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Full Length Research Paper

Association analysis of polymorphism in *KIAA1717*, *HUMMLC2B*, *DECR1* and *FTO* genes with meat quality traits of the *Berkshire* breed

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Single nucleotide polymorphisms (SNPs) in *KIAA1717*, *HUMMLC2B*, *DECR1,* and *FTO* genes have been found to be associated with some pork meat quality traits. In this study, we discovered that, in addition to meat quality traits reported previously, SNPs in these genes also are significantly associated with other meat quality traits in the *Berkshire* breed. A total of 323 *Berkshire* pigs bred under the same conditions were used for meat quality evaluation and polymerase chain reaction-amplified genes with restriction endonucleases (PCR-RFLP) genotyping analyses. The association analysis of RFLP genotyping with meat quality traits revealed that the SNPs in these 4 genes have novel associations with multiple meat quality traits ($p < 0.01$ or $p < 0.05$); a SNP in *KIAA1717* was associated with meat color (*CIE* L), backfat thickness, drip loss, water-holding capacity, and pH_{24hr}; a SNP in *HUMMLC2B* was associated with chemical composition (collagen), drip loss, shear force, and pH_{24hr}; a SNP in *DECR1* was associated with meat color (*CIE* a and b) and backfat thickness; and a SNP in *FTO* was associated with meat color (*CIE* L, a and b), protein content, drip loss, and water-holding capacity. Taken collectively, our results suggest that these 4 SNPs may be used for marker-assisted selection as a genetic marker for meat quality traits in *Berkshire* pigs.

Key words: Berkshire, genetic markers, meat quality, SNP

INTRODUCTION

During conversion of muscle to meat after slaughter, pork meat quality traits have been reported to rely on the coordination of genetic effects (Warner et al., 2010; Wood et al., 2008). For example, meat tenderness is determined by various factors such as sarcomere length, the contribution of connective tissue and post-mortem protease activity, which is influenced by genetic inheritance (Warner et al., 2010). Accordingly, there have been many efforts to identify significant associations between genetic effects and meat quality traits.

Differences in the genetic effects between individuals result from genetic variations such as DNA sequence- and structure-dependent differences (Dalvit et al. 2007; Williams 2008). Especially, the single nucleotide polymorphism

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Abbreviations: RFLP, Restriction fragment length polymorphism; **SNP,** single nucleotide polymorphism.

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Table 1. Detailed information about SNPs of 4 genes analyzed in this study.

Gene	Accession no	Location	Primer sequence F/R (5' → 3')	Tm (℃)	Restriction enzyme	PCR-RFLP pattern (bp)
KIAA1717	AY900164	C1354T	TTGCAGGGCAGCAGAATCAG GGTCCCTGGAGTTTCCCAAT	60	MspI	647/506+141
HUMMLC2B	DQ629157	A345G	AGCACTTGTAAGTGACCCCC CCTTCCCCTATGTGCTGTGA	62	MspI	440/319+121
DECR1	U94981	G114C	AGTTTTTCAGTTATGGGACAAAAA CACTGAGCACCTAGGCTGGA	55	BfaI	190/114+76
FTO	ss86352279	p.Ala198Ala (Exon 3)	TGCAGATTGAGACCATCCAG TCTTCCCCATGCCAAAGTAG	60	BstUI	240/156+84

(SNP) is the most common DNA sequence-dependent variation, which has been reported to have broad effects on meat quality traits (Gao et al. 2007). For example, SNPs in *KIAA1717*, *HUMMLC2B*, *DECR1*, and *FTO* genes have been shown to be associated with pork meat quality traits; significant associations were observed for the *KIAA1717 C1354T* SNP site with meat marbling and intramuscular fat (Xu et al. 2007), the *HUMMLC2B A345G* SNP site with meat pH, drip loss, water-holding capacity, and meat color (Xu et al. 2007), the *DECR1 G181C* SNP site with pH24hr and meat color (Amills et al. 2005), and the FTO SNP site with fatness and residual feed intake (Fan et al. 2010). Therefore, these SNPs have been considered as potential genetic markers for marker-assisted selection.

