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Effect of Single Nucleotide Polymorphisms of Acetyl-CoA Carboxylase α (ACACA) Gene on Carcass Traits in Hanwoo (Korean Cattle)

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ABSTRACT : Meat production and quality traits in beef cattle are largely affected by genetic factors. Acetyl-Coenzyme A carboxylase-α (ACACA) plays a key role in the regulation and metabolism of fatty acid biosynthesis in mammalian animals. The gene encoding ACACA enzyme was chosen as a candidate gene for carcass and meat traits. In this study, we investigated effects of single nucleotide polymorphisms (SNPs) in the ACACA gene on beef carcass and meat traits in Hanwoo (Korean cattle) populations. We have sequenced a fragment of intron I region of the Hanwoo ACACA gene and identified two SNPs. Genotyping of the two SNP markers (g.2344T>C and g.2447C>A) was carried out using PCR-SSCP analysis in 309 Hanwoo steers to evaluate their association with carcass and meat production traits. The g.2344C SNP marker showed a significant increasing effect on LW ($p = 0.009$) and CW ($p = 0.017$). Animals with the CC genotype had higher CW and LW compared with TT and TC genotypes ($p<0.05$). The g.2447A SNP marker was associated with higher MC ($p = 0.019$). Animals with the AA genotype had higher MC than animals with CC and CA genotypes ($p<0.05$). Although the degree of linkage disequilibrium (LD) was not strong between g.2344T>C and g.2447C>A in the LD analysis, four major haplotype classes were formed with two SNP information within the ACACA gene. We constructed haplotypes using the HaploView software package program and analyzed association between haplotypes and carcass traits. The haplotype of ACACA gene significantly affected the LW ($p = 0.027$), CW ($p = 0.041$) and MC ($p = 0.036$). The effect of h1 haplotype on LW and CW was larger than that of h3 haplotype. Animals with the h1 haplotype also had greater MC than did animals with h2 haplotype. Consequently, the ACACA gene could be useful as a DNA marker for meat production traits such as carcass yield and meat contents in Hanwoo. (**Key Words :** Acetyl-CoA Carboxylase Gene, SNP Marker, Carcass Traits, Hanwoo)

INTRODUCTION

A primary goal of the beef industry in Korea is to efficiently produce higher yield and higher marbling scores. Carcass traits such as meat quality and quantity in cattle are economically important traits in the beef industry and the physiological regulation of meat traits is under the control of multiple genes. In meat production, there are many genes involved in metabolic processes that control growth and differentiation of the tissue cells. Recently, the development of the field of animal genomics has stimulated interest in improving carcass and meat traits. Functional genomics and gene information provide new opportunities for understanding the molecular mechanisms and processes in muscle growth, development and meat quality traits (Bendixen, 2005; Plastow et al., 2005). Candidate genes are those with relationship between the trait of interest and known genes that may be associated with the physiological pathways underlying the trait (Gao et al., 2007). The possible effects of these genes on carcass and meat traits can be judged based upon the known involvement of the gene product in cellular or metabolic processes (Haegeman et al., 2003). In beef cattle, genes associated with fatty acid metabolism and lipogenesis are excellent candidate genes for meat production traits.

Acetyl-CoA carboxylase is the major enzyme in the regulation of fatty acid synthesis in animal tissues and is regulated by the Acetyl-CoA carboxylase-α (ACACA) gene (Travers and Barber, 2001). The ACACA is highly expressed in lipogenic tissues such as adipose tissues, lactating mammary gland and liver (Zhang et al., 2009). In

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higher animals, increases in the cellular activity of acetyl-CoA carboxylase results in an increased production of malonyl-CoA (Travers and Barber, 2001). The essential role of ACACA in fatty acid metabolism of animal tissue makes this gene an interesting candidate for explaining the influence of genetic effects on meat quality and quantity traits in beef cattle. Recently, Zhang et al. (2009) reported that SNP marker in the promoter I region of the bovine ACACA gene was associated with lipid-related traits such as beef fatty acid composition. However, the effects of this gene on any other carcass and meat traits have not been evaluated. The objective of this study was to identify SNP markers in the ACACA gene and to use them to investigate the effects of the ACACA gene polymorphisms on carcass and meat production traits in populations of Hanwoo.

