LIPID METABOLISM IN BOVINE SUBCUTANEOUS ADIPOSE TISSUE OF STEERS FED SUPPLEMENTARY PALM OIL OR SOYBEAN OIL

A Thesis

by

GYOUNG OK GANG

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Nutrition

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Approved by:

Chair of Committee,	Stephen B. Smith
Committee Members,	W. Alex McIntosh
	Tryon Wickersham
Intercollegiate Faculty Chair,	Rosemary Walzem

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ABSTRACT

Lipid Metabolism in Bovine Subcutaneous Adipose Tissue of

Steers Fed Supplementary Palm Oil or Soybean Oil. (August 2012)

Gyoung Ok Gang, B.S., Seoul Women's University;

Chair of Advisory Committee: Dr. Stephen B. Smith

We hypothesized that supplementing finishing diets with palm oil would elevate Stearoyl-CoA desaturase (SCD) activity in muscle and subcutaneous (s.c.) adipose tissue, promoting adipocyte differentiation and increase monounsaturated fatty acids (MUFA) in beef, particularly oleic acid. Soybean oil supplementation was used as a negative control. Eighteen Angus steers were assigned randomly to three groups of 6 steers and fed a basal diet without additional fat, with 3% palm oil (rich in palmitic acid), or with 3% soybean oil (rich in polyunsaturated fatty acids), top dressed daily. There were no significant differences across treatment in quality grade, REA, 12th rib fat thickness, or yield grade. Palm oil tended to increase marbling score (P = 0.33). Palm oil supplementation decreased the concentration of myristic acid (P = 0.04), and tended to decrease the concentration of *t10, c12* CLA (P = 0.07) and 18:3n-3 (P = 0.06) in s.c. adipose tissue while soybean supplementation increased *c9, t11* CLA (P = 0.02) and 18:3n-3 (P = 0.03) in muscle. Palm oil supplementation increased both glucose and acetate incorporation into total lipids of s.c. adipose tissue (both P = 0.03). Volume of s.c. adipocytes was greater in cattle supplemented with palm oil than in soybean-

supplemented cattle ($P = 0.004$). Enzyme activity of G-6-PDH tended to be greater in steers consuming palm oil supplement ($P = 0.10$).

We conclude that there was a partial interaction between palm oil supplementation and adipocyte differentiation. Palm oil supplementation increased s.c. adipocyte content without deteriorating meat quality traits and tended to increase marbling.

DEDICATION

To my family,

with love and appreciation for

memories of the past,

pleasures of the present,

and

promises of the future,

my husband,

Gwang-woong Go

my son,

David Jaewon Go

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Most important, I would like to thank my husband, Gwang-woong Go, who has been encouraging me to complete this study and supporting me with encouragement and love, and my son, Jaewon David Go, who gave me boundless happiness and the reason to live my life right and better; and my family, Yeonsook Yoon, Dongsam Ko, Kyungnan Hwang, Seokwoo Kang, Junghoon Kang, Kyunghwa Kang and Jaehoon Lee,

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NOMENCLATURE

PUFA	Polyunsaturated fatty acids
s.c.	Subcutaneous adipose
CLA	Conjugated linoleic acid
MUFA	Monounsaturated fatty acid
SFA	Saturated fatty acid
SCD	Stearoyl Co-A desaturase
TG	Triglycerides
HDL	High density lipoprotein
LDL	Low density lipoprotein
KHB	Kreb Henseleit buffer
FAME	Fatty acid methyl ester
G-6-PDH	Glucose-6-phosphate dehydrogenase
6-PGDH	6-phosphogluconate dehydrogenase
TRA	Triethanolamine
GLMM	Generalized linear mixed models
REA	Rib eye area
KPH	Kidney, pelvic and heart fat expression
ACC	Acetyl-CoA carboxylase
FAS	Fatty acid synthase
FID	Flame ionization detector

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INTRODUCTION

Beef producers would prefer to produce high quality meat with adequate marbling to both maximize profit and satisfy consumers. Factors that determine meat quality include eating quality, taste, and healthfulness, especially as related to the amount and type of fat. Variation in fatty acid composition of adipose tissue affects meat quality, determines the firmness/oiliness of adipose tissue and the stability of muscle, all of which affect flavor and meat color. Thus, fat and associated fatty acids from adipose tissue or muscle contribute to meat quality, and are important in determining the nutritional value of meat (Wood et al., 2008).

In recent years, lipid composition and fat from beef has become a subject of general interest because its close relationship with human health, particularly cardiovascular disease (Williamson and Stewart, 2005). Nutritional benefits of beef have been over-shadowed due to high levels of saturated fatty acids (relative to plant oils). Concentrations of polyunsaturated fatty acids (PUFA), which lower blood cholesterol concentrations, are low in meat (Prates et al., 2007). For these reasons, previous studies examined ways to manipulate the quality of meat and alter fatty acid composition, in particular through dietary changes (Fisher et al., 2003). One study (Pavan and Duckett, 2007) reported that feeding steers a high concentrate diet with a corn oil supplement increased lipid deposition rates and modified the fatty acid composition in subcutaneous (s.c.) adipose tissue. Andrae et al. (2001) did not observe

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This dissertation follows the style and format of the Journal of Animal Science.

changes in the percentage of stearic acid (18:0) or oleic acid (18:1n-9) when typical corn diets were replaced by high-oil corn diets. In contrast, Gillis et al. (2004) reported that when heifers were fed a high concentrate diet with 4% corn oil for 60 d, conjugated linoleic acid (CLA) concentrations increased marginally and oleic acid and total monounsaturated fatty acid (MUFA) concentrations in adipose tissues decreased.

Previous research conducted in our laboratory indicated that there was a depression in saturated fatty acid (SFA) concentration in s.c. adipose tissue due to an increase in stearoyl Co-A desaturase (SCD) gene expression in corn-fed steers (Chung et al., 2007). This effect is similar to the effects of SFA on hepatic SCD activity in humans (Adams et al., 2010), and the study (Adams et al., 2010) suggested that feeding diets abundant in either palmitic acid (16:0) or stearic acid may increase the adipose tissue concentration of oleic acid by stimulating SCD activity.