KIAA1717 encodes a H3-K4-specific methyltransferase (H3-K4-HMTase) (also called SET7/9) with 3 MORN repeats and a SET domain (Wang et al. 2001; Xu et al. 2007) and also is reported to have significant effects on heterochromatin formation and transcriptional regulation (Nishioka et al. 2002). *HUMMLC2B* encodes a Ca2+-binding protein with EF-hand calcium-binding motif (Sachdev et al. 2003) and has been suggested to be involved in the Ca2+/CaM-mediated signaling pathway for influencing pork quality (Xu et al. 2005). DECR encodes the 2,4-dienoyl-CoA reductase that participates in the fatty acid β-oxidation pathway by catalyzing the reduction of trans-2-cis-4-dienoyl-CoA to 3-enoyl-CoA (KUNAU and DOMMES 1978). FTO (fat mass and obesity-associated) encodes a protein that shares a similar sequence motif with Fe(II) and 2-oxoglutarate-dependent oxygenases and is involved in fatty acid metabolism (Gerken et al. 2007). Thus, it is assumed that these genes play important roles in the signal transduction and metabolic pathways that have broad effects on meat qualities.

In this study, we carried out a meat quality evaluation in 323 *Berkshire* pigs and polymerase chain reaction-amplified genes with restriction endonucleases (PCR-RFLP) genotyping analyses of the 4 SNPs, to assess any significant associations between SNP genotype frequencies and meat quality traits. We identified significant associations between SNPs in these 4 genes and new meat quality traits, as well as previously reported qualities, in a *Berkshire* population. These results may provide SNP resources facilitating marker-assisted selection for genetic improvement of livestock such as the *Berkshire* pig.

MATERIALS AND METHODS

Animals and meat samples

A total of 323 *Berkshire* pigs were bred under the same conditions (Da-San-Jong-Don Co. Ltd., Namwon, Korea) and then slaughtered in 10 batches when their body weight reached 110 kg, as described previously (Jin et al., 2010). Subsequently, the samples were used for meat quality evaluation and PCR-RFLP genotyping analyses.

Meat quality evaluation and statistical analysis

Pork meat quality traits such as backfat thickness, carcass weight, meat color, drip loss, cooking loss, shear force, water-holding capacity, post-mortem pH and chemical composition (fat, protein, collagen and moisture) were evaluated and subjected to statistical analysis, as described previously (Park et al., 2010; Jin et al., 2010).

To clarify the associations between genotype and meat quality traits for each of the 4 genes, statistical analysis was performed with SAS version 9.1.3 (SAS Institute Inc., Cary, NC). Only SNPs showing high SNP call rates (>95%) and more than 10% minor allele frequencies were subjected to statistical analysis. To verify significant differences of traits between genotypic frequencies, ANOVA and Kruskal-Wallis tests were used for the co-dominant model.

