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ORIGINAL ARTICLE

Effects of dietary corn oil and vitamin E supplementation on fatty acid profiles and expression of acetyl CoA carboxylase and stearoyl-CoA desaturase gene in Hu sheep

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ABSTRACT

This study was conducted to assess the effects of dietary corn oil and vitamin E supplementation on fatty acid (FA) profiles and abundances of acetyl-CoA carboxylase (ACC) and Δ^9 stearoyl-CoA desaturase (SCD) mRNA of Hu sheep. Animals were allocated to three dietary treatments: basal and supplemented with 3% corn oil (CNO), or CNO plus 500 mg/kg vitamin E (COE). The experiment lasted for 10 weeks. No differences were observed in growth performance and carcass qualities among the three treatments ($P > 0.05$). Feeding CNO and COE diets increased polyunsaturated FAs including *cis* 9 *trans* 11 conjugated linoleic acid, and decreased saturated FA in *longissimus* muscle ($P < 0.05$). The mRNA abundances of ACC and SCD as detected by real-time PCR were reduced ($P < 0.05$) in liver and subcutaneous fat by supplementary oil, while the SCD mRNA level in *longissimus* muscle was also reduced ($P < 0.05$). Inclusion of vitamin E did not have further effects on mRNA abundances of these two enzymes. It is suggested that dietary corn oil supplementation may reduce FA biosynthesis and influence FA profiles in Hu sheep through decreased expression of both ACC and SCD genes.

Key words: *Δ^9 stearoyl-CoA desaturase, acetyl-CoA carboxylase, corn oil, fatty acid, Hu sheep.*

INTRODUCTION

Consumers are becoming aware of the relationships between diet and health, which is impacting on the demand for foods containing functional components that play important roles in health maintenance and disease prevention (Scollan *et al.* 2006). Many factors such as nutrition, age and species have effect on the fatty acid (FA) composition of ruminant adipose tissues (Aurousseau *et al.* 2004; Gillis *et al.* 2004). Despite the high levels of ruminal biohydrogenation of dietary polyunsaturated FA (PUFA), nutrition is the major route for increasing the content of beneficial FA. Manipulation of FA content through dietary lipid supplementation may provide producers with increased PUFA and conjugated linoleic acid (CLA); (Griinari *et al.* 2000; Zheng *et al.* 2005; Choi *et al.* 2007). Increase in the content of PUFA can influence shelf life and sensory attributes of the meat (Lee *et al.* 2007). Vitamin E (VE) is necessary to help stabilize the effects of incorporating high levels of PUFA into meat (Scollan *et al.* 2006; Lee *et al.* 2007). In our previous study (Chen *et al.* 2008), dietary supplementation of soybean oil and VE decreased the concentrations of short- and medium-chain FA such as $C_{8:0}$, $C_{14:0}$ and $C_{15:0}$, and increase *trans-11* vaccenic acid (TVA) and *cis 9 trans 11* CLA in lamb meat. Although there have been numerous studies about the influence of the dietary oil on the FA compositions in ruminants (Dohme *et al.* 2003; Nuernberg *et al.* 2005), limited information is available in lambs (Choi *et al.* 2007).

The FA of ruminant adipose tissue can either be biosynthesized *de novo* from acetate and glucose, or from hydrolysis of circulating plasma triglyceride (Cryer 1981). In general, lipogenesis is dependent upon energy status, and enzymes such as acetyl-CoA carboxylase (ACC) and FA synthase (Gillis *et al.* 2004). In adipose tissues, the amount of FA biosynthesized *de novo* from acetate, which was catalyzed by ACC, was higher than from glucose (Smith & Crouse 1984;

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Chung *et al.* 2000). Lipid supplementation may negatively affect lipogenesis in ovine subcutaneous adipose tissue and in mammary tissue of cows (Vernon 1976; Cryer 1981; Bauman & Griinari 2003), while FA profiles are not significantly influenced by dietary oil supplementation (Gillis *et al.* 2004; Choi *et al.* 2007). Additional research is needed to assess the effects of dietary oil supplementation on FA biosynthesis and activities of lipogenic enzymes such as ACC.

