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Relationship between Single Nucleotide Polymorphisms in the Peroxisome Proliferator-Activated Receptor Gamma Gene and Fatty Acid Composition in Korean Native Cattle

Jea-young Lee[a], Jae-jung Ha[1,a], Yong-soo Park[2], Jun-koo Yi[1], Seunguk Lee[3], Seyoung Mun[4,5], Kyudong Han[4,5], J.-J. Kim[6], Hyun-Ji Kim, and Dong-yep Oh[1,*]
Department of Statistics, Yeungnam University, Gyeongbuk 712-749, Korea

ABSTRACT: The peroxisome proliferator-activated receptor gamma (*PPARγ*) gene plays an important role in the biosynthesis process controlled by a number of fatty acid transcription factors. This study investigates the relationships between 130 single-nucleotide polymorphisms (SNPs) in the *PPARγ* gene and the fatty acid composition of muscle fat in the commercial population of Korean native cattle. We identified 38 SNPs and verified relationships between 3 SNPs (g.1159-71208 A>G, g.42555-29812 G>A, and g.72362 G>T) and the fatty acid composition of commercial Korean native cattle (n = 513). Cattle with the AA genotype of g.1159-71208 A>G and the GG genotype of g.42555-29812 G>A and g.72362 G>T had higher levels of monounsaturated fatty acids and carcass traits ($p<0.05$). The results revealed that the 3 identified SNPs in the *PPARγ* gene affected fatty acid composition and carcass traits, suggesting that these 3 SNPs may improve the flavor and quality of beef in commercial Korean native cattle. (**Key Words:** Korean Native Cattle, *PPARγ*, SNP, Fatty Acid Composition, Marbling Score)

INTRODUCTION

The fatty acid composition of livestock adipose tissue is recognized as an important carcass trait affecting meat quality. The quality of fat is determined by its fatty acid composition, and beef quality depends not only on the marbling score but also on fatty acid composition. Although beef marbling is an important factor, fatty acid composition also plays an important role in the eating quality of meat (Laborde et al., 2001). About 90% of the fatty acid composition of intramuscular fat from the longissimus muscle of beef cattle is accounted for by palmitic acid (16:0) and stearic acid (18:0) from saturated fatty acid (SFA) and oleic acid (18:1) from monounsaturated fatty acid (MUFA). Oleic acid accounts for the highest proportion of MUFAs in beef cattle and is positively correlated with marbling, beef flavor, tenderness, and soft fat (Melton et al., 1982; Kim et al., 2002; Lee et al., 2004; Lee et al., 2008; Smith et al., 2009). These factors are of considerable interest because of their implications for human health. Stearic acid (18:0) is a primary determinant of fat hardness (Smith et al., 1998; Wood et al., 2004; Chung et al., 2006).

Therefore, genetic factors that enhance the conversion of stearic acid into oleic acid are expected to increase tenderness, flavor, and marbling (Yang et al., 1999). The

* Corresponding Author: Dong-yep Oh. Tel: +82-54-638-6012, Fax: +82-54-638-6013, E-mail: moocic@hanmail.net
[1] Livestock Research institute, Yeongju 750-871, Korea.
[2] Department of Equine Industry, Korea National College of Agriculture and Fisheries, Hwaseong 445-760, Korea.
[3] Biotechnology Research Center, The University of Tokyo, Bunkyo 113-8657, Tokyo.
[4] Department of Nanobiomedical Science & BK21 PLUS NBM Global Research Center for Regenerative Medicine, Dankook University, Cheonan 330-714, Korea.
[5] DKU-Theragen institute for NGS analysis (DTiNa), Cheonan 330-714, Korea.
[6] School of Biotechnology, Yeungnam University, Gyeongsan 712-749, Korea.
[a] Jea-young Lee and Jae-jung Ha are contributed equally to this work.
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fatty acid biosynthesis process is controlled by a number of transcription factors such as peroxisome proliferator-activated receptor gamma (*PPARγ*), CCAAT/enhancer binding protein alpha (*C/EBPA*), and sterol regulatory element binding proteins (*SREBPs*). Many studies have reported that genetic factors in transcription factor genes are associated with fatty acid composition and the marbling score in Korean native cattle and Japanese Black cattle (Shin et al., 2007; Hoashi et al., 2007; Lee et al., 2008; Oh et al., 2012). These findings suggest that fatty acid composition may be controlled by genetic factors such as genes related to lipid synthesis and fatty acid metabolism (Narukami et al., 2011).

PPARγ, a member of the nuclear hormone receptor superfamily, acts as a ligand-inducible transcription factor (Spiegelman, 1998; Kersten et al., 2000). *PPARγ* forms a heterodimer complex with one of the three retinoid X receptor (RXR) proteins and then binds to PPAR-responsive elements (*PPRE*) in promoters of *PPARγ* target genes (Mangelsdorf and Evans, 1995; Schulman et al., 1998).

PPARs contain general structural features of other nuclear receptor family members, including a central DNA-binding domain, a C-terminal domain mediating ligand binding, and two transcription activation function motifs (Rosen and Spiegelman, 2001). *PPARγ* is expressed abundantly in adipocytes and plays a key role in mediating adipocyte differentiation and insulin sensitivity. Many adipocyte-specific genes such as adiponectin and perilipin contain response elements for *PPARγ* in their promoter regions (Iwaki et al., 2003; Nagai et al., 2004; Guan et al., 2005). In the absence of any ligand, nuclear corepressors bind PPAR/RXR heterodimers and recruit histone deactylases to down regulate gene transcription (Yu et al., 2005). The present study evaluates the relationships between single nucleotide polymorphisms (SNPs) of intron and exon regions in the *PPARγ* gene and fatty acid composition in Korean native cattle.

MATERIALS AND METHODS

Animals and phenotypic Data

A total of 513 commercial Korean native cattle samples from Gyeungsangbuk, 96, Korea, were included in the study where 10 sires were used to produce this half sib population. Feeding conditions (slaughter age, the fattening period, forage intake, and concentration) were controlled under livestock management of each region (n = 14). They were all steers slaughtered at 941±72 days of age, and the marbling score was measured 24 h after slaughter. First, the carcass was dissected at the last rib and the first lumber vertebra according to the Animal Product Grading System of Korea. Marbling scores were measured or scored in the left carcass cut across the vertebra between the last thoracic vertebra and the first lumbar vertebra. The marbling degree was scored from 1 to 9 with a mean of 5.43 such that the higher score, the more abundant the intramuscular fat (Table 1). Genomic DNA was extracted from the longissimus muscle by using the LaboPass Tissue Mini Kit (Cosmo Genetech, Seoul, Korea).