MATERIALS AND METHODS

Animals and carcass data

A total of 309 Hanwoo steers with pedigree information and carcass data, from animals of the 32nd and 33rd progeny test, were from Hanwoo Experiment Station of the National Livestock Research Institute (NLRI). All steers of the national progeny-testing population were fed under the tightly controlled conditions of the feeding program and the means and standard deviation (SD) of phenotypic values are shown in Table 1. The carcass data analyzed were live weight (LW), carcass weight (CW), dressing percentage (DP), backfat thickness (BF), M. *Longissimus dori* area (EMA), marbling score (MS), meat color (MC), fat color (FC), texture (TEX). Genomic DNA was extracted from each animal whole blood using Salting-out protocol on whole blood (Miller et al., 1988).

Sequencing and SNP discovery

To detect SNPs in ACACA gene, primer pairs were designed based on the DNA sequence of the bovine ACACA gene GenBank accession no. AJ430417 that included intron I. The ACACA gene was amplified by PCR using the following primers: forward primer-1 (5′-GACTCCTTCTTTTCTTTCGTTTAT-3′) and reverse primer-1 (5′-TTTTTGGCCAATGAGTCTTC-3′); forward primer-2 (5′-GAACACCGAAGACTCATTGG-3′) and reverse primer-2 (5′- ACTGGCACGTGGGTTCTTT-3′). The PCR reaction was performed in a 20 μl reaction mixture containing 10 pmol of each primer, 1.5 mM $MgCl_2$, 200 μM of each dNTP and 1 unit of *Taq* DNA polymerase, 10× reaction buffer and 50 ng of genomic DNA as template. The PCR conditions were 94°C for 5 min, followed by 35 cycles of 94°C for 1 min, 51-58°C for 1 min and 72°C for 1 min, with a final extension at 72°C for 5 min. After completion of the PCR reaction, the amplified fragment was subjected to sequence analysis.

For sequencing of the ACACA gene, the PCR products were cloned into PCR 2.1 TOPO (Invitrogen B.V., Groningen, Netherlands) following the manufacturer's protocol. Positive clones were sequenced using an automated DNA sequencer (ABI 310, Perkin-Elmer, Foster City, CA, USA) with BigDye 3.1 reagents.

Table 1. Means, standard deviations (SD) and extreme values of phenotypic values measured on each trait in Hanwoo population

Traits	No.	Mean±SD	Minimum	Maximum
LW/kg	309	538.22±52.70	390.00	690.00
CW/kg	309	307.29±33.27	212.00	401.00
DP/%	309	57.10±1.64	52.60	62.40
BF/cm	309	0.70±0.29	0.20	1.80
EMA/cm^2	309	75.46±8.33	54.00	97.00
MS/1-7	309	2.22±1.37	1.00	7.00
MC/1-7	309	4.82±0.53	2.00	7.00
FC/1-7	309	2.99±0.15	2.00	4.00
TEX/1-3	309	1.31±0.66	1.00	3.00

LW = Live weight; CW = Carcass weight; DP = Dressing percentage; BF = Backfat thickness; EMA = M. *Longissimus dori* area; MS = Marbling score; MC = Meat color; FC = Fat color; TEX = Texture.

SNP genotyping using PCR-SSCP

Genotyping of two SNPs located at positions g.2344T>C and g.2447C>A (numbering was done according to GenBank accession no. AJ430417) within the intron I region of the ACACA gene was performed by a PCR-single strand conformation polymorphism (SSCP) method, because there is no restriction site for these SNPs. The PCR amplification was carried out using forward (5′-CCTCGACTCCTTCTTTTCTT-3′) and reverse (5′-GCAAAAGTGCCTATCAAATA-3′) primers designed for amplification of a 202 bp fragment including g.2344T>C SNP site, forward (5′-TGGGTGCCTATTTATTTGAT-3′) and reverse (5′-GAGGCAAGAGAAGTGAGTTG-3′) primers designed for amplification of a 214 bp fragment including g.2447C>A SNP site. The 20 μl reaction mixture contained 50 ng of genomic DNA, 0.05 μM of each primer, 10× PCR buffer, 1.5 mM $MgCl_2$, 250 μM of each dNTP and 1 unit *Taq* polymerase. Amplification conditions were 94°C for 5 min followed by 35 cycles of 94°C for 30 s, 53°C for 30 s and 72°C for 30 s, with a final extension at 72°C for 5 min in a DNA thermal cycler (Perkin Elmer Cetus, Norwalk, CT). After PCR amplification, 1 μl of PCR product was mixed with 4 μl of gel loading solution containing 95% formamide, 20 mM EDTA, 0.05% bromophenol blue and 0.05% xylene cyanol. The mixture was denaturated at 95°C for 5 min, cooled on ice for 10 min and loaded on nondenaturing 12% polyacrylamide gels (49:1 acrylamide to bis-acrylamide). Electrophoresis was performed in 1×