Δ^9 stearoyl-CoA desaturase (SCD) is a microsomal membrane bound, iron-containing enzyme required for the biosynthesis of unsaturated fatty acids (Enoch *et al.* 1976). SCD catalyze insertion of a *cis* double bond between carbons 9 and 10 of palmitoyl- and stearoyl-CoA to form the palmitoleoyl- and oleoyl-CoA, respectively (Yeom *et al.* 2003). This enzyme is also responsible for the desaturation of TVA to *cis-9*, *trans-11* CLA. The expression of SCD has been known to be regulated by dietary conditions and environmental factors such as age (Martin *et al.* 1999), insulin (Daniel *et al.* 2004a), glucose (Jones *et al.* 1998), and CLA (Choi *et al.* 2000). Some PUFA, including linoleic acid, are thought to inhibit SCD by down-regulating its gene expression (Yang *et al.* 1999).

Information is limited on the influence of dietary oil on gene expression of two key enzymes, ACC and SCD, in sheep (Daniel *et al.* 2004b). The purpose of this study was to assess the effects of dietary corn oil and VE supplementation on carcass quality, fatty acid profiles of the *longissimus* muscle, the abundances of ACC and SCD mRNA in liver, subcutaneous fat and *longissimus* muscle of Hu sheep, and to analyze the relationship between the FA profile and the two key enzyme mRNA abundances.

MATERIALS AND METHODS

Animals and experiment design

This experiment was approved by the Institutional Animal Care and Use Committee at Zhejiang University and conducted in accordance with the National Institute of Health guidelines for the care and use of experimental animals.

Twenty-four male Hu sheep, with initial body weight of 12.85 kg at age of 45 days, were allocated by live weight to three dietary treatments: (i) basal (control), (ii) supplemented with 3% corn oil supplemented (CNO), or (iii) 3% corn oil plus 500 mg/kg VE (COE). All the diets with roughage to concentrate ratio at 60:40 (DM base) were formulated to be isoenergetic and isonitrogenous (Table 1). The animals were offered feed almost *ad libitum*, but the feed intake was controlled to be similar among the three groups to avoid the differences in measured parameters resultant from growth rate. Lambs were housed individually in raised-floor pens bedded on wood, and had free access to fresh water. During the 2 weeks of adaptation and the 10 week experimental period, the roughage and concentrate were mixed and supplied twice a day at 08.00 hour and 15.00 hour in an equal quantity. Animal live weight was determined biweekly and data were used to calculate average daily live weight gain. All weighings were conducted at the same time of day (08.00 hour) to minimize the effects of diurnal variations in feed intake.

Table 1 Ingredients and chemical composition of experimental diets

Items	Diet†		
	Control	CNO	COE
Ingredient (g/kg DM)			
Chinese ryegrass hay	600	600	600
Corn	206	62	62
Wheat bran	20	200	200
Soybean meal	132	20	20
Rapeseed meal	15	53	53
NaCl	5	5	5
CaH_2PO_4	12	12	12
Urea	0	8	8
Mineral and vitamin premix‡	10	10	10
Corn oil	0	30	30
α-Tocopheryl acetate (mg/kg)	0	0	500
Chemical composition (g/kg DM)			
Crude protein	127	127	127
Ether extract	33	36	36
Neutral detergent fibre	391	442	442
Acid detergent fibre	232	250	250
Digestible energy (MJ/kg DM)	10.5	10.6	10.6

†CNO: 3% corn oil supplemented diet; COE: 3% corn oil plus 500 mg/kg vitamin E supplemented diet. ‡Mineral and vitamin premix (per kg): Zn 100 mg, Fe 90 mg, Mn 20 mg, Cu 10 mg, I 0.3 mg, Se 0.2 mg, Vitamin A 5000 IU, Vitamin D 700 IU, Vitamin E 30 IU, Vitamin B12 0.03 mg, riboflavin 10 mg, D-pantothenic acid 15 mg, niacin 25 mg.