Fatty acid composition

Total lipids were extracted from approximately 500 mg

Table 1. Means and standard deviations for carcass traits and fatty acid composition for Korean native cattle

Trait	Description	Mean±SD	Min	Max
CW (kg)	Carcass weight	427.25±43.28	321	573
BFT (mm)	Backfat thickness	13.22±5.13	3	42
MS	Marbling score	5.43±1.93	1	9
Fatty acid composition (%)				
C14:0	Myristic acid	3.63±0.65	1.68	5.52
C16:0	Palmitic acid	25.65±1.96	18.86	31.12
C18:0	Stearic acid	10.48±1.39	6.74	15.34
C14:1	Myristoleic acid	1.24±0.38	0.11	2.73
C16:1	Palmitoleic acid	6.61±0.97	4.04	10.29
C18:1	Oleic acid	44.30±2.66	36.85	53.69
C18:2n6	Linoleic acid	3.02±0.76	2.17	3.98
C18:3n3	Linolenic acid	0.35±0.20	0.14	0.89
C18:3n3/ C18:2n6	Linolenic acid/linoleic acid	1:8.62	1:2.44	1:28.43
SFA	Saturated fatty acid	40.60±2.86	30.36	48.44
MUFA	Monounsaturated fatty acid	53.50±2.96	45.82	63.46
M/S	MUFA/SFA	1.32±0.16	0.99	2.07
C14 index	[C14:1/(C14:0+C14:1)]×100	25.37±6.37	11.98	39.82
C16 index	[C16:1/(C16:0+C16:1)]×100	20.50±2.81	13.35	31.18
C18 index	[C18:1/(C18:0+C18:1)]×100	80.86±2.43	72.16	87.34

SD, standard deviation.

of the longissimus muscle with chloroform/methanol (2/1, v/v) (Folch et al., 1957) and then methylated with sodium methylate (O'Keefe et al., 1968). Samples were filtered through a filter paper in a water bath (40℃). The filtrate was mixed with distilled water, from which a layer of methanol and water was removed. After the removal of chloroform and lipid layers by using nitrogen gas, the sample was treated with BF3-methanol (14%) and then subjected to transmethylation at 65℃. Fatty acid content was analyzed using gas-chromatography (PerkinElmer, Inc., Waltham, MA, USA). Fatty acids included myristic acid, palmitic acid, stearic acid, myristoleic acid, palmitoleic acid, oleic acid, linoleic acid, and linolenic acid. The composition and function of fatty acids were used as phenotypes in the analysis of the genetic relationship (Table 1).

Genotyping

130 SNPs in *PPARγ* were selected based on the reference SNP of the bovine *PPARγ* gene (GenBank No. NC_007320.5) in dbSNP. Genotypes of 10 SNPs were subjected to a preliminary analysis. Primers for the amplification and extension were designed for the single-base extension (SBE) (Vreeland et al., 2002) by using forward, reverse, and extension primer sequences (Supplementary Table 1). Reactions of the primer extension were performed using the SNaPshot ddNTP Primer Extension Kit (Applied Biosystems, Foster City, CA, USA). To purify reactions of the primer extension, mixtures containing exonuclease I and shrimp alkaline phosphatase were added to the reaction mixture. Samples were cultured at 37℃ for 1 h and then inactivated at 72℃ for 15 min. The polymerase chain reaction product was mixed with Genescan 120 LIZ standard and HiDi formamide (Applied Biosystems, USA), followed by denaturation at 95℃ for 5 min. Electrophoresis was performed using the ABI PRISM 3130XL Genetic Analyzer, and then electrophoresis products were assayed using GeneMapper v.4.0 (Applied Biosystems, USA).

Statistic analysis

The significance of SNP allele frequency between the two groups (high and low) was analyzed using chi-square test for extremely varied 44 samples. Those SNP alleles for which there were significant differences in frequency were included in a linear discriminant analysis (Venables and Ripley, 2002) to develop a function that classified animals into two groups. Only influential fragments for discrimination (F>4.0) were included in the function.

The Hardy–Weinberg equilibrium (HWE) was tested for each SNP in the Korean native cattle population by using the chi-square statistic. Relationships between fatty acid composition and the marbling score for individual SNPs were analyzed using the following mixed model based on SPSS v19.0 (SPSS Inc., Chicago, IL, USA): $Y_{ijkl} = \mu+S_i+P_j+G_k+b\_age+e_{ijk}$, where Y_{ijkl} is the phenotype, μ is the overall mean, S_i is the random effect of sire i with the assumption of an independent and identical normal distribution, P_j is the fixed effect of calving place j (14 classes), G_k is the fixed effect of genotype k, b is the regression coefficient, age is a covariate for age in days at slaughter, and e_{ijk} is a random residual assumed to have an independent and identical normal distribution. Significant differences in mean values between different genotypes were calculated using Duncan's multiple-range test. Here $p<0.05$ was considered to be significant. Additive and dominant effects were estimated using the REG procedure in SAS version 9.2. For the haplotype analysis, the linkage disequilibrium (LD) between SNP pairs was measured according to D' and r^2 based on the HaploView software package (MIT/Harvard Broad Institute, Cambridge, MA, USA).

RESULTS AND DISCUSSION

The SNP selection of the *PPARγ* gene and the haplotype analysis of Hanwoo

All 130 SNPs at the intron and exon were identified by an NCBI-based analysis to evaluate the relationships between SNPs in the *PPARγ* gene and fatty acid composition (Figure 1). Here 129 SNPs were located at the intron, and 1, at exon 7. In addition, the phenotypic mean and standard deviation, the min and max of carcass traits, fatty acid composition, and the fatty acid index were determined for cattle (Table 1). By the SBE for the verification of 130 SNPs in 44 cattle for the high- and low-MUFA groups of Korean native cattle, 38 SNPs were identified: 37 SNPs at the intron and 1 at exon 7. Statistical analyses were conducted to determine genotypic and allelic frequency, heterozygotes, minor-allele frequency (MAF), and the HWE. MAF was lower than 0.100, and segregation was not clearly observed following the LD analysis, which reduced analytical accuracy (Eberle et al., 2006; Lee et al., 2006). The 38 identified SNPs were found to have MAF values greater than 0.100, and their genotypes did not deviate from the HWE ($p>0.05$; Table 2) (Falconer and Mackay, 1996).

Discrimination efficiency

Table 3 shows the efficiency of discrimination for the 38 SNPs in the high- and low-MUFA groups of Korean native cattle (n = 44). To classify 44 extreme animals into the high and low MUFAs groups, discriminant coefficients were calculated for the 38 SNPs, and these coefficients were derived using information on the SNP genotype and the high- or low-MUFA group. Among these SNPs, the g.1159-

