



Carcass and Meat Characteristics and Gene Expression in Intramuscular Adipose Tissue of Korean Native Cattle Fed Finishing Diets Supplemented with 5% Palm Oil

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Abstract

We hypothesized that supplementing finishing diets with palm oil would promote adipogenic gene expression but depress stearoyl-CoA desaturase (*SCD*) gene expression in intramuscular (i.m.) adipose tissues of Hanwoo steers during fattening period (from 16 to 32 mon of age). Fourteen Hanwoo steers were allotted randomly to 2 groups of 7 steers based on initial BW and fed either a basal diet (control) or the basal diet supplemented with 5% palm oil (BDSP). At slaughter, i.m. adipose tissue was harvested for analysis of adipogenic gene expression and fatty acid composition. There were no differences in BW or average daily gain between treatment groups. Supplemental palm oil had no effect on carcass quality traits (carcass weight, backfat thickness, loin muscle area, or marbling scores) or meat color values. Palm oil increased ($p<0.05$) expression of AMP-activated protein kinase- α and peroxisome proliferator-activated receptor- γ , but decreased ($p<0.05$) CAAT/enhancer binding protein- β gene expression and tended to decrease stearoyl-CoA desaturase gene expression in i.m. adipose tissue. Palm oil increased total i.m. polyunsaturated fatty acids ($p<0.05$) compared to the control i.m. adipose tissue, but had no effect on saturated or monounsaturated fatty acids. Although there were significant effects of supplemental palm oil on i.m. adipose tissue gene expression, the absence of negative effects on carcass and meat characteristics indicates that palm oil could be a suitable dietary supplement for the production of Hanwoo beef cattle.

Keywords adipose tissue, fatty acids, gene expression, palm oil, stearoyl-coenzyme A desaturase

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Introduction

Various oils are utilized as fat sources in ruminant animal feeds, including palm oil (Choi *et al.*, 2013; Lough *et al.*, 1993; Nestel *et al.*, 1978; Solomon *et al.*, 1992). In the U.S., 33% of feedlot nutritionists use plant oils as feed ingredients (Vasconcelos and Galyean, 2007) and in countries such as Korea in which palm oil is an agri-byproduct, palm oil may be a cost-effective feed additive. Oils derived

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from plants contain higher concentrations of polyunsaturated fatty acids (PUFA) than animal fats, which contain more saturated fatty acids (SFA). Addition of PUFA to animal feeds may promote fat oxidation, discoloration, and off-odors. These negative effects may be eliminated by using palm oil, which is one of the few highly saturated vegetable oils, containing approximately 40% palmitic acid (16:0) and 40% oleic acid (18:1n-9) (Truswell, 2012).

We recently demonstrated that the saturated fatty acid (SFA) palmitic acid and stearic acid (18:0) strongly promoted CCAAT enhancer binding protein-b (*CEBPb*) and carnitine-palmitoyl-CoA transferase-1 β (*CPT1 β*) gene expression in cell cultures of intramuscular (i.m.) preadipocytes (Choi *et al.*, 2015). Therefore, we hypothesized that supplementing the diets of beef cattle with palm oil, rich in palmitic acid, would increase adipogenic gene expression in i.m. adipose tissues.

While this study was being conducted in Korea, a parallel study was completed in the U.S. with Angus cross-bred steers raised to a typical U.S. endpoint (Choi *et al.*, 2013). In that study we demonstrated that, relative to soybean oil, feeding 3% palm oil to cattle increased subcutaneous (s.c.) adipocyte size and the activities of NADP-malate dehydrogenase and glucose-6-phosphate dehydrogenase (Choi *et al.*, 2013). Because of the high concentration of palmitic acid in palm oil, we had predicted that supplementing a beef cattle finishing diet with palm oil would up-regulate *SCD* gene expression. However, supplemental palm oil, which also is rich in the monounsaturated fatty acid (MUFA) oleic acid, decreased the ratio of palmitoleic acid (16:1n-7) to stearic acid (an index of *SCD* activity; Choi *et al.*, 2013), and decreased *SCD* gene expression in s.c. adipose tissue (Choi *et al.*, 2016). In preadipocyte cell cultures, oleic acid and the PUFA linoleic (18:2n-6) and α -linolenic acid (18:3n-3) depressed stearoyl-CoA desaturase (*SCD*) gene expression, so we attributed the down-regulation of *SCD* in adipose tissue of palm oil-fed steers to the unsaturated fatty acids in palm oil.

