA. The depressive effect of PUFA on SCD increases with increasing carbon chain length and double bond number within the PUFA (Ntambi, 1995). Therefore, diets designed to enhance CLA using sources of PUFA may inadvertently depress SCD and limit the effectiveness of the dietary regimen. Beaulieu et al. (2002) estimated Δ^9 -desaturase activity in lean tissues of Angus-Waygu heifers using a desaturase index developed by Malau-Aduli et al. (1997), and found that Δ^9 -desaturase activity was not affected by the addition of 5% SBO to the diet. In the current study, using the same ratio of unsaturated products to the sum of the products plus the saturated precursors, there was a trend ($P = 0.08$) for Δ^9 -desaturase activity to be depressed by the incorporation of SBO into the diet (Table 6). The decrease in Δ^9 -desaturase activity coincided with the trend ($P = 0.12$) for SBO to increase concentrations of PUFA in lean tissues (Table 6), which suggested that feeding SBO in an effort to elevate tissue CLA concentrations was detrimental to CLA accretion.

Of the studies examining CLA enhancement in muscle tissues of steers, none has reported a negative effect of linoleic acid on CLA accumulation. Enser et al. (1999), Engle et al. (2000), and Madron et al. (2002) all noted increased CLA in muscle tissues of steers with dietary addition of linseed, SBO, and extruded full-fat soybeans, respectively. Beaulieu et al. (2002) indicated that CLA concentrations in muscle tissues did not change with addition of 5% SBO to finishing diets for Angus-Waygu heifers. Stasiniewicz et al. (2000) tested addition of linseed, rapeseed oil cake, and rapeseed oil on CLA concentrations in loins of fattening bulls and found that only linseed addition was able to increase CLA concentrations compared to the control diet.

Efforts to promote increased populations of ruminal fiber-degrading bacteria by increasing dietary forage content may not elicit discernible effects on fermentation because these populations of bacteria represent <10% of the entire ruminal bacterial population (Weimer, 1998). Despite the small difference in estimated NDF intake (see Materials and Methods section) between the control diets (20% of DM as corn silage) and the forage diets (40% of DM as corn silage), there was a trend ($P = 0.08$) for increased dietary forage to

increase CLA concentrations in all tissues examined (Table 6). Increasing forage content of diets may reduce the inhibitory effect of unsaturated FA on ruminal microorganisms (Doreau et al., 1991), which may have allowed more biohydrogenation to occur, and in turn, increased the pool of CLA and VA available for utilization in CLA accretion in muscle tissues. Use of increased forage in finishing diets to elevate CLA in muscle tissue has consistently been more successful than use of plant oils or oilseeds. Shantha et al. (1997) reported increased muscle tissue CLA in grass-fed steers compared with grain-supplemented grass-fed steers. French et al. (2000) found that muscle tissue CLA increased as the proportion of grazed forage increased in the diets of finishing steers. Similar findings have been reported for increased CLA in the milkfat from dairy cattle (Kelly et al., 1998).

Effect of Muscle Group on CLA Concentration in Tissues

As expected from the literature (Marmer et al., 1984), tissue site differences in FA composition were observed with the round having a greater PUFA:saturated FA ratio than either the chuck or loin ($P < 0.0001$; data not shown). However, dietary treatment effects on CLA concentrations were observed within individual muscle groups (Table 8). Muscle group differences in CLA concentration may indicate potential tissue differences in expression or activity of Δ^9 -desaturase because the chuck, which contained the greatest concentration of CLA, was affected by dietary treatments, whereas the round and loin were unaffected by the dietary treatments (Table 8). Chang et al. (1992) suggested that greater proportions of oleic acid in tissues point toward desaturation of stearic acid by stearoyl-CoA desaturase prior to incorporation in muscle tissues and therefore less reliance on FA flow from the rumen (e.g., the chuck). Soybean oil affected ($P = 0.08$; Table 6) the calculated desaturase index for tissue samples from the current study, and there was a trend for the chuck to have greater desaturase activity than the loin or round (48.2 vs. 46.2 and 46.3, respectively; SEM = 0.75; $P = 0.13$). Tissues with less desaturase activity (e.g., the loin and round) are then more susceptible to differences in rumen outflow of FA caused by changes in ruminal biohydrogenation.

In conclusion, ruminal CLA and VA production may be influenced by a number of factors, such as biohydrogenation, population density of fiber-degrading bacteria, and PUFA limitations on ruminal fermentation. This production scheme becomes cloudier as we proceed downstream to evaluate tissue production and accretion of CLA and other FA. In the current study, dietary SBO and forage concentrations altered tissue CLA accretion, but the manner by which this occurred remains unclear.

Table 8. Effects of dietary soybean oil (SBO) and forage level on conjugated linoleic acid concentration within muscle group tissues from Angus × Hereford finishing steers

Muscle group	Lipid, % of tissue ^b	Treatment ^a				SEM	Significance (<i>P</i> -value)		
		C	C4	F4	F8		SBO	Forage	SBO linear
		—mg/100 mg of FA ^c —							
Chuck	6.39 ^e	0.39	0.30	0.33	0.38	0.01	0.01	0.15	0.18
Loin ^d	4.73 ^f	0.24	0.21	0.25	0.29	0.02	0.26	0.18	0.76
Round	3.27 ^g	0.30	0.23	0.26	0.25	0.03	0.32	0.50	0.26

^aTreatment: C = 80:20 concentrate:forage control finishing diet; C4 = control + 4% soybean oil; F4 = 60:40 concentrate:forage finishing diet + 4% soybean oil; F8 = 60:40 concentrate:forage finishing diet + 8% soybean oil.

^bSEM = 0.29.

^cFA = fatty acid.

^dSample from 12th rib.

^{e,f,g}Means within a column with different superscripts differ, *P* < 0.001.

Implications

Inclusion of soybean oil in finishing diets to enhance tissue yields of conjugated linoleic acid might be disadvantageous when dietary polyunsaturated fatty acid content is sufficient to limit ruminal production of conjugated linoleic acid and vaccenic acid or decrease tissue stearoyl-CoA desaturase expression or activity. Increasing dietary forage might boost ruminal conjugated linoleic acid and vaccenic acid by limiting polyunsaturated fatty acid toxicity, and thus, increase the substrates available for production and accretion of conjugated linoleic acid in tissues. However, it is evident that short-term feeding strategies can be used to alter fatty acid composition in muscle tissues, and future research on conjugated linoleic acid enhancement of beef does not need to focus on full-length finishing trials. Future studies should focus on potential lipid by forage interactions to alter ruminal biohydrogenation and enhance conjugated linoleic acid accretion in muscle tissues.

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