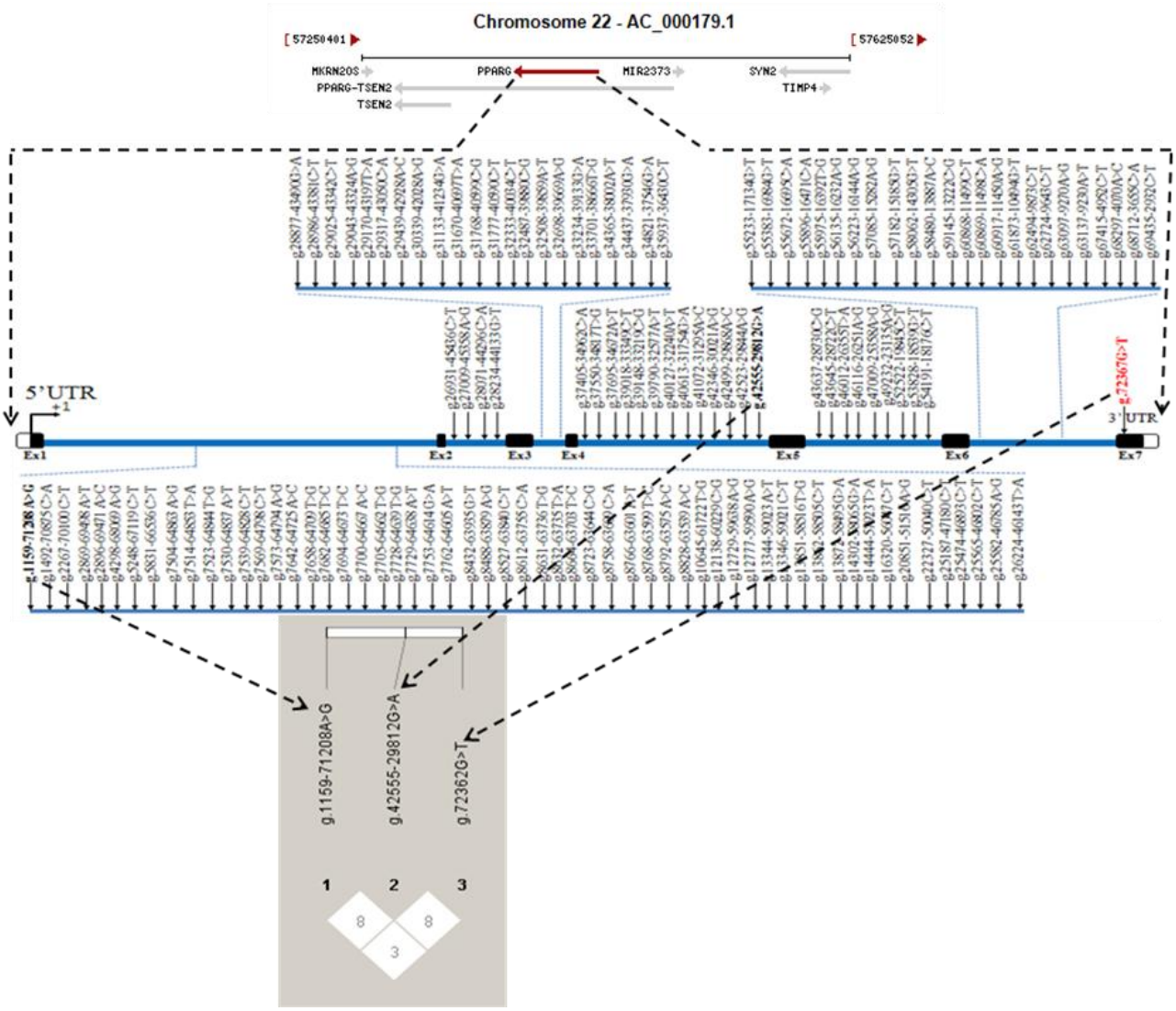

Figure 1. 130 SNPs and linkage disequilibrium (LD) values for 3 SNPs in the bovine *PPARγ* gene. The HaploView plot is color-coded using the following scheme: White represents $r^2 = 0$, and red signifies $r^2 = 1$. Numbers in cells are R^2 values. However, R^2 values of 1.0 are not shown. SNPs, single nucleotide polymorphisms; *PPARγ*, peroxisome proliferator-activated receptor gamma.

71208 A>G, g.42555-29812 G>A, and g.72367 G>T SNPs had the highest discriminant coefficients (–1.094, 0.700, and –0.941, respectively). Three SNPs showed significant relationships with MUFAs ($p<0.05$, $F>4.0$). This is equivalent to a discriminative error of 2.1% and a high correlation ratio of 0.91. These results indicated that the discriminant function successfully separated extreme Korean native cattle (Tsuji et al., 2004). Therefore, the g.1159-71208 A>G, g.42555-29812 G>A, and g.72367 G>T SNPs were selected for large-scale genotyping in commercial Korean native cattle (n = 513). Based on these results, a pairwise LD analysis of these 3 SNPs showed that the *PPARγ* gene cannot be conducted block (Figure 1).

Relationships with fatty acid composition

Previous studies have shown that the content of unsaturated fatty acid (UFA) (Alexander et al., 2007) and a high MUFA level have significant effects on beef flavor (Hoashi et al., 2007). Based on these reports, fatty acid composition, carcass phenotypes, and genetic effects were examined for a single Korean native cattle genotype (Tables 4 and 5). The results revealed significant differences according to the SNP of the *PPARγ* gene.

According to the results for carcass traits and two SNPs (g.1159-71208 A>G and g.72362 G>T), g.1159-71208 A>G were significantly related to backfat thickness (BFT), and g.72362 G>T to the marbling score (MS). The relationships between carcass traits and each SNP were based on the p-value ($p<0.05$). Yue et al. (2011) and Shin et al. (2006) reported significant effects of the bovine *PPARγ* genotype ($p<0.05$) on tenderness, BFT and water-holding capacity in *Chinese indigenous bovine* and on the longissimus muscle

Table 2. The genotype and frequency of 38 SNPs in the *PPARγ* gene of Korean native cattle

SNP	Region	Genotype (No. of head)				H	MAF	HWE[1]
		Frequency						
g.1159-71208 A>G	Intron	AA (16)	AG (14)	GG (14)	N (44)	0.499	0.420	0.016
		0.364	0.318	0.318	1.000			
g.2869-69498 A>G	Intron	AA (25)	AG (19)	GG (0)	N (44)	0.407	0.187	0.008
		0.568	0.432	0.000	1.000			
g.2896-69471 A>C	Intron	AA (0)	AC (5)	CC (39)	N (44)	0.107	0.183	0.689
		0.000	0.114	0.886	1.000			
g.5248-67119 C>T	Intron	CC (23)	CT (21)	TT (0)	N (44)	0.363	0.204	0.038
		0.523	0.477	0.000	1.000			
g.12138-60229 C>G	Intron	CC (14)	CG (25)	GG (5)	N (44)	0.496	0.455	0.029
		0.318	0.568	0.114	1.000			
g.12729-59638 A>G	Intron	AA (18)	AG (8)	GG (18)	N (44)	0.500	0.500	0.014
		0.409	0.182	0.409	1.000			
g.13344-59023 A>T	Intron	AA (14)	AT (1)	TT (29)	N (44)	0.442	0.330	0.002
		0.318	0.023	0.659	1.000			
g.22327-50040 A>G	Intron	AA (25)	AG (19)	GG (0)	N (44)	0.339	0.216	0.166
		0.568	0.432	0.000	1.000			
g.30339-42028 T>C	Intron	CC (7)	CT (19)	TT (18)	N (44)	0.469	0.375	0.776
		0.159	0.432	0.409	1.000			
g.31768-40599 C>G	Intron	CC (14)	CG (25)	GG (5)	N (44)	0.479	0.398	0.398
		0.318	0.568	0.114	1.000			
g.31777-40590 G>A	Intron	AA (14)	AG (18)	GG (12)	N (44)	0.499	0.477	0.330
		0.318	0.409	0.273	1.000			
g.32333-40034 G>A	Intron	AA (7)	AG (23)	GG (14)	N (44)	0.487	0.420	0.925
		0.159	0.523	0.318	1.000			
g.32487-39880 C>G	Intron	CC (16)	CG (23)	GG (5)	N (44)	0.469	0.375	0.718
		0.363	0.523	0.114	1.000			
g.32508-39859 A>T	Intron	AA (14)	AT (25)	TT (5)	N (44)	0.479	0.398	0.398
		0.318	0.568	0.114	1.000			
g.35937-36430 G>A	Intron	AA (0)	AG (14)	GG (30)	N (44)	0.268	0.159	0.586
		0.000	0.318	0.682	1.000			
g.39018-33349 G>A	Intron	AA (13)	AG (21)	GG (10)	N (44)	0.498	0.466	0.963
		0.295	0.478	0.227	1.000			
g.39148-33219 C>G	Intron	CC (12)	CG (26)	GG (6)	N (44)	0.491	0.432	0.329
		0.273	0.591	0.136	1.000			
g.41072-31295 T>G	Intron	GG (22)	GT (22)	TT (0)	N (44)	0.375	0.250	0.058
		0.500	0.500	0.000	1.000			
g.42346-30021 T>C	Intron	CC (15)	CT (19)	TT (10)	N (44)	0.494	0.443	0.546
		0.341	0.432	0.227	1.000			
g.42499-29868 T>G	Intron	GG (21)	GT (21)	TT (2)	N (44)	0.407	0.284	0.487
		0.477	0.477	0.046	1.000			
g.42523-29844 T>C	Intron	CC (13)	CT (19)	TT (12)	N (44)	0.500	0.489	0.497
		0.295	0.432	0.273	1.000			
g.42555-29812 G>A	Intron	AA (19)	AG (17)	GG (8)	N (44)	0.469	0.375	0.354
		0.432	0.386	0.182	1.000			

area and carcass weight in Korean native cattle. And All the mRNA region of the *PPARγ* gene within 760 individuals of four Chinese cattle breeds was scanned and four SNPs (-110G>C, -27C>T and +20A>G) of the *PPARγ* were detected in three Chinese indigenous cattle breeds (Qinchuan, Nangyang and Jiaxian cattle), rather than Chinese Holstein cattle. The mutations -110G>C, -27C>T and +20A>G located in the Exon1 of the *PPARG* and were under LD. The individuals with these three mutations had smaller body measurements (Hua et al., 2011). In the case of these five SNPs, they were located at intron 3 (C/T, 292), intron 5 (C/T, 1,064) and exon 1 (-