The effect of palm oil, which is rich in palmitic acid, on meat marbling and fatty acid composition in steers has been controversial. However, it seems to cause an increase of oleic acid in adipose tissue and promote adipocyte differentiation. Adipose tissue contains enzymes that actively elongate palmitic acid to stearic acid, which consequently is desaturated to oleic acid. Increased concentration of oleic acid will increase the healthiness of meat (Adams et al., 2010; Gilmore et al., 2011) and may also increase marbling score. Steers with higher marbling score will grade higher, and this consequentially will likely increase carcass value. Therefore, we hypothesize that palm oil will improve marbling deposition and increase oleic acid in beef.

REVIEW OF LITERATURE

General aspects of palm oil and soybean oil. Palm oil, derived from the fruits of palm trees, is edible plant oil and is one of the more saturated plant oils (Chen et al., 2011; Lopes et al., 2011). Palm oil contains several saturated and unsaturated fats including palmitic acid (44%), stearic acid (5%), oleic acid (39%), linoleic acid (18:2n-6); (10%) and α-linolenic acid (18:3n-3); (0.3%); (Cottrell, 1991). Palmitic acid is located in the sn-1 and sn-3 positions of the glycerol backbone in palm oil triglycerides (TG); (Clifton, 2011).

Dietary composition of fatty acids is known to impact human health. According to the World Health Organization, increased consumption of palmitic acid increases the higher risk of developing cardiovascular diseases, classifying it in the same category as trans-fatty acids (World Health Organization, 2003). Earlier research (Nestel et al., 1978) investigated the effects of several varieties of fat in ruminants and demonstrated a marked increase in plasma cholesterol concentration when palm oil supplements were fed to sheep and goats. Sheep fed palm oil had the greatest increase in cholesterol in the intestinal wall and serum (Nestel et al., 1978). Also, high forage diets supplemented with palm oil increased total cholesterol, high-density lipoprotein (HDL), and nonesterified fatty acids in ram lambs (Lough et al., 1994). Sharp increase in plasma lipids and carcass fat deposition were observed when palm oil was added to high-forage diets of growing ram lambs (Lough et al., 1994).

Another study (Partida et al., 2007) concluded that palm oil supplement did not increase the level of SFA in intramuscular fat in beef and PUFA/SFA ratios were in the normal range, below 0.4% (Wood et al.,2003). In an earlier study, ram lambs fed palm oil had more SFA in intramuscular fat, mainly due to an increase in palmitic acid (Solomon et al., 1992).

Soybean oil, one of the most widely consumed cooking oils, consists of linoleic acid (51%), α-linolenic acid (7~10%), oleic acid (23%), stearic acid (4%), and palmitic acid (10%); (Poth 2002). Supplementary linoleic acid increases HDL:LDL ratio in humans, whereas the effect of oleic acid is comparatively small (Katan et al., 1994). Mardron et al. (2002) indicated that adipose tissue contained more linoleic acid, a key substrate in rumen biohydrogenation, and stearic acid, and contained less palmitic and oleic acids in steers fed extruded full-fat soybeans. Extruded soybeans increased the concentration of CLA in meat. Ludden et al. (2009) indicated that fatty acid composition of s.c. adipose tissue in beef steers fed soybean oil was not different in stearic acid, oleic acid, or CLA, although palmitic acid concentration was increased by soybean oil.

Stimulating Stearoyl-CoA desaturase activity. Stearoyl-CoA desaturase plays a major role in bovine adipocyte hypertrophy (Smith et al., 1999). Stearoyl-CoA desaturase is a delta-9 fatty acid desaturase, which is encoded by the SCD gene. Stearoyl-CoA desaturase catalyzes the synthesis of MUFA by inserting a double bond in the Δ^9 positions (Bernert and Sprecher, 1977), and functions as a key regulator of metabolism (Flowers and Ntambi, 2008). Activity of SCD is positively correlated with

MUFA and negatively correlated with SFA concentrations. Onset of SCD gene expression is regarded as indicative of terminal differentiation in preadipocytes (Casimir and Ntambi, 1996). Palmitoyl-CoA and stearoyl-CoA are preferred substrates and these are desaturated to palmitoleoyl-CoA and oleoyl-CoA, respectfully. Palmitic and oleic acids are the most abundant fatty acids in cholesterol esters, phospholipids, and wax esters (Enoch et al., 1976).

When cellular SCD activity is increased, it influences fatty acid partitioning by promoting fatty acid synthesis while decreasing oxidation (Hulver et al., 2005). Modulation of SCD activity by dietary intervention or genetic manipulation significantly influences energy metabolism to affect obesity, insulin resistance, diabetes and hyperlipidemia (Flowers and Ntambi, 2008).

In bovine adipose tissue, the level of SCD gene expression indicated the extent of terminal differentiation in tailhead s.c. adipose tissue (Martin et al., 1999). Stearoyl Co-A desaturase gene expression is strongly upregulated by diets high in SFA, especially in preweaning pigs (Smith et al., 1999). Increased *cis-9, trans-11* CLA (*c9, t11* CLA) in adipose tissue of cattle fed extruded full-fat soybeans could be indicative of endogenous synthesis through SCD (Madron et al., 2002), which is comparatively active in adipose tissue than in muscle in steers (Chang et al., 1992). Chung et al. (2007) reported greater SCD activity in s.c. adipose tissue of Wagyu steers than in Angus steers, which may explain the greater MUFA:SFA ratio in Wagyu adipose tissue compared to Angus adipose tissue.