TBE buffer at 250 V for 6-7 h at room temperature. After electrophoresis, the DNA fragments in the gel were detected by silver staining.

Statistical analysis

Allele and genotype frequencies were calculated by simple allele counting method (counting the number of genes; Nei, 1987) (Falconer and Mackay, 1996). Hardy-Weinberg equilibrium (HWE) in the examined population was tested by comparing expected and observed genotype frequencies using a Chi-square test. The PROC GLM procedure of SAS (SAS, Inst. Inc., Cary NC, 2008) was used to test the association between SNP marker genotypes of the ACACA gene and carcass and meat quality traits. The linear model used was as follows:

$$Y_{ijklm} = \mu + S_i + YS_j + SP_k + A_l + G_m + e_{ijklm}$$

Where Y_{ijklm} is the observation of the carcass traits, μ is the overall mean for each trait, S_i is the effect of sire, YS_j is the effect of i_{th} year and season of calving, SP_k is the effect of slaughter place, A_l is the effect of age at slaughter (covariate), G_m is the fixed effect of SNP genotype and e_{ijklm} is the random residual effect.

Linkage disequilibrium (LD) between SNP pairs was measured using D' and r^2. HaploView software package was used for LD analysis (Barrett and Cardon, 2006). We constructed haplotypes using the HaploView software package program and analyzed association between haplotypes and carcass traits in a population of Hanwoo.

RESULTS

SNP identification and genotyping

For SNP detection of the ACACA gene in Hanwoo, a mixed DNA sample from 100 unrelated Hanwoo steers was amplified and sequenced. We identified two SNPs (g.2344T>C and g.2447C>A) by sequencing analysis of the ACACA gene (Figure 1). Genotyping of the two SNPs (g.2344T>C and g.2447C>A) within intron I of the ACACA gene was performed by a PCR-SSCP method (Figure 2). The allele and genotype frequencies are shown in Table 2. In g.2344T>C SNP, the frequency of allele T (51.7%) was almost the same that of allele C (48.3%). In g.2447C>A SNP, the frequency of allele C (56.8%) was higher than that of allele A (43.2%). The genotypic frequencies were as follows: 27.2% TT, 49.0% TC and 23.8% CC for the g.2344T>C SNP; 33.3% CC, 46.9% CA and 19.8% AA for the g.2447C>A SNP.

Gene-specific SNP marker association analysis

The results of the SNP markers association analysis are presented Table 3 and 4. At the SNP marker of g.2344T>C, the C allele showed a significant increasing effects on LW ($p = 0.009$) and CW ($p = 0.017$). Animals with the CC genotype had higher LW and CW than animals with TT or TC genotype ($p<0.05$). This SNP marker also showed a significant additive effects for the LW and CW ($p<0.05$). At