Table 2. The genotype and frequency of 38 SNPs in the *PPARγ* gene of Korean native cattle (Continued)

SNP	Region	Genotype (No. of head)				H	MAF	HWE[1]
		Frequency						
g.43637-28730 C>G	Intron	CC (15)	CG (26)	GG (3)	N (44)	0.463	0.364	0.145
		0.341	0.591	0.068	1.000			
g.43645-28722 G>A	Intron	AA (4)	AG (12)	GG (28)	N (44)	0.351	0.227	0.254
		0.091	0.273	0.636	1.000			
g.47009-25358 T>C	Intron	CC (3)	CT (26)	TT (15)	N (44)	0.463	0.364	0.145
		0.068	0.591	0.341	1.000			
g.49232-23135 T>C	Intron	CC (15)	CT (26)	TT (3)	N (44)	0.463	0.364	0.145
		0.341	0.591	0.068	1.000			
g.54191-18176 G>A	Intron	AA (16)	AG (22)	GG (6)	N (44)	0.474	0.386	0.718
		0.364	0.500	0.136	1.000			
g.56135-16232 T>C	Intron	CC (2)	CT (26)	TT (16)	N (44)	0.449	0.341	0.083
		0.045	0.591	0.364	1.000			
g.56223-16144 T>C	Intron	CC (0)	CT (17)	TT (27)	N (44)	0.312	0.193	0.293
		0.000	0.386	0.614	1.000			
g.57085-15282 T>C	Intron	CC (17)	CT (20)	TT (7)	N (44)	0.474	0.386	0.969
		0.471	0.550	0.429	1.000			
g.60868-11499 C>T	Intron	CC (20)	CT (24)	TT (0)	N (44)	0.397	0.273	0.025
		0.455	0.545	0.000	1.000			
g.60917-11450 A>G	Intron	AA (19)	AG (13)	GG (12)	N (44)	0.487	0.420	0.016
		0.432	0.295	0.273	1.000			
g.61873-10494 G>T	Intron	GG (15)	GT (25)	TT (4)	N (44)	0.469	0.375	0.309
		0.341	0.568	0.091	1.000			
g.62724-9643 C>T	Intron	CC (27)	CT (17)	TT (0)	N (44)	0.312	0.193	0.293
		0.614	0.386	0.000	1.000			
g.63097-9270 A>G	Intron	AA (8)	AG (21)	GG (15)	N (44)	0.487	0.420	0.891
		0.182	0.477	0.341	1.000			
g.63137-9230 A>T	Intron	AA (0)	AT (18)	TT (26)	N (44)	0.325	0.205	0.223
		0.000	0.409	0.591	1.000			
g.69435-2932 C>T	Intron	CC (5)	CT (22)	TT (17)	N (44)	0.463	0.364	0.902
		0.114	0.500	0.386	1.000			
g.72367 G>T	Exon 7	GG (16)	GT (22)	TT(6)	N (44)	0.474	0.397	0.718
		0.364	0.500	0.136	1.000			

SNPs, single nucleotide polymorphisms; *PPARγ*, peroxisome proliferator-activated receptor gamma; H, heterozygosity, MAF, minor allele frequence; HWE, Hardy-Weinberg equilibrium; N, total number.
[1] p value for deviation of genotype distribution from HWE.

110G>C, -27C>T, +20A>G) in the *PPARγ* gene. Although the position of these SNPs and the breed of cattle in these studies are different from those in the present study, their findings are consistent with this study's results.

As shown in Table 4 and 5, SFA in the g.1159-71208 A>G, g.42555-29812 G>A, and g.72362 G>T SNPs was observed at 41.66%, 42.01%, and 42.58% in genotypes of GG, AA, and TT, respectively ($p<0.05$). By contrast, oleic acid (C18:1) levels were significantly related to the AA genotype of g.1159-71208 A>G, the GG genotype of g.42555-29812 G>A, and the GG genotype of g.72362 G>T ($p<0.01$). In addition, the AA and GG genotypes of g.1159-71208 A>G and g.42555-29812 G>A and the GG genotype of g.72362 G>T were related to the highest oleic acid content. MUFAs account for a high proportion of fatty acid composition and are an important factor influencing meat quality. Among MUFAs, oleic acid (C18:1) is one of the major MUFAs in beef cattle and the aroma source of cooked beef (Melton et al., 1982; Mandell et al., 1998). MUFA levels (54.13%, 54.05%, and 54.03%, respectively) showed the same trends as those for oleic acid ($p<0.05$). Clinical studies have shown that long-chain omega-3 polyunsaturated fatty acids (n-3 PUFA; linolenic acid) have beneficial effects on human health. On the other hand, high levels of omega-6 PUFAs (n-6 PUFAs; linoleic acid) are closely related to certain human diseases such as cancer, cardiovascular disease, and various mental disorders (Reidiger et al., 2009). In the present study, levels of PUFAs, which included linoleic acid (C18:2n6; omega-6) and linolenic acid (C18:3n3; omega-3), were related to the three

Table 3. The efficiency of discrimination of 38 SNPs in high- and low-MUFA groups of Korean native cattle (n = 44)