The experiment was carried out at the same time as another study (Chen *et al.* 2008), and both experiments had the same control animals. Therefore, the data for control group were similar to those in the previous study (Chen *et al.* 2008).

Sample collection and analyses

At the end of experiment, blood samples were collected by jugular vein puncture, and serum metabolites were analyzed as described previously (Chen *et al.* 2008). The animals were all electrically stunned and slaughtered. Samples of liver, subcutaneous fat and *longissimus* muscle were taken immediately after animals were slaughtered, stored in liquid nitrogen until frozen, and kept at −70°C until analyzed. The growth performance, carcass quality parameters (including pH values at 1 h and 24 h, GR value and meat color), and FA profiles of *longissimus* muscle were analyzed as described previously (Chen *et al.* 2008).

Tissue total RNA preparation

A sample of 100 mg of each tissue (liver, subcutaneous fat and *longissimus* muscle) was homogenized in Trizol Reagent (Invitrogen, NY, USA). Total RNAs were extracted according to the manufacturer's instructions, and the quantity and purity were determined by measurement of absorbance at 260 and 280 nm using the spectrophotometer (Eppendorf, Hamburg, Germany).

Semi-quantitative real-time PCR analysis

Oligonucleotide primers for the ACC, SCD and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) were

Table 2 SYBR Green I primer pairs sequence of acetyl-CoA caboxylase, stearoyl-CoA desaturase and GAPDH gene segment

Gene name	Sequence	Length (bp)
Acetyl-CoA caboxylase		
Forward primer	CGGAAGGGACAGTAGAAATCA	94
Reverse primer	AGTCGCTCAGCCAAGTGGA	
Δ^9 stearoyl-CoA desaturase		
Forward primer	ACTAGATTTATCCGACCTAAGAGC	113
Reverse primer	GATACCACGGCACGAGTGT	
GAPDH (glyceraldehyde-3-phosphate dehydrogenase)		
Forward primer	TCCCTCCACGATGCCAAAG	74
Reverse primer	ATGCCTCCTGCACCACCAA	

designed based on the highly conserved amino acid sequences of *C. hircus* (ACC: DQ 370054), *O. aries* (ACC: NP 001009256; SCD: NP 998946; GAPDH: NP 001075722), *B. taurus* (ACC: NP 776649, SCD: 776384; GAPDH: NP 001029206), *H. sapiens* (ACC: NP 942133; SCD: 005054), *M. musculus* (ACC: XP 001111823) and *S. scrofa* (ACC: NP 579938; SCD: XP 001500414; GAPDH: NP 002037), which were reported in the National Center for Biotechnology Information (NCBI). The mRNA abundances of ACC and SCD were detected by quantitative real-time PCR using the iCycler apparatus (Bio-Rad). iQ™ SYBR Green supermix PCR kit (Bio-Rad) was used for real-time monitoring of amplification consisting of an initial denature at 95°C for 10 s followed by 40 cycles of 95°C for 10 s and 62°C for 20 s. All of the SYBR Green I primer pairs were designed according the cDNA fragments cloned (Table 2). The real-time PCR amplification mixtures contained 1 μL cDNA (1 in 50 dilution), 2 × SYBR Green I Master Mix buffer (12.5 μL), and 0.5 μL gene specific forward and reverse primers (10 μmol/L). Accurate amplification of the target amplicon was checked by performing a melting curve. The ACC and SCD mRNA expressions were calculated by relative threshold cycle numbers (CT) toward the GAPDH housekeeping gene following the formula: $2^{-(\Delta CT\ ACC\ or\ SCD - \Delta CT\ GAPDH)}$

Statistical analyses

All data were analyzed as a complete randomized, repeated measure designs, with individual lambs as the experimental units (SAS 1997). One-way ANOVA was used to determine the effects of diet treatment. Significance was determined at $P < 0.05$ (Tukey's test).

RESULTS

Growth performance, carcass characteristics and serum metabolites

Results of growth performance and carcass characteristics are given in Table 3. Average feed intakes, daily gains and carcass weights were not significantly different among control, CNO and COE animals ($P > 0.05$). There were also no significant differences in pH values at 1 h and 24 h and the GR value among three treatments ($P > 0.05$). The meat color L* was higher ($P < 0.05$) in lambs fed CNO and COE diets than in the control.