In the current study, we documented the effects of dietary palm oil on specific gene expression in i.m. adipose tissue in Hanwoo steers that were fed a finishing ration for an extended period of time (10 mo). The genes *CEBP β* , *SCD*, carnitine palmitoyl transferase-1 (*CPT1 β*), peroxisome proliferator-activated receptor gamma (*PPAR γ*), and AMP-activated protein kinase alpha (*AMPK α*) were selected as genetic markers of adipose tissue differentia-

tion and metabolism (Jeong *et al.*, 2015). The *CEBP β* gene product binds to promoter regions of adipogenic genes (Cao *et al.*, 1991), including *PPAR γ* . Similarly, the *PPAR γ* gene product is required for proper adipose tissue development (Tontonoz *et al.*, 1994) and is expressed abundantly in differentiating bovine adipocytes (Grant *et al.*, 2008; Smith *et al.*, 2009). AMPK α activity inactivates energy-consuming processes such as fatty acid biosynthesis, while activating energy-producing processes such as fatty acid oxidation (Hardie, 2007). Because palm oil increases carcass adiposity and lipogenesis in s.c. adipose tissue (Choi *et al.*, 2013), we hypothesized that palm oil would increase the expression of genes associated with adipogenesis (*CEBP β* , and *PPAR γ*), and decrease *SCD* and *AMPK α* gene expression. Because palm oil could potentially increase PUFA content of beef, we also measured meat quality traits.

Materials and Methods

Animals

The experimental protocol describing the management and care of animals was reviewed and approved by the Animal Care and Use at the National Institute of Animal Science (NIAS). The control diet was formulated to meet the nutrient requirements recommended by the Korean Feeding Standard for Hanwoo (NIAS, 2007). Fourteen Hanwoo steers (average BW 383.5 \pm 7.3) were assigned randomly to either a control diet (Table 1) or, the basal diet supplemented with 5% palm oil (BDSP). Each treatment group was placed in a 7.0 \times 10.0 m pen and fed its respective diet twice per day with an individual feeding stanchion. Steers were adapted to a corn-based finishing diet for 14 d and then fed either the control diet or BDSP. The fatty acid composition of palm oil was 43.6% palmitic acid, 4.6% stearic acid, 37.1% oleic acid, 10.4% linoleic acid and 0.2% α -linolenic acid. All animals had free access to water. Feed intake was recorded daily and animals were weighed monthly. Steers were fed the experimental diets for 10 mon until they attained an average BW of 753 \pm 11.5 kg.

Performance and carcass characteristics

Steers were fasted for 24 h and slaughtered at a commercial abattoir. Intramuscular adipose tissues were obtained from the 8th to 11th rib section as described previously (Choi *et al.*, 2016) and immediately snap frozen in liquid nitrogen. Carcass yield and quality including mar-

Table 1. Ingredients and chemical composition (percent, DM basis) of the experimental diets for the Hanwoo steers in mid fattening and late fattening period

Feed ingredients	Mid-fattening (400-500 kg)	Late-fattening (~750 kg)
Ingredient, % as fed		
Coarse cracked Corn	38.6	46.9
Wheat bran	20.7	12.2
Corn gluten feed	30	30
Salt	0.5	0.5
Cottonseed hulls	0.95	-
Rape seed meal	3.2	4.3
Limestone	1.6	1.6
Vitamin premix ¹	0.1	0.1
Sodium bicarbonate	0.4	0.4
Molasses	4.0	4.0
Chemical composition (% DM basis)		
Moisture	11.60	11.76
CP ²	12.96	12.34
Fat	2.62	2.57
NDF ³	24.36	21.41
TDN ⁴	76.02	76.97
NEg, Mcal/CWT ⁵	56.50	58.00