In ruminants, stearic acid is the primary fatty acid available for absorption from the small intestine (Ekeren et al., 1992). Thus the contribution of SCD to regulate the fatty acid composition in ruminant tissue is particularly important (Chang et al., 1992). Stearic acid is converted to oleic acid via SCD, and oleic acid is a major component of neutral lipids in bovine adipose tissue (Wood et al., 2008). In beef, dietary oleic acid is hydrogenated mainly to stearic acid by ruminal microorganisms, so regulation of oleic acid concentration in adipose tissue and muscle is reliant upon the activity of SCD (Smith et al., 2006). Chang et al. (1992) also found that a high-oleic acid diet significantly increased a SCD activity in muscle, liver, adipose and intestines, which probably reflected the greater duodenal concentration of stearic acid in cattle fed the high-oleic acid diet (Ekeren et al., 1992). We propose that supplementing finishing diets with palm oil will elevate SCD activity, which will promote adipocyte differentiation and increase beef MUFA. Soybean oil supplementation will be used as a negative control.

MATERIALS AND METHODS

Animals and diets. The Texas A&M University Animal Care and Use Committee, Office of Research Compliance approved the experimental procedures for this research. Eighteen Angus steers were purchased as calves, and then transported to the Texas A&M University Research Center at McGregor. Steers were grazed on native pasture until 12 mo of age. At 15 mo of age (approximately 340 kg BW), steers were allotted randomly to three treatments (n=6, per treatment): a basal diet without additional fat, basal diet plus 3% palm oil (rich in palmitic acid), or basal diet plus 3% soybean oil (rich in polyunsaturated fatty acids). Supplemental fats were added as top dressing to the basal diet at feeding. Steers were fed their treatments for 10 wk until an average BW of 500 kg. At that time, the steers were harvested at the Texas A&M University Rosenthal Meat Science and Technology Center, in College Station, TX.

Sample collection. Subcutaneous adipose tissue samples were obtained from the 8^{th} to 11^{th} rib section immediately after the hide was removed (approximately 20 min postmortem), and were placed in oxygenated 37°C, Kreb Henseleit buffer (KHB) containing 5 mM glucose and transported to the laboratory. Other samples were snap frozen in liquid nitrogen and stored at -80°C for measurement of adipose tissue cellularity, fatty acid composition, and adipogenic enzyme activities.

Lipogenesis in vitro. At sample collection, 3-h *in vitro* incubation was conducted with s.c. adipose tissue (~100 mg) as described previously (Martin et al., 1999), and adipose tissue explants were incubated with [1-^{14}C]acetate and [5,6 –

^{3}H]glucose. Scintillation vials for measurement of lipogenesis contained 5 m glucose, 5 m acetate, 10m HEPES, 1 μCi/mL [5,6-^{3}H]glucose and 1 μCi/mL[1-^{14}C] sodium acetate (American Radiolabeled Chemicals, Inc) and KHB buffer. Adipose tissues were incubated in 3 mL of media for 3 h at 37.5°C in a shaking water bath. Neutral lipids in adipose tissues were extracted using the procedure of (Folch et al., 1957) evaporated to dryness, and resuspended in 10 mL of scintillation cocktail (Bio-safe2, Research Product international Corp., Mount Prospect, IL). Radioactivity of lipid extracts was counted with a scintillation counter (Packard 1600TR Liquid Scintillation Analyzer, Downers Grove, IL). Results were reported as *n*mol/10^{5} cells.

***Fatty acid composition*.** Adipose tissue lipids were extracted by the modification of Folch method (Folch et al., 1957). Approximately 100 mg of tissue was homogenized with 5.0 mL of chloroform:methanol (2:1, v/v) in a homogenizer (Brinkmann Insruments, Westbury, NY). Total volume of homogenate was adjusted to 15 mL by adding chloroform:methanol solution. After sitting at room temperature for 30 min, the homogenate was vacuum filtered through a sintered glass filter funnel fitted with a glass microfibre filter, 691 (VWR International, England) into a glass test tube, and 8 mL of 0.74% KCl (w/v) added into the tube. Filtered sample was vortexed for 30 sec and centrifuged at 2,000 × g for 15 min for separation. After discarding the upper aqueous phase, the lower phase was evaporated at 60°C with a nitrogen flushing evaporator. Total extracted lipid was used for fatty acid analysis.

Fatty acids were methylated by the modification of (Morrison and Smith, 1964). Approximately 100 mg of total lipids extract were taken into another glass tube. Lipid

was mixed with 1 mL of 0.5 *N* of KOH in MeOH and heated in water bath at 70°C for 10 min. After cooling to room temperature, 1 mL of 14% BF_3 in MeOH (w/v) was added to sample, then heated in water bath at 70°C for 30 min and sit at room temperature. Two milliliters of HPLC grade hexane and saturated NaCl solution were added and vortexed for 30 sec. The upper phase was then transferred to 20 mL glass tube containing anhydrous Na_2SO_4 to remove aqueous molecules. Total volume of hexane was determined for optimal fatty acid methyl ester (FAME) concentrations. FAME was analyzed by GC-FID (model CP-3800 equipped with a CP-8200 auto-sampler, Varian Inc, CA). Separation of FAME was accomplished on a fused silica capillary column (100 m x 0.25 mm ID) (model CP-3800, Varian Inc, CA) with the helium as carrier gas (flow rate = 1.7 mL/min). One microliter of sample was injected with the split ratio of 100:1 at 270°C. Oven temperature was set at 165°C for 65 min and then increased to 235°C (2°C/min) and held for 15 min. Flame ionization detector (FID) detected the signal at 270°C. Standard (GLC 68-D, Nu-chek Prep, MN) was used to identify each peak.

Enzyme assays. We measured glucose-6-phosphate dehydrogenase (G-6-PDH), 6-phosphogluconate dehydrogenase (6-PGDH), and NADP-malate dehydrogenase (malic enzyme) as indices of adipogenesis. G-6-PDH and 6-PGDH were measured using the assay system by Bergmeyer (1974). A buffer containing 0.1 mL $NADP^+$, 0.015 mL 1 *M* $MgCL_2$, 0.635 mL H_20 and 1.5 mL 0.4 *M* triethanolamine (TRA) buffer was added to each cuvette with 0.05 mL homogenate to give a total volume of 2.3 mL. Baseline activity was recorded, and 0.1 mL 6-PG was added to each cuvette to measure

the enzyme activity of 6-PGDH, which converted 6-phosphogluconate to ribulose-5-P. Rate was measured using a Beckman DU-7400 Spectrophotometer (Palo Alto, CA) set at 339nm. In the same cuvette, 0.1 mL G-6-P was added to measure the activity of G-6-PDH, which catalyzes G-6-P to 6-phosphogluconate, and the change in enzyme activity was measured.