The effects of dietary corn oil and VE supplementation on serum metabolites are shown in Table 4. The concentrations of total cholesterol, high density

Table 3 Effect of dietary supplementation of corn oil and vitamin E on growth performance and carcass characteristics in Hu sheep

Items	Diet†			
	Control‡	CNO	COE	SEM
Diet intake (g DM/day)	733	729	712	13.5
Initial body weight (kg)	13.06	12.93	12.57	0.651
Average daily gain (g)	106	103	105	7.8
Carcass weight (kg)	8.68	8.35	8.14	0.812
pH value at				
1 h	6.47	6.49	6.50	0.575
24 h	5.60	5.63	5.71	0.519
Meat color§				
*L**	28.84[b]	40.61[a]	34.39[a]	1.046
*a**	22.67	14.95	18.69	2.348
*b**	11.05	8.59	7.94	0.759
GR value	1.03	1.01	1.05	0.104

†CNO: 3% corn oil supplemented diet; COE: 3% corn oil plus 500 mg/kg vitamin E supplemented diet. ‡The data were from Chen *et al.* (2008). §Measured by color meter. *L**: lightness; a*: redness; *b**: yellowness. GR value: the depth of muscle and fat tissue from the surface of the carcass to the lateral surface of the 12th rib 110 mm from the midline. [a,b]Means with different letters within the same row differ at $P < 0.05$.

Table 4 Effect of dietary supplementation of corn oil and vitamin E on serum metabolites in Hu sheep

Iems	Diet†			
	Control‡	CNO	COE	SEM
Total protein (g/L)	57.3	62.8	62.3	0.94
Albumin (g/L)	33.0	35.5	34.0	0.45
Triglyceride (mmol/L)	0.25	0.32	0.29	0.02
Cholesterol (mmol/L)				
Total	1.58[b]	2.53[a]	2.43[a]	0.14
High density lipoprotein-cholesterol	1.04[b]	1.70[a]	1.72[a]	0.08
Low density lipoprotein-cholesterol	0.51	0.74	0.63	0.05
Non-esterified fatty acids (mmol/L)	331[b]	452[a]	490[a]	10.8
Glucose (mmol/L)	4.31[a]	3.09[b]	2.91[b]	0.15
Urea nitrogen (mmol/L)	7.30	7.55	7.98	0.71

†CNO: 3% corn oil supplemented diet; COE: 3% corn oil plus 500 mg/kg vitamin E supplemented diet. ‡The data were from Chen *et al.* (2008). [a,b]Means with different letters within the same row differ at $P < 0.05$.

lipoprotein-cholesterol (HDL-C) and non- esterified FA (NEFA) increased, while glucose decreased significantly in both CNO and COE diets compared to the control ($P < 0.05$). The contents of other serum metabolites showed no significant differences among the three groups ($P > 0.05$).

FA profiles of *longissimus* muscle

The profiles of FA in *longissimus* muscle from lambs fed different diets are presented in Table 5. Dietary oil supplementation did not have marked effect on total lipid concentration of meats ($P > 0.05$). The dominant three fatty acids, oleic ($C_{18:1}$), palmitic acid ($C_{16:0}$), and stearic acid ($C_{18:0}$

FAs, *de novo* synthesis from precursors, and desaturation rate by SCD (Choi *et al.* 2007). In the present study, supplementation of linoleic-rich corn oil (53%) to the diet increased PUFA and decreased the SFA in *longissimus* muscle of Hu sheep (Table 5). Raes *et al.* (2004) suggested that the PUFA to SFA ratio is mainly influenced by genetics, and less by nutrition, but even so the effect of nutrition on the ratio is important (Demirel *et al.* 2006). The VE has been fed to ruminants to protect the diet PUFA against biohydrogenation, and to increase the potential for intestinal absorption (Scollan *et al.* 2006; Lee *et al.* 2007). In the current study, COE-fed lambs showed more PUFA and less SFA than those on CNO.