SNP	Region	Genotype (No. of head)						Discriminant coefficient	F-value	p-value
		High MUFAs group			Low MUFAs group					
		Frequency			Frequency					
g.1159-71208 A>G	Intron	AA (7)	AG (4)	GG (11)	AA (9)	AG (10)	GG (3)	–1.094	5.469	0.025
		0.438	0.286	0.786	0.562	0.714	0.214			
g.2869-69498 A>G	Intron	AA (12)	AG (10)	GG (0)	AA (13)	AG (9)	GG (0)	–0.183	0.092	0.761
		0.480	0.526	0.000	0.520	0.474	0.000			
g.2896-69471 A>C	Intron	AA (0)	AC (2)	CC (20)	AA (0)	AC (3)	CC (19)	–0.223	0.223	0.635
		0.000	0.400	0.513	0.000	0.600	0.487			
g.5248-67119 C>T	Intron	CC (10)	CT (12)	TT (0)	CC (13)	CT (9)	TT (0)	0.532	0.797	0.365
		0.435	0.571	0.000	0.565	0.429	0.000			
g.12138-60229 C>G	Intron	CC (7)	CG (11)	GG (4)	CC (7)	CG (14)	GG (1)	–0.400	1.000	0.340
		0.500	0.440	0.800	0.500	0.560	0.200			
g.12729-59638 A>G	Intron	AA (9)	AG (4)	GG (9)	AA (9)	AG (4)	GG (9)	0.000	0.000	1.000
		0.500	0.500	0.500	0.500	0.500	0.500			
g.13344-59023 A>T	Intron	AA (7)	AT (0)	TT (15)	AA (7)	AT (1)	TT (14)	0.284	0.284	0.596
		0.500	0.000	0.517	0.500	1.000	0.483			
g.22327-50040 A>G	Intron	AA (13)	AG (9)	GG (0)	AA (12)	AG (10)	GG (0)	0.183	0.092	0.761
		0.520	0.474	0.000	0.480	0.526	0.000			
g.30339-42028 T>C	Intron	CC (3)	CT (10)	TT (9)	CC (4)	CT (9)	TT (9)	0.000	0.000	1.000
		0.429	0.526	0.500	0.571	0.474	0.500			
g.31768-40599 C>G	Intron	CC (7)	CG (11)	GG (4)	CC (7)	CG (14)	GG (1)	–0.403	1.008	0.340
		0.500	0.440	0.800	0.500	0.560	0.200			
g.31777-40590 G>A	Intron	AA (7)	AG (9)	GG (6)	AA (7)	AG (9)	GG (6)	0.000	0.000	1.000
		0.500	0.500	0.500	0.500	0.500	0.500			
g.32333-40034 G>A	Intron	AA (4)	AG (11)	GG (7)	AA (3)	AG (12)	GG (7)	0.000	0.000	1.000
		0.571	0.478	0.500	0.429	0.522	0.500			
g.32487-39880 C>G	Intron	CC (8)	CG (11)	GG (3)	CC (8)	CG (12)	GG (2)	0.050	0.025	0.885
		0.500	0.478	0.600	0.500	0.522	0.400			
g.32508-39859 A>T	Intron	AA (7)	AT (12)	TT (3)	AA (7)	AT (13)	TT (2)	0.086	0.043	0.887
		0.500	0.480	0.600	0.500	0.520	0.400			
g.35937-36430 G>A	Intron	AA (0)	AG (7)	GG (15)	AA (0)	AG (7)	GG (15)	0.000	0.000	1.000
		0.000	0.500	0.500	0.000	0.500	0.500			
g.39018-33349 G>A	Intron	AA (6)	AG (11)	GG (5)	AA (7)	AG (10)	GG (5)	0.000	0.000	1.000
		0.462	0.524	0.500	0.538	0.476	0.500			
g.39148-33219 C>G	Intron	CC (6)	CG (14)	GG (2)	CC (6)	CG (12)	GG (4)	0.433	0.216	0.663
		0.500	0.538	0.333	0.500	0.462	0.667			
g.41072-31295 T>G	Intron	GG (10)	GT (12)	TT (0)	GG (12)	GT (10)	TT (0)	0.350	0.350	0.546
		0.455	0.545	0.000	0.545	0.455	0.000			
g.42346-30021 T>C	Intron	CC (8)	CT (11)	TT (3)	CC (7)	CT (8)	TT (7)	–0.405	1.005	0.343
		0.533	0.579	0.300	0.467	0.421	0.700			
g.42499-29868 T>G	Intron	GG (11)	GT (10)	TT (1)	GG (10)	GT (11)	TT (1)	0.000	0.000	1.000
		0.524	0.476	0.500	0.476	0.524	0.500			
g.42523-29844 T>C	Intron	CC (7)	CT (10)	TT (5)	CC (6)	CT (9)	TT (7)	0.111	0.056	0.793
		0.538	0.526	0.417	0.462	0.474	0.583			
g.42555-29812 G>A	Intron	AA (9)	AG (12)	GG (1)	AA (10)	AG (5)	GG (7)	0.700	4.200	0.024
		0.474	0.706	0.125	0.526	0.294	0.875			
g.43637-28730 C>G	Intron	CC (8)	CG (12)	GG (2)	CC (7)	CG (14)	GG (1)	–0.129	0.065	0.758
		0.533	0.462	0.667	0.467	0.538	0.333			
g.43645-28722 G>A	Intron	AA (2)	AG (6)	GG (14)	AA (2)	AG (6)	GG (14)	0.000	0.000	1.000
		0.500	0.500	0.500	0.500	0.500	0.500			
g.47009-25358 T>C	Intron	CC (2)	CT (12)	TT (8)	CC (1)	CT (14)	TT (7)	0.111	0.056	0.758
		0.667	0.462	0.533	0.333	0.538	0.467			
g.49232-23135 T>C	Intron	CC (8)	CT (12)	TT (2)	CC (7)	CT (14)	TT (1)	0.105	0.052	0.758
		0.533	0.462	0.667	0.467	0.538	0.333			

Table 3. The efficiency of discrimination of 38 SNPs in high- and low-MUFA groups of Korean native cattle (n = 44) (Continued)

SNP	Region	Genotype (No. of head)						Discriminant coefficient	F-value	p-value
		High MUFAs group			Low MUFAs group					
		Frequency			Frequency					
g.54191-18176 G>A	Intron	AA (8)	AG (11)	GG (3)	AA (8)	AG (11)	GG (3)	0.000	0.000	1.000
		0.500	0.500	0.500	0.500	0.500	0.500			
g.56135-16232 T>C	Intron	CC (1)	CT (12)	TT (9)	CC (1)	CT (14)	TT (7)	0.000	0.000	1.000
		0.500	0.462	0.562	0.500	0.538	0.438			
g.56223-16144 T>C	Intron	CC (0)	CT (8)	TT (14)	CC (0)	CT (9)	TT (13)	–0.177	0.089	0.757
		0.000	0.471	0.519	0.000	0.529	0.481			
g.57085-15282 T>C	Intron	CC (8)	CT (11)	TT (3)	CC (9)	CT (9)	TT (4)	0.839	0.042	0.818
		0.471	0.550	0.429	0.529	0.450	0.571			
g.60868-11499 C>T	Intron	CC (10)	CT (12)	TT (0)	CC (10)	CT (12)	TT (0)	0.000	0.000	1.000
		0.500	0.500	0.000	0.500	0.500	0.000			
g.60917-11450 A>G	Intron	AA (9)	AG (8)	GG (5)	AA (10)	AG (5)	GG (7)	–0.231	0.347	0.583
		0.474	0.615	0.417	0.526	0.385	0.583			
g.61873-10494 G>T	Intron	GG (7)	GT (12)	TT (3)	GG (8)	GT (13)	TT (1)	0.338	0.507	0.575
		0.467	0.480	0.750	0.533	0.520	0.250			
g.62724-9643 C>T	Intron	CC (0)	CT (14)	TT (8)	CC (0)	CT (13)	TT (9)	0.177	0.089	0.757
		0.000	0.519	0.471	0.000	0.481	0.529			
g.63097-9270 A>G	Intron	AA (4)	AG (11)	GG (7)	AA (4)	AG (10)	GG (8)	0.000	0.000	1.000
		0.500	0.524	0.467	0.500	0.476	0.533			
g.63137-9230 A>T	Intron	AA (0)	AT (8)	TT (14)	AA (0)	AT (10)	TT (12)	0.362	0.362	0.540
		0.000	0.444	0.538	0.000	0.556	0.462			
g.69435-2932 C>T	Intron	CC (3)	CT (10)	TT (9)	CC (2)	CT (12)	TT (8)	0.177	0.089	0.802
		0.600	0.455	0.529	0.400	0.545	0.471			
g.72367 G>T	Exon 7	GG (13)	GT (6)	TT (3)	GG (3)	GT (16)	TT (3)	–0.941	5.642	0.005
		0.812	0.273	0.500	0.188	0.727	0.500			

SNPs, single nucleotide polymorphisms; MUFA, monounsaturated fatty acid.