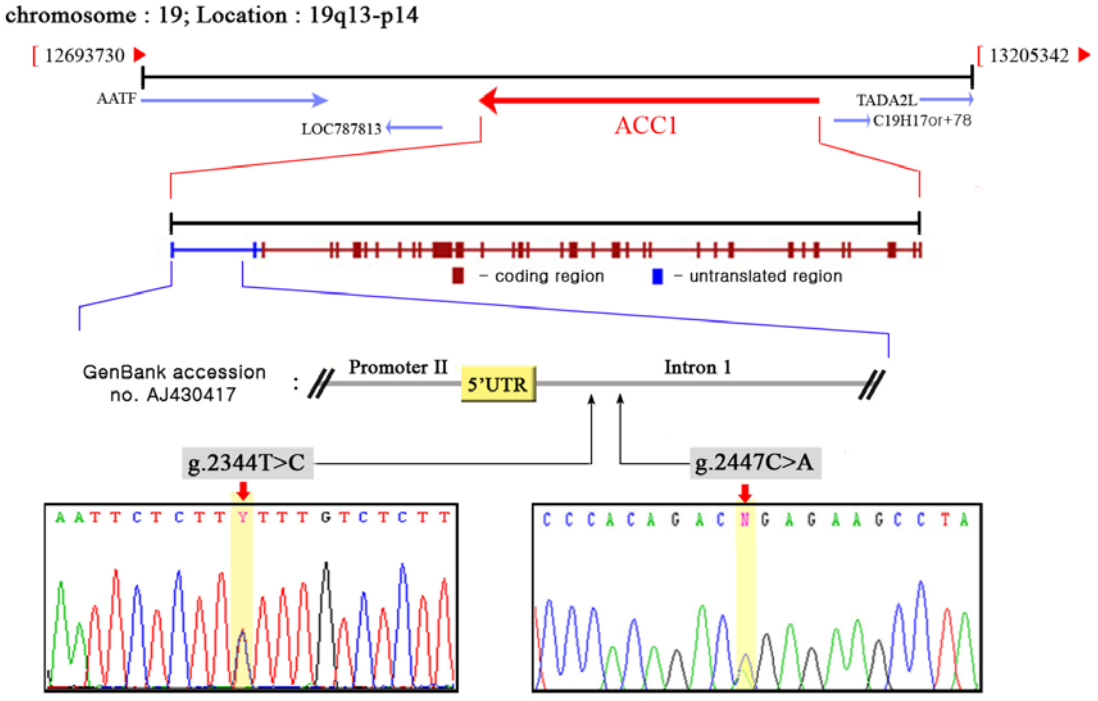

Figure 1. SNP map of ACACA gene in Hanwoo. Two SNPs were (g.2344T>C and g.2447C>A) identified by DNA sequencing.

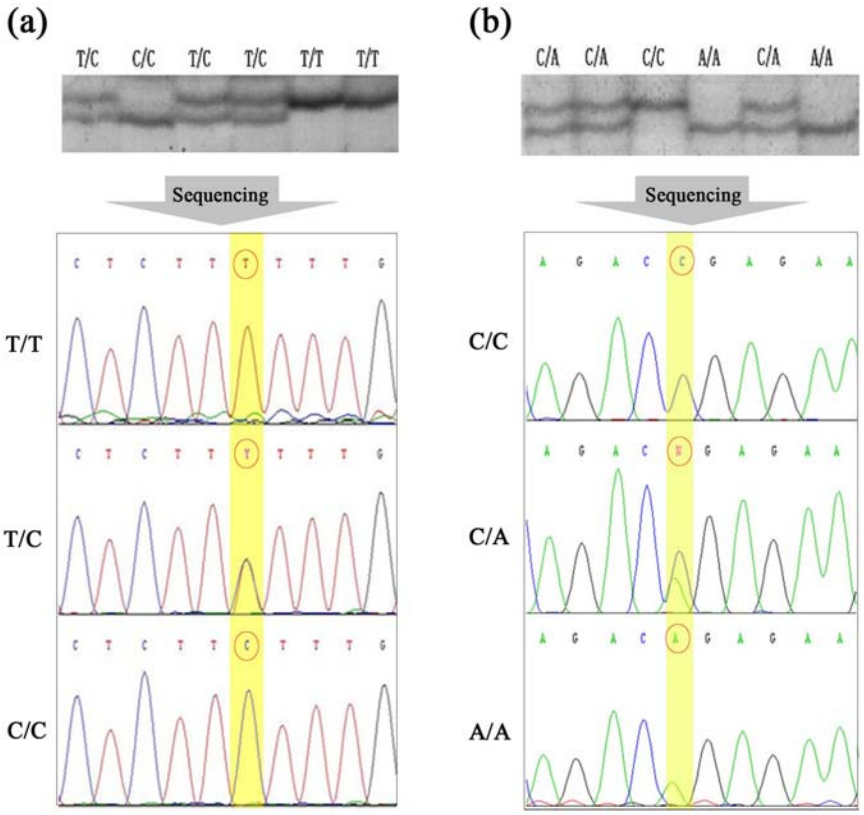

Figure 2. PCR-SSCP and DNA sequencing results for two SNPs of the ACACA gene in Hanwoo. (a) Demonstration of all three genotypes (T/T, T/C and C/C) for g.2344T>C SNP. (b) Demonstration of all three genotypes (C/C, C/A and A/A) for g.2447C>A SNP.