The contents of TVA and *cis 9 trans 11* CLA were also increased by supplementary corn oil, similar to the result with soybean oil (Chen *et al.* 2008). Generally, dietary linoleic acid are mostly converted to monounsaturated fatty acid, such as oleic acid (C18:1 n-9) and TVA, and to SFA (such as stearic acid, $C_{18:0}$) through the process of biohydrogenation in rumen. Scollan *et al.* (2001) reported that about 92% of linolenic acid and 90% of linoleic acid were biohydrogenated in cattle. Only small amounts of dietary linoleic acid can escape from rumen biohydrogenation and then be absorbed and synthesized to tissular FA, thereby contributing to the content of meat PUFA (Demirel *et al.* 2006).

Serum metabolites

The serum concentrations of total cholesterol and HDL-C were increased by oil supplementation (Table 4). Dietary lipids have the capacity to regulate cholesterol and lipoprotein metabolism in a manner dependent on the FA they contain (Salter & Tarling 2007). Diets rich in SFA are associated with elevated plasma concentrations of LDL-C, while those rich in PUFA reduced it. Wang *et al.* (2006) observed slightly increased contents of cholesterol and HDL-C proportion in intramuscular regions when a soybean oil-supplemented diet was fed to steers, which is in consistent with the present result.

The serum NEFA increased, but glucose decreased significantly in animals fed the CNO or COE diets when compared to the control ($P < 0.05$). It is well established that the ratio of dietary concentrate to forage may affect major volatile FA such as acetate and propionate in the rumen (Beaulieu *et al.* 2002). In this study, when the lambs were fed the control diets containing high levels of easily fermentable carbohydrates such as ground maize (Table 1), large quantities of serum glucose were formed from propionate produced in the rumen (Demirel *et al.* 2004), while the animals fed CNO and COE may absorb more volatile FA in the intestines.

ACC gene expression and FA synthesis

Adipose tissues including subcutaneous and intramuscular are the primary sites of lipogenesis in ruminants, while the liver may play an important role in the remodeling of FAs (Gillis *et al.* 2004). The FA in adipose tissues can be either biosynthesized *de novo*, using acetate by ACC and FAS, or be created from hydrolysis of circulating plasma triglycerides (Cryer 1981). In the present study, the abundance of ACC mRNA was reduced markedly in liver and subcutaneous fat by dietary corn oil supplementation. This lead to reduced FA *de novo* boisynthesis in adipose tissues, probably resulting in decreased concentrations of short- and medium-chain FAs in oil supplemented lambs (Table 5). Cryer (1981) and Vernon (1976) also found that lipid supplementation negatively affects the activities of lipogenic enzymes and *de novo* fatty acid synthesis in ovine subcutaneous adipose tissues. The decrease in proportion of medium-chain FA may be due to decreases in gene expression and activity of lipogenic enzymes such as ACC and fatty acid synthase (Kim *et al.* 2007). Madsen *et al.* (2005) indicated that dietary n-3 PUFAs may decrease adipose tissue mass and suppress the development of obesity in rodents by targeting a set of key regulatory transcription factors involved in adipogensis, such as ACC, SCD and FA synthase, and by enhanced expression of lipolytic genes. However, Gillis *et al.* (2004) observed that the effects of supplemental rumen-protected CLA or soybean oil were not significant on FA composition of adipose tissues in beef cattle. Choi *et al.* (2007) suggested that synthesis of short- and medium-chain FAs were not suppressed, and *in vitro* lipogenesis of subcutaneous adipose tissue might be enhanced by supplementation with oils. Therefore, the depressing effect of dietary oil on *de novo* FA biosynthesis is inconsistent and further study is needed to clarify it.

The abundance of ACC mRNA in *longissimus* muscle in CNO and COE-fed animals was not reduced significantly compared with the control (Table 6), indicating that response of ACC genes to supplemental oil was in a tissue-specific manner. This may explain the conflicts mentioned above that supplementation of oil to ruminant diets had different effects on FA biosynthesizes and ACC mRNA levels in different studies, at least to a certain extent.