¹Vitamin A, 2,650,000 IU/kg; Vitamin D, 3,530,000 IU/kg; Vitamin E, 1,050 IU/kg; Niacin, 10,000 mg/kg; Mn, 4,400 mg/kg; Zn, 4,400 mg/kg; Fe, 13,200 mg/kg; Cu, 2,200 mg/kg; I, 440 mg/kg; Co, 440 mg/kg; Butylated hydroxy toluene, 10,000 mg/kg. ²Crude Protein. ³Neutral Detergent Fiber. ⁴Total Digestible Nutrients. ⁵Net Energy, Carcass Weight.

bling score were graded by meat graders using criteria provided by Livestock Quality Assessment (KAPE, 2007). Meat color attributes Hunter L (lightness), a (redness) and b (yellowness) and CIE $L^*a^*b^*$ were determined by Chroma Meter (CR-10, Minolta Corporation, Ltd., Japan). Each sample was measured at 4 different locations on the muscle surface and an average score was taken.

Gene expression analysis with Real-time PCR

Real-time PCR was conducted as previously described (Park *et al.*, 2009). Briefly, mRNA from i.m. adipose tissue was isolated using TRIzol reagent (Invitrogen, USA) and cDNA was made using the random primed cDNA synthesis. Real-time quantification of *AMPK α* , *CTP1 β* , *C/EBP β* , *PPAR γ* , and *SCD* transcripts was performed with the 7500 Fast Real-Time PCR System (Applied Biosystems, USA). Final reaction mix included 1X Fast SYBR Green Master Mix (Applied Biosystems, USA). The relative amount of mRNA was first normalized to ribosomal protein S9 (*RPS9*) and then expression of each transcript from palm oil group was normalized with that from the control group. Target primer sets designed using Primer-

BLAST (National Center for Biotechnology Information) for these genes were: forward 5'-ACC ATT CTT GGT TGC TGA AAC TG-3' and reverse 5'-CAC CTT GGT GTT TGG ATT TCT G-3' for *AMPK α* ; forward 5'-TGG CTC TGG ATG AGG AGT CT-3' and reverse 5'-GGA CTT GTC GAA CCA CCT GT-3' for *CTP1 β* ; forward 5'-CCA GAA GAA GGT GGA GCA ACT G-3' and reverse 5'-TCG GGC AGC GTC TTG AAC-3' for *C/EBP β* ; forward 5'-ATC TGC TGC AAG CCT TGG A-3' and reverse 5'-TGG AGC AGC TTG GCA AAG A-3' for *PPAR γ* ; forward 5'-TGC CCA CCA CAA GTT TTC AG-3' and reverse 5'-GCC AAC CCA CGT GAG AGA AG-3' for *SCD*; and forward 5'-GAG CTG GGT TTG TCG CAA AA-3' and reverse 5'-GGT CGA GGC GGG ACT TCT-3' for *RPS9*. Relative standard curves containing 0.2-200 ng of cDNA were used to determine primer efficiency, which ranged from 97 to 106%.

Fatty acid composition of intramuscular adipose tissue

Approximately 100 mg of intramuscular adipose tissue was isolated from loin muscle at slaughter. Total lipids were extracted by the method (Folch *et al.*, 1957). Adipose tissue lipids were extracted in chloroform:methanol (2:1, vol/vol) and fatty acid methyl esters (FAME) were analyzed by gas chromatography according to 2013 (Choi *et al.*, 2013). FAME were analyzed by GC-FID (model CP-3800 equipped with a CP-8200 auto-sampler, Varian Inc, USA). Separation of FAME was accomplished on a fused silica capillary column (100 m \times 0.25 mm ID; model CP-3800, Varian Inc, USA) 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. An authentic standard (GLC 68D, Nu-chek Prep, USA) was used to confirm the identity of each peak.

Statistical analysis

Data were analyzed by *t*-test. Probability values less than 0.05% were considered significant. Each animal was considered an experimental unit.