SNPs evaluated ($p<0.05$). Linolenic acid had the highest content in GG, AA, and TT genotypes, but the opposite trend was observed for linoleic acid. Variations in linolenic acid showed trends similar to those in oleic acid and MUFA

Table 4. Effects of 2 SNPs at the intron on the fatty acid composition of intramuscular fat

Trait	g.1159-71208 A>G						g.42555-29812 G>A						Total
	AA (N = 134)	AG (N = 303)	GG (N = 76)	p-value	Genetic effect		AA (N = 83)	AG (N = 113)	GG (N = 317)	p-value	Genetic effect		(N = 513)
	LSM±SE	LSM±SE	LSM±SE		Additive	Dominance	LSM±SE	LSM±SE	LSM±SE		Additive	Dominance	LSM±SE
CW (kg)	422.49±3.52	430.25±2.52	423.66±5.09	0.165	-0.586±3.52	7.179±2.52	424.88±4.82	422.81±3.84	429.44±2.46	0.325	2.283±2.47	-4.348±3.84	427.25±1.91
BFT (mm)	12.70±0.46^{a}	13.07±0.27^{a}	14.71±0.66^{b}	0.018	-1.005±0.46	-0.633±0.28	13.53±0.59	12.59±0.47	13.36±0.28	0.330	-0.085±0.29	-0.852±0.48	13.22±0.22
MS	5.38±0.16	5.48±0.11	5.29±0.23	0.705	0.046±0.17	0.147±0.11	5.01±0.22	5.47±0.17	5.52±0.11	0.101	0.254±0.11	0.203±0.17	5.43±0.08
Fatty acid composition (%)													
C14:0	3.51±0.05^{a}	3.64±0.03^{a}	3.85±0.08^{b}	0.002	-0.166±0.05	-0.042±0.04	3.80±0.07^{b}	3.74±0.05^{a}	3.55±0.03^{a}	0.002	-0.119±0.04	0.070±0.06	3.63±0.02
C16:0	25.24±0.16^{a}	25.68±0.11^{a}	26.25±0.22^{b}	0.001	-0.506±0.16	-0.064±0.11	26.69±0.21^{c}	25.91±0.19^{b}	25.28±0.10^{a}	0.000	-0.707±0.1	-0.071±0.2	25.65±0.08
C18:0	10.44±0.10	10.44±0.08	10.72±0.16	0.260	-0.143±0.1	-0.142±0.08	10.88±0.17^{b}	10.56±0.12^{ab}	10.35±0.07^{a}	0.007	-0.265±0.08	-0.055±0.13	10.48±0.06
C14:1	1.27±0.02	1.23±0.02	1.26±0.03	0.562	0.003±0.03	-0.036±0.02	1.22±0.04	1.21±0.03	1.26±0.02	0.407	0.018±0.02	-0.035±0.03	1.24±0.01
C16:1	6.49±0.07	6.65±0.05	6.65±0.11	0.452	-0.043±0.07	0.085±0.06	6.50±0.11	6.49±0.08	6.67±0.05	0.128	0.087±0.05	-0.099±0.08	6.61±0.04
C18:1	45.00±0.22^{c}	44.32±0.14^{b}	42.94±0.30^{a}	0.000	1.031±0.22	0.356±0.15	43.09±0.28^{a}	43.83±0.25^{b}	44.79±0.14^{c}	0.000	0.848±0.14	-0.111±0.26	44.30±0.11
C18:2n6	2.95±0.07^{a}	3.01±0.04^{ab}	3.18±0.08^{b}	0.048	-0.112±0.07	-0.051±0.04	3.23±0.06^{b}	3.13±0.07^{ab}	2.93±0.04^{a}	0.001	-0.150±0.04	0.050±0.07	3.02±0.03
C18:3n3	0.41±0.02^{b}	0.33±0.01^{a}	0.32±0.02^{a}	0.001	0.044±0.02	-0.028±0.01	0.33±0.01	0.34±0.01	0.46±0.01	0.027	0.015±0.01	-0.008±0.02	0.35±0.01
SFA[1]	40.01±0.23^{a}	40.60±0.16^{a}	41.66±0.33^{b}	0.000	-0.825±0.23	-0.235±0.16	42.01±0.33^{c}	40.99±0.28^{b}	40.09±0.14^{a}	0.000	-0.954±0.15	-0.061±0.29	40.60±0.12
MUFA[2]	54.13±0.23^{b}	53.58±0.17^{b}	52.07±0.33^{a}	0.000	1.027±0.24	0.483±0.17	52.23±0.34^{a}	52.92±0.28^{a}	54.05±0.15^{b}	0.000	0.909±0.16	-0.219±0.28	53.50±0.13
M/S[3]	1.36±0.01^{b}	1.33±0.01^{b}	1.25±0.01^{a}	0.000	0.052±0.01	0.020±0.01	1.25±0.17^{a}	1.30±0.01^{b}	1.36±0.01^{c}	0.000	0.051±0.01	-0.002±0.02	1.33±0.01
C14 index[4]	26.54±0.53^{b}	25.01±0.37^{ab}	24.75±0.67^{a}	0.044	0.896±0.53	-0.641±0.38	24.26±0.82^{a}	24.35±0.57^{a}	26.03±0.34^{b}	0.012	0.886±0.34	-0.795±0.57	25.37±0.28
C16 index[5]	20.55±0.21	20.57±0.16	20.12±0.31	0.455	0.215±0.22	0.228±0.17	19.59±0.34^{a}	20.08±0.25^{a}	20.88±0.15^{b}	0.000	0.642±0.15	-0.164±0.26	20.50±0.12
C18 index[6]	81.15±0.18^{b}	80.94±0.14^{b}	80.00±0.28^{a}	0.003	0.573±0.18	0.355±0.14	79.83±0.31^{a}	80.56±0.22^{b}	81.23±0.12^{c}	0.000	0.699±0.13	0.034±0.23	80.85±0.10

SNPs, single nucleotide polymorphisms; LSM, least square mean; SE, standard error; CW, carcass weight; BFT, backfat thickness; MS, marbling scores from 1 to 9 (a larger score indicates more abundant intramuscular fat); SFA, saturated fatty acid; MUFA, mono unsaturated fatty acid; M/S, mono unsaturated fatty acid/saturated fatty acid ratio.

I_{C14} [C14:1/(C14:0+C14:1)]×100, I_{C16} [C16:1/(C16:0+C16:1)]×100, I_{C18} [C18:1/(C18:0+C18:1)]×100.

Mean values with different superscripts in the same row for each SNP indicate statistical differences ($p<0.05$); * $p<0.05$, ** $p<0.01$, and *** $p<0.001$.

Table 5. Effects of the g.72362 G>T genotype at exon 7 on the fatty acid composition of intramuscular fat