SCD gene expression and FA profiles

The SCD plays an important role in transformation of SFA into unsaturated FA and catalyzation of desaturation of TVA to *cis 9 trans 11* CLA (Yeom *et al.* 2003). It has been intensively researched in humans and mice, focused mostly on human metabolic syndromes such as obesity, hyperinsulinemia and arteriosclerosis (Biddinger *et al.* 2005). Works in rodents have shown that PUFA inhibit liver and embryo 3T3-L1 adipocyte

SCD gene expression (Ntambi *et al.* 1988; Waters & Ntambi 1996). The SCD gene expression is directly modulated by sterol regulatory element binding protein-1, and also regulated by other factors such as PUFAs through the interaction with this binding protein (Le Lay *et al.* 2002; Daniel *et al.* 2004b). Løchsen *et al.* (1997) observed that high-fat diets down-regulated the hepatic level of Δ^9 SCD mRNA in rats, and that inclusion of fish oil and soybean oil decreased the enzymatic activity by 85 and 50%, and the abundance of SCD mRNA by 90 and 60%, respectively. These results support the present finding that the expression levels of SCD mRNA were reduced significantly by dietary oil supplementation in subcutaneous fat, *longissimus* muscle and liver in Hu sheep (Table 6).

To date, limited information is available on the effect of dietary PUFA on SCD gene expression in ruminants. Moreover, studies on this topic in ruminants mainly focus on the effect of CLA on SCD enzyme activity and mRNA expression, and the results vary. Choi *et al.* (2000) and Baumgard *et al.* (2002) have shown that CLA reduced both SCD enzyme activity and mRNA levels. However, Park *et al.* (2000) observed that CLA decreased the SCD activity directly without change in gene expression. Also, no change was found in SCD mRNA levels by feeding rumen-protected CLA to sheep (Wynn *et al.* 2006).

One purpose of our study was to analyze the relationship between SCD mRNA levels and the FA profiles. In both present and previous studies (Chen *et al.* 2008), corn oil or soybean oil supplemented diets increased the contents TVA and CLA in *longissimus* muscle, but the absolute increase in CLA extent was minor. *Cis* 9 *trans 11* CLA originates from either ruminal biohydrogenation of dietary linoleic acid or endogenous synthesis from TVA by SCD (Yeom *et al.* 2003). There was a positive relationship between TVA and *cis 9 trans 11* CLA in mammary cells and intramuscular lipids (Daniel *et al.* 2004b). The major proportion of *cis* 9 *trans 11* CLA in ruminant products was formed through the action of SCD on TVA, but the higher level of CLA would suppress the expression of SCD gene (Griinari *et al.* 2000). Lipid supplementation may decrease SCD activity in adipose tissues, which in turn would lower the conversion of TVA to CLA (Gillis *et al.* 2004). In the present study, the abundance of SCD mRNA was reduced significantly by dietary corn oil supplementation. These results indicate that dietary lipid supplementation in sheep can increase CLA in adipose tissues by increased conversion of TVA to CLA, while high levels of CLA suppressed the expression of the SCD gene, thus the CLA was increased only marginally.

The expression of SCD mRNA was also regulated by insulin and glucose (Waters & Ntambi 1996; Jones *et al.* 1998). Daniel *et al.* (2004a) shown that insulin significantly increased the expression of ovine SCD gene and synthesis of monounsaturated FA from acetate in cultured ovine adipose tissue explants. The serum glucose contents were decreased in oil supplemented lambs in both present and previous studies (Chen *et al.* 2008). These results may make some contributions to the inhibition of SCD mRNA expression.

In conclusion, feeding corn oil supplemented diets increased PUFA, TVA and *cis 9 trans 11* CLA, and decreased the SFA, the $C_{8:0}$, $C_{14:0}$ and $C_{15:0}$ fatty acids in *longissimus* muscle of Hu sheep. Addition of vitamin E had effects on the FA profiles. The dietary oil may reduce FA biosynthesis and influence FA profiles in Hu sheep through the decreased expression of both ACC and SCD genes

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