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ARTICLE

Association of *−867G>C*, *−877Gdel*, and *Exon 5G>T* Polymorphisms in the Stearoyl-CoA Desaturase (*SCD*) Gene with Fatty Acid Composition in the *M. longissimus dorsi* Muscle of Hanwoo (Korean Cattle)

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Abstract

This study aimed to identify genetic polymorphisms associated with fatty acid composition in Hanwoo beef. In this study, three SNPs (-867G>C, -877Gdel and 878T>C) were detected in SCD gene by DNA sequencing and PCR-RFLP. Statistical analysis revealed that 878T>C SNP was significantly associated with total saturated (p=0.016), unsaturated (p=0.016), and monounsaturated fatty acid (p=0.026) composition. However, the other two SNPs (-867G>C and -877Gdel) that are detected in the regulatory region of the SCD gene have no association with the fatty acid composition of Hanwoo meat. The 878C (alanine type) allele was found to be associated with 2.2% higher monounsaturated fatty acid, 1.5% lower saturated fatty acid, and 1.4% higher unsaturated fatty acid content than those associated with the 878T (valine type) allele. These results indicate that the non-synonymous SNP (878T>C) in the SCD gene could be a causal mutation that contributes to the MUFA variation in Hanwoo beef.

Key words: Hanwoo, monounsaturated fatty acid, saturated fatty acid, single nucleotide polymorphism, stearoyl-CoA desaturase

Introduction

Dietary factors are believed to be linked with the incidence of coronary heart disease. In particular, a high intake of saturated fatty acids can lead to health problems such as coronary artery disease. Of the saturated fatty acids, lauric acid (C12:0), myristic acid (C14:0), and palmitic acid (C16:0) are key risk factors for cardiovascular disease (Keys *et al*., 1974). A study of the relationship between fatty acid composition and LDL-cholesterol levels reported by Woollett *et al.* (1992) proposed that polyunsaturated fatty acid (PUFA) and monounsaturated fatty acid (MUFA) decrease the circulating concentration of LDL cholesterol by elevating hepatic low density lipoprotein (LDL) receptor activity.

Fatty acid composition in cattle can be modified by diet (Kim *et al.*, 2004; Mandell *et al.*, 1998), gender (Zembayashi *et al.*, 1995), age (Lee *et al.*, 2005), breed (Siebert *et al.*, 1996), and genetics (Taniguchi *et al.*, 2004; Zhang *et al.*, 2008). Cattle fed with grass have higher levels of saturated fatty acid than do grain-fed cattle (Melton, 1990). Two Asian *Bos taurus* breeds, Hanwoo (Korean cattle) and Wagyu (Japanese black cattle) have exceptionally high levels of MUFA (oleic acid; C18:1), which may be because of the high grain concentration fed during the finishing period. Daniel *et al*. (2004) showed that a vitamin A-elevated diet results in increased oleic acid composition possibly because vitamin A is an up-regulator of stearoyl-CoA desaturase (SCD) gene expression.

Two genes have been reported in conjunction with the single nucleotide polymorphism (SNP) effect on fatty acid composition in cattle. Zhang *et al*. (2008) reported an effect of a DNA polymorphism in fatty acid synthase (FAS) on fatty acid composition. The g.17924GG genotype was significantly associated with lower saturated fatty acid (myristic acid; C14:0 and palmitic acid; C16:0) and higher MUFA (oleic acid; C18:1) contents in the total and triacylglyceride fraction. Moreover, Taniguchi *et al.* (2004) suggested that the *878C>T* SNP in exon 5 of SCD had a significant effect on MUFA (oleic acid; C18:1) in

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1003 Japanese black cattle. Thus, FAS and SCD are functional candidate genes affecting fatty acid composition of beef meat.

In this study, we resequenced the 5 μ-regulatory and exon 5 regions of the SCD gene and found regulatory and non-synonymous SNPs, which might modify gene expression and protein activity. We then examined the association of the SNP with fatty acid composition in the *M. longissimus dorsi* muscle of Hanwoo steers.

Materials and Methods

Animals and phenotype data

Three different populations were used to study the frequency and associations of the SCD gene polymorphisms. Twenty four unrelated Hanwoo bulls were selected for SNP identification and blood samples were collected at the National Institute of Animal Science (NIAS). The allele frequencies for 7 cattle breeds (Asian and European) were examined using DNA extracted from semen. Phenotypic data and blood samples were obtained from 90 Hanwoo steers representing 9 sires from NIAS for association test of genetic polymorphisms with phenotypic variation.