Trait	g.72362 G>T			p-value	Genetic effect		Total
	GG (N = 302)	GT (N = 160)	TT (N = 51)				(N = 513)
	LSM±SE	LSM±SE	LSM±SE		Additive	Dominance	LSM±SE
CW (kg)	428.70±2.49	423.38±3.36	430.80±6.32	0.375	–1.054±2.49	–6.375±3.37	427.25±1.91
BFT (mm)	12.99±0.28	13.25±0.42	14.49±0.72	0.153	–0.752±0.29	–0.488±0.42	13.22±0.22
MS	5.62±0.11^{b}	5.27±0.15^{ab}	4.80±0.28^{a}	0.010	0.406±0.11	0.059±0.15	5.43±0.08
Fatty acid composition (%)							
C14:0	3.54±0.03^{a}	3.70±0.05^{a}	4.01±0.10^{b}	0.000	–0.238±0.03	–0.067±0.05	3.63±0.02
C16:0	25.34±0.10^{a}	25.81±0.16^{a}	26.95±0.30^{b}	0.000	–0.800±0.1	–0.332±0.16	25.65±0.08
C18:0	10.47±0.07^{a}	10.34±0.11^{a}	11.02±0.22^{b}	0.009	–0.278±0.08	–0.407±0.11	10.48±0.06
C14:1	1.23±0.02^{ab}	1.29±0.03^{b}	1.15±0.05^{a}	0.057	0.037±0.02	0.101±0.03	1.24±0.01
C16:1	6.57±0.05	6.73±0.08	6.46±0.15	0.127	0.057±0.05	0.216±0.08	6.61±0.04
C18:1	44.90±0.13^{c}	44.02±0.21^{b}	41.58±0.31^{a}	0.000	1.660±0.14	0.780±0.22	44.30±0.11
C18:2n6	2.94±0.04^{a}	3.03±0.06^{a}	3.46±0.10^{b}	0.000	–0.260±0.04	–0.164±0.06	3.02±0.03
C18:3n3	0.37±0.01^{b}	0.34±0.01^{ab}	0.28±0.02^{a}	0.019	0.041±0.01	0.010±0.02	0.35±0.01
SFA[1]	40.23±0.14^{a}	40.67±0.23^{a}	42.58±0.46^{b}	0.000	–1.172±0.15	–0.733±0.23	40.60±0.12
MUFA[2]	54.03±0.15^{b}	53.44±0.25^{b}	50.57±0.38^{a}	0.000	1.729±0.15	1.142±0.25	53.50±0.13
M/S[3]	1.35±0.01^{b}	1.32±0.01^{b}	1.19±0.02^{a}	0.000	0.078±0.01	0.051±0.01	1.33±0.01
C14 index[4]	25.64±0.37^{b}	25.81±0.47^{b}	22.38±0.82^{a}	0.002	1.628±0.37	1.803±0.48	25.37±0.28
C16 index[5]	20.59±0.15^{b}	20.69±0.23^{b}	19.34±0.41^{a}	0.007	0.624±0.15	0.732±0.23	20.50±0.12
C18 index[6]	81.10±0.13^{b}	80.97±0.19^{b}	79.07±0.38^{a}	0.000	1.014±0.13	0.885±0.2	80.85±0.10

LSM, least square mean; SE, standard error; CW, carcass weight; BFT, backfat thickness; MS, marbling scores from 1 to 9 (a larger score indicates more abundant intramuscular fat); SFA, saturated fatty acid; MUFA, mono unsaturated fatty acid; M/S, mono unsaturated fatty acid/saturated fatty acid ratio.
IC14 [C14:1/(C14:0 + C14:1)] *100, IC16 [C16:1/(C16:0 + C16:1)] *100, IC18 [C18:1/(C18:0 + C18:1)] *100.
Mean values with different superscripts in the same row indicate significant differences ($p<0.05$); * $p<0.05$, ** $p<0.01$, and *** $p<0.001$.

content. However, the opposite trend was observed for linoleic acid. These results suggest that the consumption of meat from Korean native cattle with specific SNPs that alter levels of different fatty acids may enhance human health.

As shown in Table 4, g.1159-71208 A>G and g.42555-29812 G>A had additive effects on oleic acid, linoleic acid, linolenic acid, SFAs, and MUFAs ($p<0.05$). In addition, g.72362 G>T had an additive effect on MS, oleic acid, SFAs, and MUFAs. In particular, oleic acid (C18:1), an important factor influencing beef flavor, had significant additive effects (1.031, 0.848, and 1.660, respectively) on quantitative traits, and these effects were positive.

In general, *PPARγ* is a type of nuclear receptor superfamily with the N-Terminal domain, the DNA-binding domain, and the ligand-binding domain. Previous studies have reported that *PPARγ*, whose ligand-binding domain is bound by the ligand, forms a dimer with RXR, which is a 9-cis-retinoic acid receptor, and thus that it controls adipocyte differentiation by combining with the peroxisome proliferator response element (*PPRE*), which belongs to the area of the cis-acting element relevant to adipocyte differentiation (Kodera et al., 2000; Christine et al., 2005; Shanika et al., 2009). This ligand-binding domain consists of 154 amino acids ranging from the 321st valine to the 474th valine in Hanwoo (Jeoung et al., 2004). In particular, g.72367 G>T SNP (Gln1344His) is the 448th glutamine included in the ligand-binding domain. In addition, it may become a non-synonymous SNP that changes into histidine from glutamine as the CAG nucleotide changes into CAT (Oh et al., 2012). This suggests that fatty acid content may vary depending on the level of change in the amino acid of the ligand-binding domain because it affects adipocyte differentiation.

In conclusion, Korean native cattle with AA, GG, and GG genotypes at the g.1159-71208 A>G, g.42555-29812 G>A, and g.72362 G>T SNPs in the *PPARγ* gene had higher proportions of MUFAs and lower proportions of SFAs. In addition, animals with the GG genotype of g.72362 G>T had higher MSs. These individual SNPs may be effective genetic targets for improving beef quality and have considerable influence on the Korean native cattle industry.

CONFLICT OF INTEREST

We certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

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REFERENCES

Alexander, L. J., M. D. MacNeil, T. W. Geary, W. M. Snelling, D. C. Rule, and J. A. Scanga. 2007. Quantitative trait loci with additive effects on palatability and fatty acid composition of meat in a Wagyu-Limousin F_2 population. Anim. Genet. 38: 506-513.

Christine, Y., M. Kathleen, A. T. Karla, D. Dianne, J. B. Matthew, and N. C. Ronald. 2005. The nuclear receptor corepressors NCoR and SMRT decrease peroxisome proliferator-activated receptor γ transcriptional activity and repress 3T3-L1 adipogenesis. J. Biol. Chem. 280:13600-13605.

Chung, K. Y., D. K. Lunt, C. B. Choi, S. H. Chae, R. D. Rhoades, T. H. Adams, B. Booren, and S. B. Smith. 2006. Lipid characteristics of subcutaneous adipose tissue and *M. longissimus thoracis* of Angus and Wagyu steers fed to US and Japanese endpoints. Meat Sci. 73:432-441.

Eberle, M. A., M. J. Rieder, L. Kruglyak, and D. A. Nickerson. 2006. Allele frequency matching between snps reveals an excess of linkage disequilibrium in genic regions of the human genome. PLoS Genet. 2:e142.

Falconer, D. S. and T. F. C. Mackay. 1996. Introduction to Quantitative Genetics, fourth ed. Longman, London, England.

Fan, Y. Y., L. S. Zan, C. Z. Fu, W. Q. Tian, H. B. Wang, Y. Y. Liu, and Y. P. Xin. 2011. Three novel SNPs in the coding region of *PPARγ* gene and their associations with meat quality traits in cattle. Mol. Biol. Rep. 38:131-137.

Folch, J., M. Lee, and G. H. S. Stanley. 1957. A simple method for the isolation and purification of total lipides from animal tissues. J. Biol. Chem. 226:487-509.

Guan, H. P., T. Ishizuka, P. C. Chui, M. Lehrke, and M. A. Lazar. 2005. Corepressors selectively control the transcriptional activity of PPAR gamma in adipocytes. Genes Dev. 19: 453-461.

Hoashi, S., N. Ashida, H. Ohsaki, T. Utsugi, S. Sasazaki, M. Taniguchi, K. Oyama, F. Mukai, and H. Mannen. 2007. Genotype of bovine sterol regulatory element binding protein-1 (SREBP-1) is associated with fatty acid composition in Japanese Black cattle. Mamm. Genome 18:880-886.

Hua, L., J. Wang, F. Chen, S. Hu, and H. Chen. 2011. The peroxisome proliferators-ativated receptor gamma (PPARG) gene polymorphisms and associations with body measurements of cattle. Afr. J. Biotechnol. 10:2785-2790.

Iwaki, M., M. Matsuda, N. Maeda, T. Funahashi, Y. Matsuzawa, M. Makishima, and I. Shimomura. 2003. Induction of adiponectin, a fat-derived antidiabetic and antiatherogenic factor, by nuclear receptors. Diabetes 52:1655-1663.