Malic enzyme was quantified with the same procedure mentioned above. A 0.1 mL aliquot of homogenate was added into each cuvette with 0.1 mL NADP, 1.0 mL H_2O and 1.2 mL 0.4 *M* TRA buffer. Baseline activity was read on the spectrophotometer, and 0.1 mL malate was added in the same cuvette to measure malic enzyme activity. Change in absorbance was noted.

Fatty acid synthetase was measured by adding 0.1 mL homogenate to each cuvette with 0.1 mL NADPH, 0.9 mL H_2O and 1.3 mL 0.4 *M* TRA buffer, the total volume was 2.4 mL. Background was recorded on the spectrophotometer, and the combination of 0.1 mL AcCoA + MalCoA was added to each cuvette. Change in absorbance was recorded.

Cellularity. Subcutaneous adipose tissue was collected immediately from the steers and frozen at -80°C for determination of cellularity by osmium fixation, counting, and sizing (Morrison and Smith, 1964). A 25-mg sample was sliced into sections 1 mm thick while being kept on ice at all times. Exact weights of the samples were recorded and then samples were transferred to 20 mL scintillation vials. Tissues were rinsed 3 times with 37°C 0.154 *M* NaCl at 1-h intervals to eliminate free triacylglycerol. After the last rinse, 0.5 mL of 50 mM collidine-HCl buffer (pH 7.4) was added to break up the

tissue samples and then 0.8 mL of 3.0% osmium in collidine buffer was added. Samples were placed in 37°C water bath for 96 h with swirling occasionally. After incubation, the osmium was removed and 10 mL of 0.154 *M* NaCl were added using a Pasteur pipet. The samples were rinsed continuously with NaCl until the solution was clear. Ten milliliters of 8 *M* urea were added and incubated at room temperature for 24-96 h with occasional swirling. After degradation of connective tissue with urea, tissues were rinsed three times with 0.154 *M* NaCl. The fixed adipocytes, resuspended with 0.01% Triton in 0.154 *M* NaCl, were used for determination of cell size, volume, and cells/100 mg tissue, using a bright-field microscope (Olympus Vanox ABHS3, Olympus, Tokyo, Japan) and CCD Color Video Camera (DXC-960MD, Sony, Japan).

Statistical analysis. Data was analyzed using the General linear mixed models (GLMM) of SPSS statistics 20 (IBM, Armonk, NY) as appropriate for completely randomized designs. The model tested main effects of palm oil and soybean oil compared to control group. Means were separated and statistically analyzed to see if different dietary treatments had any statistical significance ($P < 0.05$).

RESULTS

Carcass traits. Neither palm oil nor soybean oil supplementation affected marbling score, quality grade, actual fat thickness, adjusted fat thickness, rib eye area (REA), kidney, pelvic and heart fat (KPH), carcass weight and yield grade (Table 2). However, overall maturity was significantly affected by supplemental palm oil. Skeletal maturity was lower by 25.9% in steers supplemented with palm oil than in steers receiving only basal diet ($P = 0.04$). Lean maturity was decreased by 28.3% with palm oil treatment than with soybean oil treatment ($P = 0.02$). Overall maturity in steers with palm oil supplemented was 24.2% lower than steers fed basal diet and 19.8% lower than steers fed soybean supplement respectively ($P = 0.01$).

Incorporation of glucose and acetate into lipids in vitro. The rate of acetate incorporation into total lipids was approximately 2-fold greater than the rate of glucose incorporation in s.c. adipose tissue, so more acetate was used for lipid synthesis rather than glucose in bovine s.c. adipose tissue (Table 3). Palm oil supplementation increased lipid synthesis from glucose ($P = 0.03$) whereas soybean oil supplementation had no effect on lipid synthesis from glucose, compared to the control group. Rate of acetate incorporation into lipids was much higher in steers fed palm oil that in soybean oil-fed steers ($P = 0.03$).

Enzyme activities. Oil supplements had no effect on the activities of 6-PGDH, NADP-MDH or FAS in s.c. adipose tissue (Table 3). G-6-PDH tended to be greater in steers consuming palm oil supplement ($P = 0.10$).

Cellularity. Adipocyte volume in s.c adipose tissue was not affected in steers supplemented with palm oil but was decreased by soybean oil supplementation (P = 0.004); (Table 3).

Fatty acid composition. Myristic acid was significantly decreased by palm oil supplementation in s.c. adipose tissue (P = 0.04); (Table 4). The *t*10, *c*12 CLA isomer and 18:3n-3 tended to be decreased by palm oil supplementation in s.c. adipose tissue (P = 0.07 and P = 0.06, respectively). However, neither palm oil nor soybean oil affected other fatty acid concentration in s.c. adipose tissue in steers.

Palm oil supplementation decreased the concentration of *c*9, *t*11 CLA (P = 0.02) and 18:3n-3 (P = 0.03) in muscle (Table 4). Subcutaneous adipose MUFA ranged from 46%-49% among treatments whereas total MUFA in muscle were 43% among treatments. Total SFA concentration was greater in muscle tissue than one in s.c. adipose tissue, so the ratio of MUFA:SFA was slightly higher in s.c. adipose tissue than in muscle.

Simple correlations. There was no correlation between marbling scores and adjusted fat thickness (Table 5). Nor were any in vitro measures of lipid synthesis correlated with adjusted fat thickness ($P > 0.10$). However, marbling score was significantly correlated with glucose and acetate incorporation into fatty acids and NADP-MDH ($P < 0.05$). FAS activity tended ($P < 0.10$) to be correlated with marbling scores.

DISCUSSION

Effects of seed oils on carcass composition. This study demonstrated that supplemental palm oil promoted adipogenesis and adiposity, whereas soybean oil supplementation had no effect on adipogenesis. Volume of s.c. adipocytes in cattle fed the palm oil diet was significantly larger than in soybean oil diet, and carcass traits also demonstrated that the palm oil-fed steers possibly had more adipocytes or larger adipocytes, as indicated by trends toward higher marbling scores and increased quality grade compared with soybean oil-fed steers.