The steers in the second trial received *ad libitum* intake of a total mixed concentrate diet and rice straw with ratios in the total feed of about 1.5:1, 2:1, and 4.5:1 for the growing period (4-12 mon), finishing period I (13-18 mon), and finishing period II (19-24 mon), respectively. Crude protein (CP) and total digestible nutrients (TDN) of the concentrate were 14-16, 11-13, and 11% and 68-70, 71-73, and 72-73%, respectively, for the three periods. Fatty acid composition in this study was measured in *M. longissimus dorsi* muscle taken from the eleventh and twelfth rib junction. Table 1 summarizes the fatty acid compositions.

Table 1. Summary statistics of the fatty acid composition

Traits (Fatty acid)	Phenotype	
	Mean	SD
Myristic acid (C14:0)	2.91	0.87
Palmitic acid (C16:0)	28.3	4.57
Palmitoleic acid (C16:1)	4.9	1.04
Stearic acid (C18:0)	10.6	1.9
Oleic acid (C18:1)	49.5	7.68
Saturated fatty acid (SFA)	41.9	6.62
Unsaturated fatty acid (UFA)	58.0	8.9
Monounsaturated FA	55.4	8.5
Polyunsaturated FA	2.65	0.65

Identification of regulatory and non-synonymous SNPs in the SCD gene

Genomic DNA was isolated from 24 Hanwoo bulls to identify the SNP of the SCD gene. Three primer sets were designed based on the SCD genomic sequences to amplify the 5'-regulatory and exon 5 regions of the SCD gene (GenBank Acc No. AY241932) using the *Primer3* program (http://frodo.wi.mit.edu/). The primer sets used for the PCR amplification were as follows: SCD-Promoter-F; 5'-CAACGACCCGACGTTCTAAT-3', SCD-Promoter-R; 5'-CCTCGGCTTCTCTTACATCG-3', and SCD-Exon5-F; 5'-ATGTATGGATACCGCCCTTATGAC-3', SCD-Exon5-R; 5'-TTCTGGCACGTAACCTAATACCCTAAGC-3'. PCR amplification was performed with a thermal cycler (PTC-225, MJ Research, Co., Waltham, MA, USA). The PCR reaction started at 95°C for 5 min for pre-denaturation, followed by 35 cycles of 94°C for 1 min, 58°C for 1 min, and 72°C for 1 min, with a final extension step at 72°C for 10 min. The amplified DNA fragments were directly sequenced in an ABI 3730XL genetic analyzer (Applied Biosystems, Foster City, CA, USA), and SNPs were detected using the Phred/Phrap/Polyphred program (Nickerson *et al.*, 1997).

Genotyping and haplotype construction

Three SNPs (*-867G>C*, *-877Gdel*, and *Exon5G>T*) were genotyped using the PCR-restriction fragment length polymorphism (RFLP) with *Fau* I and *Hsp*92II restriction enzymes. The two primer sets used for the PCR-RFLP were the same primer sets used for direct sequencing and generated 500 and 700 bp DNA fragments including the restriction enzyme site. The PCR amplification reactions were performed with 1.5 mM $MgCl_2$, 2.5 mM deoxyribonucleotides (dNTPs), 10 pM of each primer, 1 μL of the genomic DNA (50 ng), and 0.5 U Taq DNA polymerase (Promega, Co., Madison, WI, USA) in a 20 μL volume. The PCR reaction profile for the PCR-RFLP was 94°C for 5 min and 35 cycles of 94°C for 1 min, 58°C for 1 min, and 72°C for 1 min. The regulatory SNP (-867G>C; 500 bp) in the promoter was digested with *Fau I*, whereas the second SNP (878T>C; 700 bp) in exon 5 was digested with *Hsp92II*. The restriction enzyme digestions were performed with 20 μL of PCR product mixed with three units of the appropriate restriction enzyme and were then incubated at 65°C and 37°C for 5 h, respectively. Haplotypes were constructed with the PHASE program (Stephens *et al.*, 2001).