Table 2. Genotype and allele frequencies of two SNPs within the ACACA gene in Hanwoo population

SNP	Frequencies (%)					He	PIC	x^2	HWE*
	Genotype			Allele					
g.2344T>C	TT	TC	CC	T	C	0.499	0.375	0.144	0.930
	27.2	49.0	23.8	51.7	48.3				
g.2447C>A	CC	CA	AA	C	A	0.491	0.370	0.585	0.746
	33.3	46.9	19.8	56.8	43.2				

He = Heterozygosity, PIC = Polymorphic information contents. * p-values of Hardy-Weinberg equilibrium.

Table 3. Least square means and standard errors for carcass traits of different g.2344T>C SNP genotype of ACACA gene in Hanwoo population

Traits	SNP genotype			p-value	Effect	
	TT	TC	CC		Additive	Dominance
LW/kg	538.000±7.879[b]	537.500±5.872[b]	567.714±8.423[a]	0.009	29.714±11.534*	30.714±16.462
CW/kg	307.389±5.077[b]	307.525±3.784[b]	325.400±5.428[a]	0.017	17.875±7.432*	18.147±10.608
DP/%	57.132±0.246	57.126±0.183	57.280±0.263	0.881	0.147±0.360	0.159±0.515
BF/cm	0.655±0.043	0.618±0.032	0.691±0.046	0.417	0.036±0.063	0.110±0.090
EMA/cm^2	75.075±1.298	74.500±0.967	76.485±1.388	0.503	1.410±1.900	2.560±2.713
MS/1-7	1.950±0.196	2.000±0.146	2.342±0.209	0.320	0.392±0.287	0.292±0.409
MC/1-7	4.825±0.086	4.791±0.064	4.885±0.092	0.707	0.060±0.126	0.127±0.180
FC/1-7	3.000±0.029	2.986±0.021	2.942±0.031	0.374	-0.057±0.042	-0.029±0.060
TEX/1-3	1.300±0.101	1.277±0.075	1.257±0.108	0.959	-0.042±0.148	0.001±0.212

LW = Live weight; CW = Carcass weight; DP = Dressing percentage; BF = Backfat thickness; EMA = M. *Longissimus dori* area; MS = marbling score; MC = Meat color; FC = Fat color; TEX = Texture.
* Effect was significant at p<0.05. [a, b] Within a row, means with different superscript letter differ (p<0.05).

the SNP marker of g.2447C>A, the A allele showed a significant increasing effect on MC (p = 0.019). Animals with the AA genotype had higher MC than animals with CC or CA genotype (p<0.05). This SNP marker also showed a significant additive effect for the MC (p<0.05).

Haplotype association analysis

To determine the effects of combined SNPs, haplotypes were constructed by these SNPs. HaploView software package (Barrett and Cardon, 2006) was used for LD analysis of the SNP markers. We investigated an association between haplotype of the ACACA gene and carcass traits in a population of Hanwoo. Results of the haplotype association analysis are presented in Table 5. Although the degree of LD was not strong between g.2344T>C and g.2447A>T, four major haplotype classes were formed with the two SNP information within the ACACA gene. We constructed haplotypes using the HaploView software package program and analyzed association between haplotypes and carcass traits.

As shown in Table 5, the haplotypes of ACACA gene significantly affected the LW (p = 0.027), CW (p = 0.041) and MC (p = 0.036). Animals with the h1 haplotype had higher LW and CW than animals with h3 haplotype (p<0.05) and higher MC compared with h2 haplotype (p<0.05). In this population, haplotype h3 was dominant with a frequency of 58.6% of the total expressed haplotypes, whereas the frequency of h1 haplotype was found only 12.9%.