Marbling is the important factor in determining carcass quality. Difference in marbling at the 12^{th} rib interface is closely related to the eating quality of beef (Smith et al., 2004). Consumers prefer to purchase meats with high marbling scores because greater marbling suggests more tender, juicy and flavorful meat than lower levels of marbling.

Carcass quality is calculated primarily from marbling scores and firmness of lean in relation to maturity. Thus, the evaluation of maturity (i.e., the physiological age of the carcass) is important for the determination of meat quality. Main indicators of maturity include color, size, and shape of rib bones. Also, lean tends to be darker and less tender as cattle mature. Both skeletal maturity and lean maturity were lowest in steers fed palm oil supplementation. It is possible that the saturated fatty content of muscle from cattle fed the palm oil supplement was sufficiently elevated to increase the

melting point of the muscle lipids. This would have increased muscle firmness, resulting in a lower maturity score.

Previous research indicates that dietary supplementation with positively affected carcass composition. Partida et al., (2007) demonstrated that steers fed dietary palm oil produced more tender meat, while beef flavor of all diets remained similar. Lambs fed palm oil increased s.c. fat thickness and body wall fat thickness, and this indicated a higher degree of SFA in s.c. adipose tissue (Solomon et al., 1992). Teye et al. (2006) indicated that pigs fed palm kernel oil produced firmer fat than ones fed soyabean oil. Gillis et al. (2004) reported that a diet containing added 4% corn oil did not affect carcass characteristics including BW, fat depth, REA, yield grade and quality grade. Neither a soybean oil supplementation (Ludden et al., 2009) nor a corn-based diet (Nelson et al., 2008) affected carcass traits such as marbling scores and quality grade in steers. However, steers fed high-oil corn diet had increased marbling scores and quality grades (Andrae et al., 2001).

Effects of seed oils on fatty acid composition of muscle and adipose tissue. Palm or soybean oil did not effect on fatty acid profiles in s.c. adipose tissue. St John et al. (1991) confirmed that dietary supplementation cannot easily modify a fatty acid composition in bovine tissue. St John et al. (1987) reported that a high-oleate rapeseed diet did not significantly change the fatty acid composition of bovine s.c. adipose tissue, even though rapeseed is regarded as less susceptible to ruminant biohydrogenation.

Palm oil supplementation significantly decreased the concentration of myristic acid in s.c. adipose tissue, and tended to decrease *t*10, *c*12 CLA isomer and 18:3n-3 in

our study. Pavan and Duckett (2007) demonstrated that steers with corn oil supplementation had a reduced proportion of myristic acid in s.c. adipose due to the increase of total linoleic acid intake.

Previous research has demonstrated an effect of dietary palm oil supplementation on ruminants. Rams fed palm oil had significantly more SFA in s.c. adipose tissue, mainly due to an increased palmitic acid, but palm oil lowered myristic and linolenic fatty acids (Solomon et al., 1992), similar to this study. Partida et al. (2007) demonstrated an increase in palmitic acid in intramuscular fat of bulls after supplementing hydrogenated palm oil, although the total SFA concentration remained similar to control animals.

In general, the amounts of n-3 fatty acids tended to be low in diets containing high corn or soybean because of rich linoleic acid, which is a precursor of the n-6 (Partida et al., 2007). Linoleic (18:2n-6) and a-linolenic acid (18:3n-3) are essential fatty acids, and they are important for the structure of cellular membrane and metabolic processes. Soybean oil supplementation maintained *c*9, *t*11 CLA level and increased 18:3n-3 in muscle while palm oil decreased *c*9, *t*11 CLA and 18:3n-3. Similarly, Gillis et al. (2004) demonstrated a decrease in oleic acid and total MUFA after heifers were fed corn oil or rumen-protected CLA salt, whereas total PUFA was higher in heifers supplemented with corn oil. Pavan and Duckett (2007) found that *c*9, *t*11 CLA was greater in s.c. adipose tissue of steers after an administration of corn oil supplementation. Although corn oil supplementation did not affect total SFA or the PUFA:SFA ratio, it reduced the level of myristic and palmitic acids. According to Oliveira et al. (2011), the

compositions of fatty acids are affected by dietary fats. Ground cottonseed treatment increased myristic acid while decreasing oleic acid in s.c. adipose tissue, with no effect on CLA concentration. Ground soybeans increased 18:2n-6 and 18:3n-3 in muscle and s.c. adipose as soybeans had the great percentages of these two fatty acids. Ground linseed oil also increased 18:3n-3 in muscle and adipose tissue.

Bovine s.c. adipose tissue is a major site for SCD activity in cattle (St John et al., 1991), and is required for the conversion of palmitic to oleic acid. Also, SCD activity increases as steers get fatter (Duckett et al., 2009). Yang et al. (1999) investigated the change of SCD activity in s.c. adipose tissue from different feeding styles, such as pasture-feeding or feedlot, and pasture-fed steers exhibited elevated SCD activity and total unsaturated fatty acids, and also lowered total saturated fatty acids. According to Chung et al. (2006), palmitoleic acid content of bovine adipose tissue is primarily determined by SCD activity because diets normally fed to steers contain such small amount of palmitoleic acid. In ruminant adipocytes, *de novo* lipogenesis converts acetate into myristic acid, or primarily palmitic acid, which are SFA. Joseph et al. (2010) indicated that the high intake of corn oil in cattle resulted in lower de novo fatty acid synthesis and decreased palmitic acid production by down regulating ACC (acetyl-CoA carboxylase) and FAS (fatty acid synthase).