Results

Growth performance and carcass quality traits

There was no significant difference in growth perfor-

Table 2. Performance and carcass quality traits of control and supplementary palm oil (5%) fed to Hanwoo steers

Items	Control ¹	Palm oil	Pooled SEM ²
Performance			
Initial BW, kg	549.3	548.8	8.37
Final BW, kg	749.5	756.0	11.46
Total BW gain, kg	200.3	207.3	7.60
Average daily gain, kg	0.626	0.648	0.024
Carcass quality traits			
Live weight, kg	749.5	756.0	11.46
Carcass weight, kg	453.3	454.3	6.91
Backfat thickness, mm	18.3	17.0	1.6
Loin muscle area, cm ²	100.0	82.0	4.67
Yield index	62.1	62.2	1.16
Marbling score ³	6.7	6.0	0.42

¹Control feed was formulated based on Korean Feeding Standard for Hanwoo. ²Pooled standard error of the mean over all samples (n= 14). ³9 = most abundant, 1 = devoid.

Table 3. Effect of palm oil supplementation on the instrumental color values of meat

	Control	Palm oil	SEM ¹
CIE L*	38.09±0.78	39.19±0.64	0.4774
a*	18.32±0.72	19.03±0.98	0.4718
b*	7.73±0.49	7.8±0.06	0.3049
Hunter L	31.86±0.69	32.84±0.57	0.4224
a	14.21±0.53	14.94±0.89	0.4177
b	5.09±0.30	5.2±0.42	0.2011

¹Standard error of the mean

mance including BW and average daily gain (ADG) between treatment groups (Table 2). Carcass quality traits

Table 4. Fatty acid profile of intramuscular adipose tissues from Hanwoo steers fed on control and supplementary palm oil (5%) diets

Fatty acid, g/100 g total fatty acids	Control ¹	5% Palm oil	Pooled SEM ²
14:0	2.92	2.50	0.06
16:0	27.15	26.31	0.28
16:1n-7	4.42	4.11	0.08
18:0	11.55	12.17	0.16
18:1n-9	51.17	51.65	0.34
18:1n-7	0.11	0.13	0.003
18:2n-6	1.92	2.38	0.02
18:3n-6	0.04	0.05	0.007
18:3n-3	0.07	0.08	0.007
20:1n-9	0.54	0.45	0.008
20:4n-6	0.12	0.12	0.001
Total SFA	41.61	40.98	1.50
Total MUFA	56.24	56.33	1.57
Total PUFA	2.15	2.69*	0.23
SCD index	0.385	0.339	

¹Control feed was formulated based on Korean Feeding Standard for Hanwoo. ²Pooled standard error of the mean (n=14). **p*<0.05, significantly different from control.

also were unaffected by supplemental of palm oil. Supplemental palm oil also did not affect meat color attributes (Table 3). There was no difference in feed intake for both control and palm oil groups (data not shown).

Adipogenic gene expression in intramuscular adipose tissue

Supplemental palm oil increased (*p*<0.05) *AMPKα* and

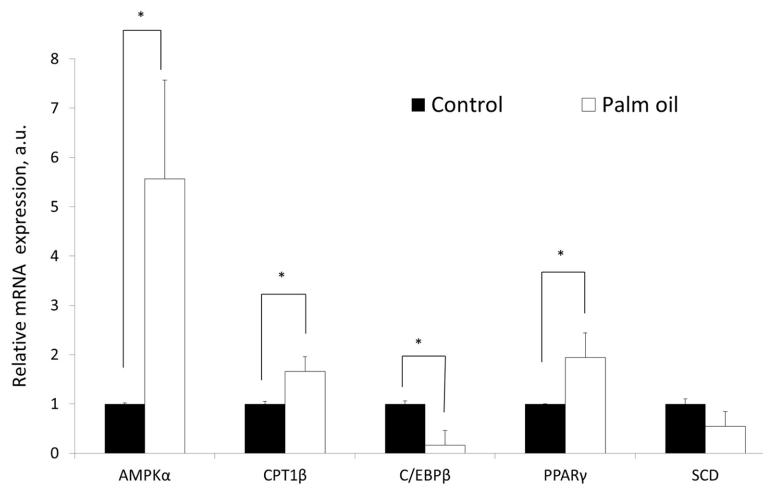


Fig. 1. Relative mRNA levels of AMP-activated protein kinase-α (*AMPKα*), carnitine palmitoyl-transferase-1β (*CPT1β*), CAAT/enhancer binding proteins β (*C/EBPβ*), peroxisome proliferator-activated receptor-γ (*PPARγ*) and stearoyl-CoA desaturase (*SCD*) in i.m. adipose tissue from control and palm oil-fed Hanwoo steers. **p*<0.05.