Table 4. Least square means and standard errors for carcass traits of different g.2447C>A SNP genotype of ACACA gene in Hanwoo population

Traits	SNP genotype			p-value	Effect	
	CC	CA	AA		Additive	Dominance
LW/kg	538.000±7.235	546.027±6.204	553.793±9.500	0.405	15.793±11.941	-0.265±17.221
CW/kg	307.640±4.650	312.985±3.987	315.758±6.105	0.521	8.118±7.675	-2.571±11.068
DP/%	57.150±0.220	57.269±0.188	56.944±0.288	0.641	-0.205±0.036	-0.443±0.523
BF/cm	0.618±0.038	0.670±0.033	0.634±0.050	0.573	0.016±0.064	-0.088±0.092
EMA/cm^2	74.040±1.159	75.250±0.993	76.724±1.521	0.371	2.684±1.913	0.264±2.758
MS/1-7	2.020±0.175	1.985±0.150	2.344±0.230	0.406	0.324±0.290	0.394±0.418
MC/1-7	4.800±0.075[b]	4.735±0.064[b]	5.068±0.099[a]	0.019	0.268±0.124*	0.398±0.179
FC/1-7	2.960±0.026	2.985±0.022	3.000±0.034	0.612	0.400±0.043	-0.010±0.062
TEX/1-3	1.300±0.090	1.205±0.077	1.413±0.118	0.329	0.113±0.148	0.302±0.214

LW = Live weight; CW = Carcass weight; DP = Dressing percentage; BF = Backfat thickness; EMA = M. *Longissimus dori* area; MS = Marbling score; MC = Meat color; FC = Fat color; TEX = Texture.
* Effect was significant at p<0.05. [a, b] Within a row, means with different superscript letter differ (p<0.05).

Table 5. Least square means and standard errors for carcass traits of different haplotypes of ACACA gene in Hanwoo population

Traits	Haplotype				p-value
	h1 (12.9%)*	h2 (21.7%)	h3 (58.6%)	h4 (6.8%)	
LW/kg	573.157±11.480[a]	543.125±8.846[ab]	517.000±15.824[b]	542.441±5.396[ab]	0.027
CW/kg	327.157±7.411[a]	312.312±5.710[ab]	294.100±10.215[b]	310.127±3.483[ab]	0.041
DP/%	57.021±0.357	57.443±0.275	56.800±0.492	57.134±0.167	0.622
BF/cm	0.684±0.062	0.643±0.048	0.540±0.086	0.650±0.029	0.599
EMA/cm^2	78.105±1.880	74.562±1.449	74.100±2.592	74.802±0.883	0.402
MS/1-7	2.526±0.284	2.062±0.219	2.000±0.392	1.976±0.133	0.382
MC/1-7	5.105±0.122[a]	4.687±0.094[b]	5.000±0.169[ab]	4.790±0.057[ab]	0.036
FC/1-7	3.000±0.041	2.906±0.032	3.000±0.057	3.000±0.019	0.088
TEX/1-3	1.368±0.147	1.281±0.113	1.500±0.202	1.232±0.069	0.571

LW = Live weight; CW = Carcass weight; DP = Dressing percentage; BF = Backfat thickness; EMA = M. *Longissimus dori* area; MS = Marbling score; MC = Meat color; FC = Fat color; TEX = Texture.
[a, b] Within a row, means with different superscript letter differ ($p<0.05$). * Haplotype frequencies.

DISCUSSION

Meat quality and quantity are of economic importance in farm animals and are controlled by multi- genes and various environmental factors. Recently, advances in molecular genetics and genomic technologies have led to the identification of genes or markers associated with genes that affect the meat quality and quantity traits in beef cattle (Gao et al., 2007). Genes related to lipid metabolism of the beef cattle are potential markers because of their important role in fat deposition and synthesis. So far, several genes involved in the meat quality and quantity traits have been reported in cattle. DNA markers such as thyroglobulin, leptin, calpain, calpastatin and stearoyl-CoA desaturase genes associated with meat quality traits have become commercially available in beef industry (Gao et al., 2007). Because the meat production trait is a complex trait controlled by multi-genes and the environment, although there are some commercially available markers for beef meat, further marker gene information associated with meat production traits is required for improving carcass traits by using marker-assisted selection.