In ruminants, the double bonds in polyunsaturated fatty acids of diets are hydrogenated by the microbes before the absorption in the small intestine (Ekeren et al., 1992). Despite the ruminal modification, Chang et al. (1992) demonstrated that, after feeding a corn-based diet with 20% high oleate sunflower seed, SCD activity increased

in both muscle and adipose, and the concentrations of oleic, myristic, and stearic acid were higher in perianal adipose than in steers fed only the corn-based diet. Chung et al. (2006) demonstrated that steers fed a hay-based diet had reduced oleic acid in adipose tissue, compared to corn-fed steers. They also indicated that s.c. adipose tissue of corn-fed steers had more MUFA and PUFA than hay-fed steers. Duckett et al. (1993) indicated that steers fed a high-concentrate diet for a longer period had decreased PUFA concentrations, but increased oleic acid concentrations and MUFA content. The increase in oleic acid might have been due to an increased microsomal desaturase activity or a decreased ruminal biohydrogenation with grain feeding.

For fat accumulation and adipocyte hypertrophy, fatty acids originate from either de novo lipogenesis or dietary supplementation (Joseph et al., 2010). Although the current study demonstrated that lipogenesis in bovine adipose tissue was sensitive to dietary fats, the effect of dietary fatty acids on lipogenesis did not seem to correlate with changes in the tissue concentration of fatty acids. Moreover, our research indicated that the fatty acids derived from dietary supplementation did not noticeably affect the fatty acid profiles in s.c. adipose tissue.

Comparison of 1-^{14}C acetate to 5,6-^{3}H glucose. In ruminants, the major lipogenic site is s.c. adipose tissue (Ingle et al., 1972; Joseph et al., 2010; Rhoades et al., 2007; St John et al., 1991). Acetate is the major carbon source for *de novo* lipogenesis in s.c. adipose tissue (Hanson and Ballard, 1967; Ingle et al., 1972; Smith and Crouse, 1984). Our results confirmed that the incorporation of acetate into s.c. adipose tissue was almost 2.5-fold greater than that of glucose. This was consistent with previous

research conducted in our labaratory (Smith and Crouse, 1984; Smith and Prior, 1986). Rhodes et al. (2007) reported that rates of acetate and glucose incorporation into lipids were similar in s.c. adipose tissue. Although acetate and lactate together did not affect total glucose utilization in bovine s.c. adipose, acetate provided 72-82% of the acetyl for fatty acid synthesis, which was dependent on the substrate concentration (Smith and Prior, 1986).

The current study indicates that palm oil supplementation significantly increased lipogenesis from both acetate and glucose in s.c. adipose tissue by 75.7% and 74.6% , respectively, to compare to control group. Other investigators also demonstrated that lipogenesis from acetate was increased in bovine s.c. adipose tissue after steers were fed a high-concentrate diet for 6 months (Martin et al., 1999) and 3 months (Prior, 1983), or after steers were fed corn-based diets rather than hay-fed (Chung et al., 2007). Earlier, Pothoven et al. (1975) reported that steers fed *ad libitum* had a higher rate of acetate incorporation into lipids in adipose tissue than steers fed energy-restricted diets.

Soybean oil supplementation did not increase lipogenesis from either glucose or acetate in s.c. adipose tissue, which in turn resulted in 7% smaller adipocyte volumes compared to adipocytes from cattle fed palm oil diets. Whole cottonseed fed to steers reduced the rate of acetate incorporation into lipids in s.c. adipose tissue, indicating the depression of lipogenesis by dietary fat (Page et al., 1997).

Despite the lack of effect of diet on FAS, which is a key enzyme regulating the rate of lipogenesis in bovine adipose tissue (Prior, 1980; Smith and Prior, 1986), the results obtained from this study suggest that palm oil supplementation enhanced

lipogenesis in bovine s.c. adipose tissue. Increased lipogenic activity in s.c. tissue in palm oil-fed steers promoted s.c. adipocyte volume in this study.

In an earlier study, adipocyte volume gradually increased and peaked at 18 mo of age in steers fed a high concentrate diet for 6 mo (Martin et al., 1999). This represented a period of adipocyte hyperplasia. Chung et al. (2007) examined Wagyu and Angus steers with a short feeding time and a long feeding time (4 mo longer than short feeding) and found that adipocyte volume was greater in long-fed than in short-fed Wagyu steers, while Angus steers exhibited reduced adipocyte volume after the long feeding time.

Other investigators have demonstrated that there was no effect on cellularity in bovine s.c. adipose tissue by dietary supplementations such as hay-based or corn grain-based diets (Pavan and Duckett, 2007; Rhoades et al., 2007) or by breeds (St John et al., 1991). Prior (1983) indicated that a concentrate diet tended to reduce mean adipocyte diameter and volume in comparison to a hay diet, in s.c. adipose tissue.

Taken together with the increase in lipogenesis after palm oil supplementation, palm oil, unlike soybean oil, enhanced adiposity in s.c. tissue as this study indicated that adipocyte volume was significantly greater in palm oil-fed steers than in soybean oil-fed ones.

Importance of FAS, NADP-MDH, G-6PDH and 6-PGDH. We chose to measure 6-PGDH, NADP-MDH, FAS and G-6PDH, which are lipogenic enzymes involved in adipose tissue metabolism. Activity of G-6PDH was almost two-fold greater in the palm oil group than in the control group, and all other enzyme activities indicated a tendency to be increased in steers fed palm oil.

Although not significant ($P \leq 0.26$), the highest activities of G-6PDH, NADP-MDH and FAS were observed in s.c. adipose tissue of cattle fed palm oil. Similarly, s.c. fat thickness, marbiling scores, and yield grade were numerically greater in palm oil-fed steers. Smith and Prior (1986) observed that the activity of fatty acid synthetase was sufficient to support maximal rates of lipogenesis from acetate and lactate in bovine adipose tissue. Thus, FAS was not only a key enzyme which affected by the various treatments, but also important in regulating the rate of lipogenesis in bovine adipose tissue (Prior, 1980; Smith and Prior, 1986). Furthermore, Prior (1980) indicated that the activity of FAS was greater in small type cattle than in large cattle, and this might explain the relatively low activity of FAS in s.c. adipose, as the average BW of steers in current studies were very close to the average BW of large cattle in their study (Prior, 1980).