Association test of SNPs, haplotype, and fatty acid composition

The association study for the three fatty-acid composition SNPs was analyzed using a linear mixed model in ASReml (Gilmour *et al.*, 2006). The factors, treatment (three levels), age at slaughter, and genotype were fitted as fixed effects, and the animals were fitted as random effects. The following linear models were used to estimate the association between fatty acid composition and the three SCD gene polymorphisms:

$$Y_{ijkl} = \mu + T_i + bD_{ijk} + G_{ij} + a_{ijkl} + e_{ijkl} \quad (1)$$

where Y_{ijkl} is the observation for the trait, μ is overall mean, T_i is the fixed effect of i^{th} treatment, G_{ij} is the fixed term of the i^{th} genotype for the *SCD* SNPs and k is genotype class within locus i (k=1-3), D_{ijk} is covariate for age of days at slaughter, a_{ijkl} was fitted as random effect and e_{ijkl} is the random residual error. Genetic covariances among animals were fitted through a numerator relationship matrix (A): (Var (a) = $A\sigma_a$). Association of reconstructed three main haplotypes with fatty acid composition was evaluated by the model [1] for SNP analysis, replacing SNP genotype by haplotype using ASReml (Gilmour *et al.*, 2006).

Results

Identification of the 5'-regulatory and non-synonymous SNPs in the SCD gene

We resequenced the 5'-regulatory (1.2 kb) and exon 5 (900 bp) regions of the SCD gene to identify functional SNPs that might modify gene expression and protein activity. Two SNPs were detected in the 1.2 kb regulatory region at -867 and -877 bp from the mRNA start site. These two SNPs were in a complete linkage disequilibrium state and located quite close to each other. Compared to the 1.2 kb regulatory region sequence of the human promoter region, we found the key transcription factor binding sites for lipid metabolism such as the sterol regulatory element (SRE), nuclear factor Y, and CCAAT enhancer binding protein alpha (C/EBPalpha) (Fig. 1). Taniguchi *et al.* (2004) also searched for a regulatory SNP in the 5' upstream region (around 1.1 kb) of the Japanese black cattle SCD gene; however, they found no mutations in that region. Compared with the region reported by the Japanese group, these two regulatory SNPs in Hanwoo were detected about 100 bp away from the region that the Japanese group searched. However, one SNP (878C>T) was identified in exon 5, and it was a non-synonymous SNP that caused an amino acid change (valine>alanine). This non-synonymous SNP (878C>T) was the same SNP detected in Japanese black cattle.

Comparison of allele frequencies among six cattle breeds

Table 2 shows the gene frequency in the six other cattle breeds (Asian, European, and African cattle) for the two SNP types in the SCD gene. The -877G and 878C allele frequencies of Hanwoo (0.27 and 0.43) were similar to those of Japanese Brown cattle (0.27 and 0.58) and Yanbian cattle (0.27 and 0.55). However, the -877G allele frequency was not polymorphic in the European cattle

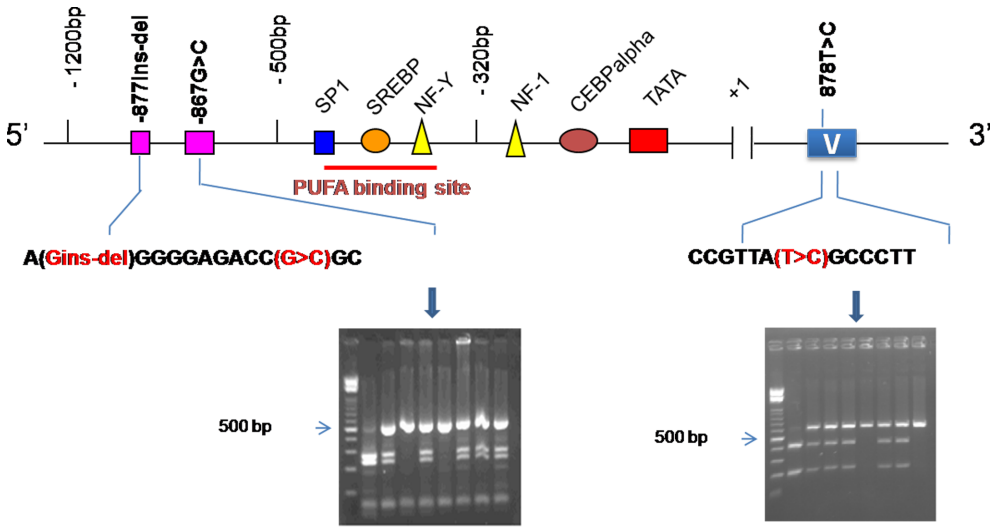

Fig. 1. Transcription factor site and single nucleotide polymorphism (SNP) map of the stearoyl-CoA desaturase (SCD) gene on BTA26.