Jeoung, Y. H., S. M. Lee, H. Y. Pack, D. H. Yoon, J. G. Choi, S. J. Moon, and M. J. Kang. 2004. Molecular Cloning mRNA Expression of the Bovine Peroxisome Proliperator Recepter Gamma (*PPARγ*). J. Anim. Sci. Technol. (Kor). 46:23-30.

Kersten, S., S. Mandard, P. Escher, F. J. Gonzalez, S. Tafuri, B. Desvergne, and W. Wahli. 2000. The peroxisome proliferator-activated receptor α regulates amino acid metabolism. FASEB J. 15:1971-1978.

Kim, J. H., C. H. Kim, and Y. D. Ko. 2002. Influence of dietary addition of dried wormwood (Artemisia sp.) of the performance and carcass characteristics of Hanwoo steers and the nutrient digestibility of sheep. Asian Australas. J. Anim. Sci. 15:390-395.

Kodera, Y., K. Takeyama, A. Murayama, M. Suzawa, Y. Masuhiro, and S Kato. 2000. Ligand type-specific interactions of peroxisome proliferatoractivated receptor γ with transcriptional coactivators. J. Biol. Chem. 275:33201-33204.

Laborde, F. L., I. B. Mandell, J. J. Tosh, J. W. Wilton, and J. G. Buchanan-Smith. 2001. Breed effects on growth performance, carcass characteristics, fatty acid composition, and palatability attributes in finishing steers. J. Anim. Sci. 79:355-365.

Lee, M. A., O. M. Keane, B. C. Glass, T. R. Manley, N. G. Cullen, K. G. Dodds, A. F. McCulloch, C. A. Morris, M. Schreiber, J. Warren, A. Zadissa, T. Wilson, and J. C. McEwan. 2006. Establishment of a pipeline to analyse non-synonymous SNPs in *Bos Taurus*. BMC Genomics 7:298.

Lee, S. H., D. H. Yoon, S. H. Hwang, E. Y. Cheong, O. H. Kim, and C. S. Lee. 2004. Relationship between monounsaturated fatty acid composition and stearoyl-CoA desaturase mRNA level in Hanwoo liver and loin muscle. J. Anim. Sci. Technol. (Kor). 46:7-14.

Lee, S. H., Y. M. Cho, S. H. Lee, B. S Kim, N. K. Kim, Y. H Choy, K. H. Kim, D. Yoon, S .K Im, S. J Oh, and E. W. Park. 2008. Identification of marbling-related candidate genes in M. longissimus dorsi of high- and low marbled Hanwoo (Korean Native Cattle) steers. BMB Rep. 41:846-851.

Mandell, I. B., J. G. Buchanan-Smith, and C. P. Campbell. 1998. Effects of forage vs grain feeding on carcass characteristics, fatty acid composition, and beef quality in Limousin-cross steers when time on feed is controlled. J. Anim. Sci. 76: 2619-2630.

Mangelsdorf, D. J. and R. M. Evans. 1995. The RXR heterodimers and orphan receptors. Cell 83:841-850.

Melton, S. L., M. Amiri, G. W. Davis, and W. R. Backus. 1982. Flavor and chemical characteristics of ground beef from grass-, forage-grain- and grain-finished steers. J. Anim. Sci. 55:77-87.

Nagai, S., C. Shimizu, M. Umetsu, S. Taniguchi, M. Endo, H. Miyoshi, N. Yoshioka, M. Kubo, and T. Koike. 2004. Identification of a functional peroxisome proliferator-activated receptor responsive element within the murine perilipin gene. Endocrinology 145:2346-2356.

Narukami, T., S. Sasazaki, K. Oyama, T. Nogi, M. Taniguchi, and H. Mannen. 2011. Effect of DNA polymorphisms related to fatty acid composition in adipose tissue of Holstein cattle. Anim. Sci. J. 82:406-411.

Oh, D., Y. Lee, C. Lee, E. Chung, and J. Yeo. 2012. Association of bovine fatty acid composition with missense necleotide polymorphism in exon7 of *peroxisome proliferator-activated receptor gamma* gene. Anim. Genet. 43:474.

O'Keefe, P. W., G. H. Wellington, L. R. Mattick, and J. R. Stouffer. 1968. Composition of bovine muscle lipids at various carcass locations. J. Food Sci. 33:188-192.

Reidiger, N. D., R. A. Othman, M. Suh, and M. H. Moghadasian. 2009. A systemic review of the roles of n-3 fatty acids in health and disease. J. Am. Diet. Assoc. 109:668-679.

Rosen, E. D. and B. M. Spiegelman. 2001. PPAR gamma: a nuclear regulator of metabolism, differentiation, and cell growth. J. Biol. Chem. 276:37731-37734.

Schulman, I. G., G. Shao, and R. A. Heyman. 1998. Transactivation by retinoid X receptor-peroxisome proliferator-activated receptor γ (*PPARγ*) heterodimers:

intermolecular synergy requires only the *PPARγ* hormone-dependent activation function. Mol. Cell. Biol. 18:3483-3494.

Shanika, P. S., M. S. Maria, M. D. Arpad, N. J. Daniel, J. B. Matthew, and N. C. Ronald. 2009. Altering PPAR ligand selectivity impairs adipogenesis by thiazolidinediones but not hormonal inducers. Obesity 17:965-972.

Shin, S. C. 2006. The Development of DNA Markers Related to Carcass and Meat quality Traits in Korean Cattle. MS thesis, Sang Ji University, Wonju, Korea.

Shin, S. C., M. J. Kang, and E. R. Chung. 2007. Identification of a novel SNP associated with meat quality in C/EBPα gene of Korean cattle. Asian Australas. J. Anim. Sci. 20:466-470.

Smith, S. B., C. A. Gill, D. K. Lunt, and M. A. Brooks. 2009. Regulation of fat and fatty acid composition in beef cattle. Asian Australas. J. Anim. Sci. 22:1225-1233.

Smith, S. B., A. Yang, T. W. Larsen, and R. K. Tume. 1998. Positional analysis of triacylglycerols from bovine adipose tissue lipids varying in degree of unsaturation. Lipids 33:197-207.

Spiegelman, B. M. 1998. PPAR-gamma: adipogenic regulator and thiazolidinedione receptor. Diabetes 47:507-514.

Tsuji, S., K. Itoh, S. Sasazaki, H. Mannen, K. Oyama, M. Shojo, and F. Mukai. 2004. An association study using AFLP markers and application to a beef cattle breeding population. Anim. Genet. 35:40-43.

Venables, W. N. and B. D. Ripley. 2002. Modern Applied Statistics with S. 4th Edition. Springer, New York, USA.

Vreeland, W. N., R. J. Meagher, and A. E. Barron. 2002. Multiplexed, high-throughput genotyping by single-base extension and end-labeled free-solution electrophoresis. Anal. Chem. 74:4328-4333.

Wood, J. D., R. I. Richardson, G. R. Nute, A. V. Fisher, M. M. Campo, E. Kasapidou, P. R. Sheard, and M. Enser. 2004. Effects of fatty acids on meat quality: A review. Meat Sci. 66: 21-32.

Yang, A., T. W. Larsen, S. B. Smith, and R. K. Tume. 1999. ∆9-desaturase activity in bovine subcutaneous adipose tissue of different fatty acid composition. Lipids 34:971-978.

Yu, C., K. Markan, K. A. Temple, D. Deplewski, M. J. Brady, and R. N. Cohen. 2005. The nuclear receptor corepressors NCoR and SMRT decrease peroxisome proliferator-activated receptor gamma transcriptional activity and repress 3T3-L1 adipogenesis. J. Biol. Chem. 280:13600-13605.