CPT1 β gene expression in i.m. adipose tissue relative to control i.m. adipose tissue (Fig. 1). *C/EBP β* expression was lower and *PPAR γ* expression was higher (both $p < 0.05$) in i.m. adipose tissue of palm oil-fed steers than in i.m. adipose tissue of control steers. *SCD* gene expression was not affected by palm oil supplementation ($p > 0.05$).

Fatty acid composition of intramuscular adipose tissue

Myristic acid (14:0), palmitic acid, stearic acid, oleic acid, cis-vaccenic acid (18:1n-7), linoleic acid, γ -linoleic acid (18:3n-6), and α -linolenic acid were unaffected by supplemental palm oil (Table 4; $p > 0.05$). There also was no difference in eicosenoic acid (20:1n-9) or arachidonic acid (20:4n-6) between treatments. The proportion of total PUFA was higher ($p < 0.05$) in i.m. adipose tissue of palm oil-fed steers than in control adipose tissue. Intramuscular adipose tissue of palm oil-fed steers had greater ($p < 0.05$) levels of $\omega 3$ fatty acids but lower ($p < 0.05$) $\omega 6:\omega 3$ ratio than control group.

Discussion

The production of Hanwoo beef cattle differs from beef cattle production in the U.S. in that Hanwoo cattle are fed to heavier BW (approximately 750 kg vs 550 kg), and energy density of the diet is increased in stages in the Korean beef cattle production system to ensure adequate i.m. fat accumulation. However, the long-term feeding of Hanwoo beef cattle results in poorer feed efficiencies and increased feed costs. It is possible that agri-byproducts such as palm oil could reduce feed costs for the Hanwoo beef cattle industry, but there is little information available about the effects of palm oil on growth, carcass composition, and meat composition of beef cattle.

Because it is readily available, soybean oil has been tested extensively in beef cattle production systems. Engle *et al.* (2000) reported that 4% supplementary soybean oil had no effect on average daily gain (ADG), average daily feed intake (ADFI), or gain-to-feed ratio (G:F), but depressed marbling scores. Ludden *et al.* (2009) later reported that 5% supplemental soybean oil had no effect on production or carcass traits of Gelbvieh x Angus crossbred steers. In a study with Korean Hanwoo cattle, Song *et al.* (2010) reported that 7% supplemental soybean oil (DM basis) depressed feed intake, ADG, and G:F, and we subsequently reported that 3% soybean oil depressed ADG, and the G:F in Angus crossbred steers (Choi *et al.*, 2013).

It is likely that the high concentration of PUFA in soybean oil depresses ruminal fermentation, reducing its efficacy as a feed supplement for beef cattle.

Previous studies with lambs demonstrated that supplemental palm oil increased backfat thickness (Lough *et al.*, 1993; Solomon *et al.*, 1992). Relative to soybean oil-fed steers, palm oil-fed Angus crossbred steers had greater marbling scores and slightly greater 12th rib fat thickness (Choi *et al.*, 2013). Supplemental palm oil promoted lipid synthesis *in vitro* and increased lipogenic enzyme activities and adipocyte sizes in s.c. adipose tissue (Choi *et al.*, 2013; Nestel *et al.*, 1978). In the current study, palm oil supplementation had no effect on carcass quality traits or feed efficiency of Hanwoo steers, nor did it affect meat color attributes.