Table 2. Allele frequencies of -867G>C, -877Gindel and 878T >C in the SCD gene in 7 cattle breeds

Breeds	N	-867 G	-877G	878 C
Hanwoo	90	0.27	0.27	0.43
Japanese Brown Cattle	11	0.27	0.27	0.58
Yanbian	25	0.32	0.32	0.55
Hereford	20	0.00	0.00	0.83
Simmental	27	0.07	0.07	0.89
Brown Swiss	19	0.00	0.00	0.82
Zebu	9	0.00	0.00	0.00

(Hereford, Simmental, and Brown Swiss), and the 878C allele in the Hereford (0.83), Simmental (0.89), and Brown Swiss (0.82) cattle revealed a much higher allele frequency than in the Northeastern Asian cattle. These two SNPs were not detected in African Zebu cattle.

Association test of SNPs, haplotype, and fatty acid composition

Among the three SNPs identified in the 5'-regulatory and exon 5 regions of the SCD gene, the 878T>C SNP was significantly associated with total saturated fatty acids (p=0.016), unsaturated fatty acids (p=0.016), and MUFAs (p=0.026) (Table 3). There was no effect between the regulatory SNPs (-867G>C and -877Gdel) and fatty acid composition in Hanwoo meat. However, the SNP interaction analysis between -867G>C and 878T>C showed a significant effect of monounsaturated fatty acid composition (p=0.043). Table 4 shows the least square mean of the 878T>C genotype for single and total fatty acid composition. In particular, muscle containing the 878C (alanine type) allele had 2.2% higher monounsaturated fatty acid (MUFA), 1.5% lower saturated fatty acid (SFA), and 1.4% higher unsaturated fatty acid (UFA) contents than did muscle containing the 878T (valine type) allele.

Four haplotypes for the three selected SNPs were identified in 90 Hanwoo cattle. Of the four reconstructed haplotypes, three were predominant with frequencies of 0.34, 0.35, and 0.26. The other haplotype (GdelT) had minor frequencies of less than 0.05 (Table 5). The three main haplotype effects on fatty acid composition were estimated using regression analysis, but there was no significant effect (Table 5). However, the CGT haplotype showed a suggestive effect of increased saturated fatty acid (p= 0.067) and decreased unsaturated fatty acid (p=0.067). This finding suggested that 878C>T SNP, which is a non-

Table 3. *P-values* of all associations tested between the two single nucleotide polymorphisms (SNPs) in the promoter and the exon 5 region of the SCD gene with fatty acid composition and fat traits (n=90). Significant (p<0.05) traits are listed with an asterisk (*)

Traits (Fatty acid)	SNPs (p value)			
	Promoter (*-867G>C*)	Promoter (*-877Gdel*)	Exon5 (*878T>C*)	SNP interaction (-867G>C/878T>C)
Myristic acid (C14:0)	0.5	0.5	0.1	0.42
Palmitic acid (C16:0)	0.8	0.8	0.47	0.23
Palmitoleic acid (C16:1)	0.91	0.91	0.9	0.5
Stearic acid (C18:0)	0.65	0.65	0.065	0.108
Oleic acid (C18:1)	0.725	0.725	0.08	0.126
Saturated fatty acid (SFA)	0.68	0.68	0.016*	0.058
Unsaturated fatty acid (UFA)	0.068	0.068	0.016*	0.059
Monounsaturated FA	0.62	0.62	0.026*	0.043*
Polyunsaturated FA	0.85	0.85	0.5	0.39

Table 4. Association of *878T>C* polymorphisms with fatty acid composition in the *M. longissimus dorsi* muscle of Hanwoo steers (n = 90).

SNP	Fatty acid composition (%)					
	N	C18:0	C18:1	SFA	UFA	MUFA
			878T>C genotype least square mean			
TT(3)_VV	11	11.3±0.34	48.1±0.71	43.8±0.70	56.9±0.71[a]	53.7±0.69[a]
TC(2)_VA	49	10.7±0.21	49.5±0.38	41.8±0.37	58.1±0.37[b]	55.4±0.37[b]
CC(1)_AA	30	10.4±0.21	50.0±0.47	41.4±0.47	58.5±0.47[b]	55.9±0.46[b]
			P-value for SNP			
878T>C		0.065	0.08	0.016*	0.016*	0.026*

C18:0, stearic acid; C18:1, oleic acid; SFA, saturated fatty acid; UFA, unsaturated fatty acid; MUFA, monounsaturated fatty acid.