In the production of meat there are many genes involved in metabolic processes that control growth and differentiation of the composite cells (Arnyasi et al., 2006). ACACA is a key enzyme in the regulation of fatty acid synthesis and is subject to both acute control, via reversible phosphorylation and chronic control that results in the regulation of synthesis of the enzyme (Travers and Barber, 2001). The gene for ACACA highly expressed in lipogenic tissues such as adipose tissues, lactating mammary gland and liver (Ponce-Castaneda et al., 1991; Abu-Elheiga et al., 1995). The complete sequence of the bovine ACACA cDNA was reported by Mao et al. (2001). This sequence is 7,041 bp, maps to chromosome 19, and encodes a protein with a high similarity to those of human, rat, sheep and chicken (Mao et al., 2001). The control of ACACA in the adipose tissue of ruminants is of special interest because the products of their metabolic pathway play an important role in energy storage and may also be mobilized for oxidation to meet dietary energy deficits or for increased thermogenic requirements (Moibi et al., 2000). Because of the specific role of ACACA in adipose tissue, we hypothesized that variations of the ACACA gene among individuals would be a candidate for differences in carcass traits of beef cattle.

In the present study, we identified two novel SNPs in intron I of the ACACA gene and the associations of these SNPs with various carcass trait data including live weight, carcass weight, dressing percentage, backfat thickness, M. *Longissimus dori* area, marbling score, meat color, fat color and texture were investigated. In both single and combined SNPs of ACACA gene, the SNP marker had a significant effect on LW, CW and MC. Animals expressing genotype CC had increased LW and CW at g.2344T>C, whereas genotype AA animals had a higher MC at g.2447C>A. In the combined SNPs effect, haplotype h1 had higher LW, CW and MC compared with other haplotypes. The haplotype analysis can be more powerful than individual SNP analysis (Pannier et al., 2009). Therefore, gene-specific SNPs identified in this study may be a potential candidate DNA marker for meat quantity of Korean cattle. However, meat quality traits such as BACKFAT THICKNESS, M. *LONGISSIMUS DORI* AREA and marbling score were not affected by ACACA gene polymorphisms in this population examined. The ACACA gene is known to influence the biosynthesis of fatty acids. Therefore, we expected that the novel SNPs influenced meat quality traits such as marbling and backfat thickness.

However, the ACACA gene polymorphisms have proved to influence meat quantity such as live and carcass weights, instead of meat quality. It is possible that ACACA SNP marker is in linkage disequilibrium with QTL that causes either gene expression or phenotypic variation on muscle growth and carcass weight. However, additional analysis using different population is needed to confirm the effect of SNP marker of ACACA gene.

Recently, Zhang et al. (2009) identified eight novel SNPs in the promoter I region of the ACACA gene in cross-bred cattle, which were AJ276223:g.2064T>A, g.2155C>T, g.2203G>T, g.2268T>C, g.2274G>A, g.2340A>G, g.2350T>C and g.2370A>G. The genotypes of SNP were significantly associated with adjusted backfat thickness, triacylglycerol content and fatty acid composition of *longissimus dorsi* muscle in Brangus-, Romosinuano- and Bonsmara-sired cattle. Cattle with g.2203GG genotype had greater concentrations of triacylglycerol content, total lipid, total saturated fatty acid and total monounsaturated fatty acid than did cattle with g.2203GT genotype. The genotypes of g.2350T>C were significantly associated with fatty acid composition of *longissimus dorsi* muscle. Cattle with genotype g.2350TC had greater amounts of several fatty acids in *longissimus dorsi* muscle than cattle with genotype g.2350CC. Their results suggested that the SNPs of ACACA gene are associated with variations in the fatty acid contents in *longissimus dorsi* muscle. Since promoter region of ACACA gene is also good candidate SNP marker for carcass traits, investigation using the markers of promoter would be important in beef cattle population. On the other hand, a few studies detected SNPs in the promoter or exon region of ACACA gene in sheep (Moioli et al., 2005; Federica et al., 2008) and goat (Badaoui et al., 2007), and investigated the associations of SNP marker with milk production traits. Results from their studies showed that the SNP marker was associated with fat yield, lactose content and somatic cell count.

In conclusion, although no significant effects on other carcass traits except for LW, CW and MC, results of the present study suggested that the SNPs and haplotypes in the intron I region of ACACA gene were significantly associated with some carcass traits in Hanwoo. Therefore, the ACACA gene could be useful as a DNA marker for meat production traits such as carcass yield and meat contents in Hanwoo. However, further studies are needed to evaluate the possible association between SNP markers of ACACA gene and other carcass traits, especially in meat quality traits. Also, our results show that PCR-SSCP analysis is a simple and efficient technique for the detection of single base substitution and can be employed for evaluating SNP markers of ACACA gene in Hanwoo populations.

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