Results of enzyme activity affected by treatments might be related to regulating the fatty acid profile in this study. Lipogenic enzyme activities measured in this study tended to be greater in palm oil supplementation compared to other diets. Thus, this result correlated with the increase by palm oil supplementation in lipogenesis.

We chose to measure the enzymes FAS, NADP-MDH, 6-PGDH, and G6PDH based on previous research from this laboratory. As indicated previously, FAS probably is rate-limiting to fatty acid biosynthesis in bovine adipose tissue (Smith and Prior, 1986). Additionally, the incorporation of both acetate and glucose carbon into fatty acids is dependent of the activities of NADP-MDH and the pentose phosphate enzymes (Prior et al., 1981; Smith, 1983; Smith and Prior, 1981; Smith et al., 1984; Smith et al.,

1992). Glucose carbon incorporation into fatty acids includes flux through NADP-MDH, and NADP-MDH provides as much as 40% of the NADPH required for fatty acid biosynthesis from acetate and glucose (Smith, 1983). Also, the activities of all of these enzymes are sensitive to differences in energy intake (Smith et al., 1984; Smith et al., 1992).

Unlike previous studies in which ^{14}C-labeled glucose was used as a precursor for lipid synthesis, we chose to use [5,6-^{3}H]glucose. After conversion of the glucose carbon to pyruvate, only ^{3}H labeling at carbon 6 remains. Once the pyruvate enters the mitochondria and is converted to acetyl-CoA or oxaloacetate (Smith and Prior, 1981), the ^{3}H labeling remains at either carbon 2 (acetyl-CoA) or carbon 3 (oxaloacetate). After condensation with oxaloacetate to produce citrate, the ^{3}H labeling can be incorporated into fatty acids attached to carbon 2 of acetyl-CoA via the combined activities of ATP-citrate lyase and NADP-MDH. Alternatively, the ^{3}H can be incorporated into NADPH via NADP-MDH or NADP-isocitrate dehydrogenase, and the ^{3}H labeling subsequently can be incorporated into fatty acids via FAS. The very high correlation between [5,6-^{3}H]glucose and [1-14C]acetate incorporation into fatty acids ($r = 0.99$) suggests that a substantial amount of the ^{3}H labeling from [5,6-^{3}H]glucose was incorporated into fatty acids as NADPH, although this was not measured directly.

It was unexpected that NADP-MDH activity would be correlated with marbling score but not fat thickness, as the latter is an s.c. adipose tissue depot. The data suggest that marbling scores and NADP-MDH activity were both sensitive to the palm oil supplementation, whereas subcutaneous fat thickness was not.

CONCLUSIONS

To date, there is little published information about the effects of dietary palm oil supplementation on carcass quality or lipid metabolism in cattle. The goal of this research was to promote adipocyte differentiation and to increase beef MUFA by supplementing finishing diets with palm oil. We hypothesized that palm oil supplementation would elevate SCD activity, which in turn would increase oleic acid in beef and elevate marbling deposition. The increased oleic acid not only would increase the healthfulness of the beef, but also would increase carcass value.

In our study, we investigated the effects of palm oil supplementation on fatty acid composition, lipogenic enzyme activities, adipose tissue cellularity, and lipid metabolism in vitro in bovine subcutaneous adipose tissue. The results of this study confirm that fatty acid synthesis was greater from acetate than from glucose in bovine s.c. adipose tissue. The rates of acetate and glucose incorporation into total lipids in steers fed palm oil was 75% greater than in steers fed soybean oil. Although palm oil supplementation increased lipogenic capacity, it had no effect on the concentration of oleic acid in s.c. adipose tissue. Palm oil supplementation decreased myristic acid, the *t*10, *c*12 CLA isomer and 18:3n-3 in s.c. adipose tissue and c9, t11 CLA and 18:3n-3 in muscle. Soybean oil supplementation had greater c9, t11 CLA and 18:3n-3 in muscle and 18:3n-3 in s.c. adipose tissue than palm oil. This was expected, as palm oil is lower in polyunsaturated fatty acids than the soybean oil diet.

Taken together, palm oil supplementation is involved, at least in part, in the effects of adiposity and substrate utilization, and appears to be correlated with marbling. The results of this study partially support the hypothesis that palm oil supplementation promotes adipogenesis and marbling.

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APPENDIX

TABLE 1 Ingredients and chemical composition of the high-energy, corn-based diet

Item	g/100 g corn-based diet
Ground sorghum	20.00
Ground corn	48.05
Cottonseed meal	6.00
Cottonseed hulls	15.00
Molasses	7.50
Limestone	0.96
Trace mineralized salt[1]	0.56
Dicalcium phosphate	0.23
Potassium chloride	0.16
Zinc oxide	0.01
Ammonium sulfate	0.25
Vitamin premix[2]	0.08
R-1500[3]	1.20
Total	100.0
Nutrient composition[4]	
Dry matter, %	89.13
Crude protein, %	11.16
NEm (Mcal/kg)	1.81
NEg (Mcal/kg)	1.19
Acid detergent fiber, %	14.12
Calcium, %	0.52
Phosphorus, %	0.36

[1]Trace mineralized salt: NaCl, 98%; Zn, 0.35%, Mn 0.28%; Fe, 0.175%; Cu, 0.035%; I, 0.007%; Co, 0.0007%.
[2]Vitamin Premix: vitamin A, 2,200,000 IU/kg; vitamin D, 1,100,000 IU/kg; vitamin E, 2,200 IU/kg.
[3]R-1500: 1.65g monensin sodium (Rumensin) per kg.
[4]Percentage of dry matter. Calculated values based on NRC (1996).