Table 5. Haplotype frequencies among three SNPs, and its association with fatty acid composition in Hanwoo cattle

Traits	*Haplotypes*[1]	df	Regression coefficients	*F-value*	*p-value*
C14:0	GdelC	1	0.19±0.24	0.77	0.38
	CGT	1	0.49±0.29	2.83	0.09
	CGC	1	0.49±0.36	2.05	0.16
C16:0	GdelC	1	-1.01±0.61	2.38	0.12
	CGT	1	0.25±0.71	0.12	0.73
	CGC	1	0.58±0.86	0.61	0.43
C16:1	GdelC	1	-0.23±0.21	0.85	0.36
	CGT	1	-0.10±0.32	0.11	0.74
	CGC	1	-0.36±0.38	0.78	0.38
C18:0	GdelC	1	-0.03±0.32	1.33	0.25
	CGT	1	0.66±0.45	2.15	0.15
	CGC	1	0.63±0.47	1.63	0.21
C18:1	GdelC	1	1.10±0.72	2.51	0.12
	CGT	1	-0.91±0.86	1.06	0.30
	CGC	1	-1.40±1.04	2.13	0.15
SFA	GdelC	1	-0.79±0.69	1.30	0.26
	CGT	1	1.60±0.85	3.52	0.06
	CGC	1	1.51±1.06	2.21	0.14
UFA	GdelC	1	0.81±0.70	1.33	0.25
	CGT	1	-1.60±0.85	3.52	0.06
	CGC	1	-1.51±1.06	2.18	0.14
MUFA	GdelC	1	0.96±0.67	2.07	0.15
	CGT	1	-1.35±0.84	2.56	0.11
	CGC	1	-1.76±1.04	3.06	0.09

[1]Frequencies of the three main haplotypes (GdelC, CGT, and CGC) were 0.344, 0.350, and 0.261, respectively.

synonymous SNP, might have a larger effect on fatty acid composition than the regulatory SNPs (-867G>C and -877 Gdel) in Hanwoo.

Discussion

Fatty acid profiles are important factors for determining meat quality, such as the visual manifestation of marbling during processing (Smith *et al.*, 1998), fat softness, and meat flavor (Melton *et al.*, 1982), as well as a human health problem. In cattle, MUFA composition can be modified by many factors, including animal gender (Clemens *et al.*, 1973), nutritional treatments (Daniel *et al.*, 2004; Chung *et al.*, 2007) and genetic factors (Perry *et al.*, 1998). Yang *et al*. (1999) reported that SCD enzyme activity is positively correlated with UFA content in bovine fat tissue. The SCD gene is the main gene that produces MUFAs from stearic acid (C18:0) and palmitic acid (C16:0) by catalyzing a double bond at the ninth carbon chain of saturated fatty acids.

In this study, we identified one non-synonymous SNP in exon 5 and two SNPs in the 5'-regulatory region of the SCD gene. As shown in Table 1, the non-synonymous SNP ($878C^{ala}>T^{val}$) was significantly associated with MUFAs, which are composed of oleic acid (C18:1) and palmitoleic acid (C16:1). This result agrees with the findings from Taniguchi *et al.* (2004) that the 878C allele (alanine type, AA) had a 1.7% higher total MUFA composition than the 878T allele (valine type, VV) in Japanese black cattle. In the Hanwoo population, muscle with the 878C allele revealed 2.2% higher total MUFA composition than that in Japanese black cattle, whereas the SCD genotype explained about 5% of the MUFA phenotypic variation (R^2 =0.05) in this study. We identified two regulatory SNPs in a 300 bp upstream region from the PUFA binding site, which is a region that enhances SCD gene expression through the SREBP-1c transcriptional factor. In the linear mixed model to fit each SNP effect as a fixed effect, two SNPs (-867G>C and -877Gdel) were not significantly associated with fatty acid composition. However, -867G>C had a significant SNP interaction effect with 878C>T, which was significant with MUFAs.

Haplotypes were constructed in the PHASE program to estimate haplotype effects. As shown in Table 3, three main haplotypes were detected in the Hanwoo population. Regression analysis was implemented to estimate the haplotype effect, but there was no significant haplotype effect on MUFAs. However, the haplotype (GdelC) effect (0.96%) was larger than the haplotype (CGC) effect (-1.76%) in the MUFA percentage. The difference between the two haplotype effects was 2.72% and larger than the 878C>T single SNP effect. This result indicates that MUFA composition in Hanwoo meat might not only be affected by the non-synonymous SNP (878C>T) but also by an interaction effect between the non-synonymous (878C>T) and regulatory SNP (-867G>C) SNP.

In conclusion, the non-synonymous SNP (878T>C) in the SCD gene was a functional SNP that explained about 5% of the MUFA phenotypic variation, and there was an SNP interaction effect between the non-synonymous SNP (878T>C) and the regulatory SNP (-867G>C). In addition, the effect (2.72%) between the GdelC and CGC haplotypes was greater than the single SNP (878C>T) effect (2.2%).

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