AMPK α , *C/EBP β* , *CPT1 β* , *PPAR γ* , and *SCD* were selected as genetic markers for differentiation and metabolism of adipose tissue based on previous research (Smith *et al.*, 2012). As in our study with Angus crossbred cattle (Choi *et al.*, 2016), supplemental palm oil decreased *C/EBP β* gene expression and caused a small decrease in *SCD* gene expression. The marked increase in *AMPK α* gene expression in i.m. adipose tissue in response to supplemental palm oil is of interest because AMPK regulates many metabolic processes including glucose uptake, fatty acid synthesis, and lipid oxidation (Park *et al.*, 2009). AMPK activity decreases malonyl-CoA concentrations by phosphorylating and thereby inhibiting acetyl CoA carboxylase, the rate-limiting enzyme of malonyl-CoA synthesis, and by enhancing the degradation of malonyl-CoA via malonyl CoA decarboxylase (Thomson and Winder, 2009). Malonyl-CoA is an allosteric inhibitor of CPT1, the enzyme that controls the transfer of long chain fatty acyl-CoA into the mitochondria. The markedly increased *AMPK α* and *CPT1 β* gene expression caused by palm oil supplementation should have promoted fatty acid oxidation, but there was only a small, nonsignificant reduction in backfat thickness in the palm oil-fed steers relative to the control steers. We recently demonstrated that SFA strongly up-regulated *AMPK α* gene expression in cultures of i.m. preadipocytes and 3% supplemental palm oil increased plasma palmitic acid over 40% in beef cattle (Choi *et al.*, 2016). However, unlike the results of the current study, supplemental palm oil decreased *AMPK α* gene expression in s.c. adipose tissue of Angus crossbred steers relative to control steers (Choi *et al.*, 2016), which was consistent with the small increases in 12th rib fat thickness and marbling scores observed in these cattle (Choi *et al.*, 2013).

In the current study, *C/EBP β* gene expression was decreased but *PPAR γ* gene expression was increased in i.m. adipose tissue by palm oil. The lack of significant effects of palm oil on carcass adiposity indicated that 5% supplementary palm oil administration can alter adipogenic gene expression, but not sufficiently to elicit changes in adipose tissue accretion. This is in spite of the fact that the Hanwoo steers were fed supplemental palm oil for 10 mo.

Palm oil supplementation caused only a small decrease in *SCD* gene expression in the current study, but this was of similar magnitude to the depression in *SCD* gene expression in s.c. adipose tissue caused by palm oil in Angus crossbred cattle (approximately 25%; Choi *et al.*, 2016). Similarly, supplemental palm oil decreased the SCD index (ratio of palmitoleic acid:stearic acid) from 0.49 to 0.32 in the previous study (Choi *et al.*, 2016) and from 0.39 to 0.34 in the current study. Adipose tissue is the primary site for SCD activity (St John *et al.*, 1991) and *SCD* gene expression increases with time on a finishing diet (Adams *et al.*, 2010). Rams fed a diet containing palm oil had significantly more SFA in their i.m. lipid compared to control lambs, mainly due to the high concentration of palmitic acid in palm oil (Solomon *et al.*, 1992). However, the previous and the current study have demonstrated that palm oil has little effect on the proportions of SFA in bovine adipose tissue (Partida *et al.*, 2007). However, palm oil supplementation to Hanwoo steers increased i.m. adipose tissue PUFA, which might be responsible for the small depression in *SCD* gene expression.

Conclusions

It is not possible to make direct comparisons of the current study to our previous studies of the effects of palm oil on gene expression in adipose tissue of Korean Hanwoo and U.S. beef cattle. In previous studies (Choi *et al.*, 2013; Choi *et al.*, 2016), Angus crossbred steers were fed 3% palm oil for 10 wk, rather than 10 mo, and the Angus crossbred steers weighed approximately 570 kg at slaughter, rather than 750 kg for the Hanwoo steers. Adipose tissue MUFA are higher in Hanwoo steers than in U.S. domestic cattle (Smith *et al.*, 2009), and adipose tissue MUFA increase with time on a finishing diet in beef cattle (Chung *et al.*, 2006; Kim *et al.*, 2016). For these reasons, i.m. adipose tissue from Hanwoo steers of the current study contained over 55 g MUFA per 100 g total fatty acids, versus 40 g MUFA per 100 g total fatty acids in i.m. adipose tissue of Angus crossbred steers (Choi *et al.*, 2016). Simi-

larly, it has not been possible to modify carcass composition with supplemental palm oil, even though this and our previous studies documented significant changes in adipogenic gene expression. It is likely that other factors, such as time on feed and other dietary components, attenuated any effects on carcass adiposity suggested by the observed changes in adipose tissue gene expression. We can conclude, however, that palm oil, an agri-byproduct in Korea, can be used as a feed supplement without negative effects on Hanwoo beef cattle production or carcass characteristics.

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