TABLE 2 Carcass characteristics of Angus steers at different times on a high-energy, corn based diet (N=28)

Item	Treatment[1]			SEM	*P*-values
	Control	Palm oil	Soybean oil		
Skeletal maturity	54.0[b]	40.0[a]	44.4[ab]	2.42	0.04
Lean maturity	46.0[ab]	36.7[a]	51.1[b]	2.15	0.02
Overall maturity	50.6[b]	38.3[a]	47.8[b]	1.67	0.01
Marbling score[2]	479.0	508.9	455.6	14.16	0.33
Quality grade[3]	425.8	437.7	416.3	5.90	0.36
Actual fat, cm	1.87	1.95	1.72	0.09	0.62
Adjusted fat, cm	1.97	2.05	1.82	0.09	0.58
REA[4], cm^2	81.8	81.1	80.8	1.17	0.94
KPH[5], %	2.30	2.61	2.50	0.12	0.54
Carcass weight, kg	341.5	341.7	343.0	5.64	0.99
Yield grade	3.70	3.87	3.66	0.11	0.72

[1]Control = basal diet only, Palm oil = basal diet + 3% palm oil, Soybean oil = basal diet + 3% soybean oil.
[2]Marbling score, 400 = Small; 500 = Modest.
[3]Quality grade, 400 = Choice.
[4]REA = rib eye area.
[5]KPH = kidney, pelvic and heart fat expressed as percent of carcass weight ranged from 1 to 6.

TABLE 3 Adipose tissue cellularity, glucose and acetate incorporation into lipids and adipogenic enzyme activity in subcutaneous adipose tissue of steers fed palm oil and soybean oil (N=18)

Item	Treatment[1]			SEM	P-value
	Control	Palm oil	Soybean oil		
Lipogenesis[2]					
Glucose	29.59[a]	51.65[b]	23.48[a]	4.02	0.03
Acetate	73.98[a]	130.05[b]	56.21[a]	10.63	0.03
Cellularity[3]					
Adipocyte vol, pL	4276[a]	4379[a]	4072[b]	38.3	0.004
Enzyme activity[4]					
6-PGDH	2.55	4.02	4.20	0.50	0.36
G-6-PDH	3.90	7.52	6.15	0.64	0.10
NADP-MDH	0.22	0.35	0.28	0.03	0.13
FAS	0.17	0.33	0.30	0.04	0.26

[1]Control = basal diet only, palm oil = basal diet + 3% palm oil, soybean oil = basal diet + 3% soybean oil.
[2]Subcutaneous adipose tissue metabolism, nanomoles of acetate and glucose incorporated·$3h^{-1}$·10^5 $cells^{-1}$·
[3]Adipocyte volume, pL
[4]6-phosphogluconate dehydrogenase (6-PGDH), glucose-6-phosphate dehydrogenase (G-6-PDH), NADP-malate dehydrogenase (NADP-MDH), and fatty acid synthetase (FAS), μmol·min^{-1}·10^5 $cells^{-1}$

TABLE 4 Fatty acid composition of subcutaneous adipose tissue and muscle of control steers and steers fed palm oil and soybean oil (g/100g total lipids); (N=18)

Fatty acids	Subcutaneous adipose tissue					Muscle				
	Control	Palm oil	Soybean oil	SEM	*P*-values	Control	Palm oil	Soybean oil	SEM	*P*-values
14:0	3.35[ab]	2.68[a]	3.53[b]	0.13	0.04	3.33	2.97	3.48	0.14	0.34
14:1n-5	1.38	0.92	1.24	0.09	0.16	0.82	0.64	0.76	0.07	0.57
16:0	26.12	26.00	24.78	0.36	0.22	27.52	27.94	27.15	0.36	0.67
16:1n-7	4.69	3.82	4.01	0.23	0.31	3.34	2.94	3.33	0.15	0.50
18:0	9.76	11.82	11.1	0.46	0.21	14.69	15.20	13.98	0.49	0.60
18:1*trans*[2]	3.36	3.47	3.43	0.30	0.99	2.76	2.77	3.38	0.17	0.26
18:1*cis*-9	40.21	41.30	38.94	0.84	0.37	36.88	37.78	37.06	0.49	0.57
18:1*cis*-11	1.71	1.33	1.47	0.06	0.08	1.34	1.19	1.33	0.05	0.33
18:2n-6	1.73	1.82	1.88	0.08	0.73	2.86	2.74	3.51	0.16	0.15
18:2*c*-9,*t*-11	0.63	0.52	0.58	0.04	0.53	0.36[b]	0.21[a]	0.36 [b]	0.02	0.02
18:2*t*-10,*c*-12	0.08	0.04	0.07	0.01	0.07	0.08	0.07	0.13	0.01	0.36
18:3n-3	0.08	0.05	0.10	0.01	0.06	0.09[ab]	0.07[a]	0.15[b]	0.01	0.03
20:4n-6	0.04	0.03	0.04	0.01	0.35	0.67	0.72	0.83	0.05	0.48
MUFA	48.62	47.88	45.63	0.94	0.42	42.75	42.76	42.25	0.53	0.90
SFA	39.23	40.71	39.41	0.36	0.22	45.53	46.10	44.60	0.39	0.32
MUFA:SFA[3]	1.24	1.17	1.16	0.03	0.51	0.95	0.93	0.95	0.02	0.94

[a-c]Means in rows not bearing a common superscript differ, $P < 0.05$.

[1]Control = basal diet only, palm oil = basal diet + 3% palm oil, soybean oil = basal diet + 3% soybean oil.

[2]Sum of amount of 18:1 *t9*, 18:1 *t10*, and 18:1 *t11*.

[3]MUFA:SFA = (14:1 n5 + 16:1 n7 + 18:1 *c9* + 18:1 *c11* + 18:2 *c9, t11*) / (14:0 + 16:0 + 18:0 + 18:1 *trans*).

TABLE 5 Simple correlation coefficients among variables[1] (N=28)

Item	Fat thickness	Marbling score	Glucose incorp.	Acet incorp.
Fat thickness	---			
Marbling score	0.14	---		
Glucose incorp.	0.30	0.47**	---	
Acetate incorp.	0.28	0.47**	0.99***	---
6-PGDH	0.01	0.10	0.01	0.01
G6PDH	0.08	0.26	0.02	0.03
NADP-MDH	0.02	0.50**	0.22	0.23
FAS	-0.14	0.39*	-0.25	0.24

[1]Data are from 18 total observations. *$P \leq 0.10$; **$P \leq 0.05$; ***$P \leq 0.01$.

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