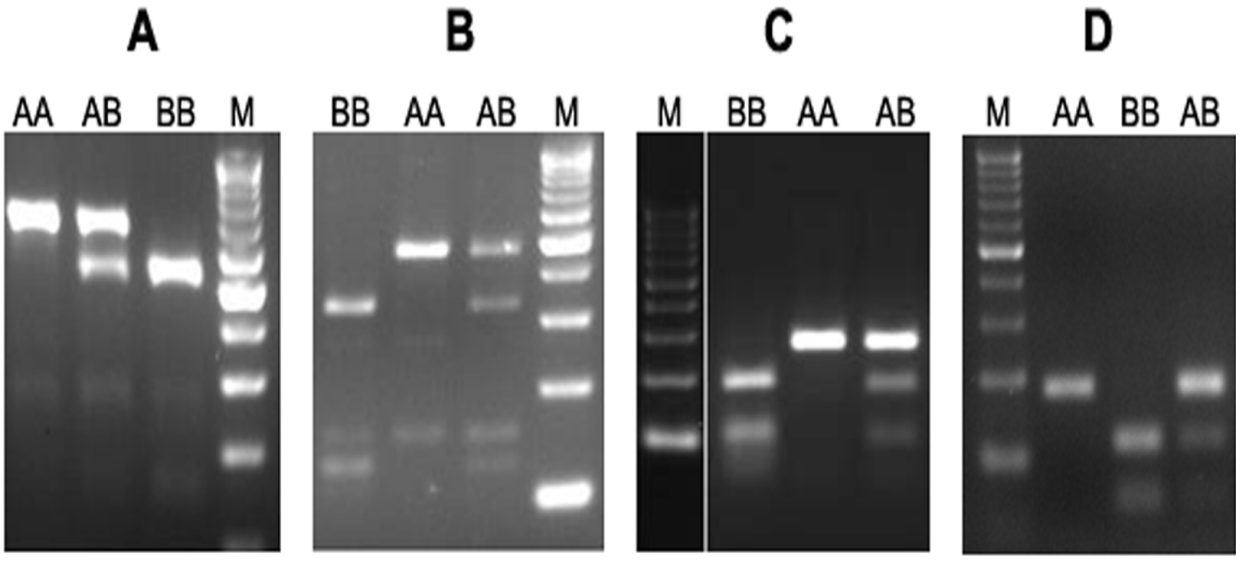

Figure 1. Agarose gel electrophoresis showing polymorphisms in polymerase chain reaction (PCR) fragments of *KIAA1717*, *HUMMLC2B*, *DECR1* and *FTO* genes. *Msp* I restriction fragment length polymorphism (RFLP) in *KIAA1717* (A) and *HUMMLC2B* (B), *Bfa I* RFLP in *DECR1* (C), and *BstU* I RFLP in *FTO* (D) PCR products were shown by agarose gel electrophoresis (3%). (A) AA (647 bp), BB (506 + 141 bp) and AB (647 + 506 + 141 bp) in *KIAA1717*. (B) AA (440 bp), BB (319 + 121 bp) and AB (440 + 319 + 21 bp) in *HUMMLC2B*. (C) AA (190 bp), BB (114 + 76 bp) and AB (190 + 114 + 76 bp) in *DECR1*. (D) AA (240 bp), BB (156 + 84 bp) and AB (240 + 156 + 84 bp) in *FTO*. M; 100 bp ladder DNA size marker (Solgent Co., Daejeon, Korea).

PCR- RFLP analysis

A pair of primers was synthesized to identify polymorphisms of *KIAA1717*, *HUMMLC2B*, *DECR1* and *FTO* genes (Table 1). A volume of 25 µl of the PCR mixture was prepared by mixing 1 X PCR buffer, 100 µM dNTPs, 0.5 µM primer pair, and 50 ng genomic DNA and ddH_2O; PCR amplification included initial denaturation at 95°C for 5 min followed by 35 repeats of a cycle consisting of annealing at 95°C for 1 min, 60°C for 1 min (for *HUMMLC2B*, 62°C and for *DECR1*, 55°C), and at 72°C for 1 min, and finally, elongation at 72°C for 5 min (GeneAmp PCR system 9600/9700; Applied Biosystems, USA). PCR products were digested with *Msp*I restriction enzyme for *KIAA1717* and *HUMMLC2B*, with *Bfa*I for *DECR1*, and with *BstU*I for *FTO*, and subsequently, genotypes A and B were identified using 3% agarose gel electrophoresis (Figure 1). In genotypes of all genes used in this study, "cut" and "uncut" types are indicated as B and A, respectively.

RESULTS AND DISCUSSION

Meat quality evaluation in *Berkshire* loins

Mean values for various meat quality parameters of 323 *Berkshire* loins are shown in Table 2. The *Berkshire* meat generally exhibited a high post-mortem pH value and water-holding capacity and low drip and cooking losses when compared with other breeds (Suzuki et al., 2003), indicating that the *Berkshire* breed has excellent meat quality. Moreover, meat quality evaluation revealed that each individual sample had significantly different meat quality traits, which may be induced by genetic effects.

Genotyping analysis of SNPs in *KIAA1717*, *HUMMLC2B*, *DECR1* and *FTO* genes

To identify the associations between genetic effects and the meat quality traits listed in Table 2, genotyping analysis was carried out by PCR-RFLP. Genotyping revealed high SNP call rates (100%) at the 4 SNPs, and in this sample population, frequencies of the *A* allele at the *KIAA1717 (C1354T)*, *HUMMLC2B (A345G)*, *DECR1 (G181C)* and *FTO (p.Ala198Ala)* SNP sites were 0.76, 0.69, 0.24, and 0.31, respectively; the 4 SNPs showed more than 10% minor allele frequency (Table 3). Moreover, permutation-based Chi-square tests (Table 3) revealed that the sample population used in this study was in Hardy-Weinberg equilibrium at the 4 SNPs. Therefore, these results indicate that our genotyping analyses exhibited high accuracy.

Association analysis of genotypes with meat quality traits in *Berkshire* pigs

In this *Berkshire* population, SNPs in the 4 genes showed significant associations with multiple meat quality traits; a SNP in *KIAA1717* was associated with meat color (*CIE* L) ($p < 0.05$), backfat thickness ($p < 0.05$), drip loss ($p < 0.05$), water-holding capacity ($p < 0.05$), and pH_{24hr} ($p < 0.05$) (Table 4); a SNP in *HUMMLC2B* was associated with chemical composition (collagen) ($p < 0.01$), drip loss

Table 2. Character of meat quality traits in Berkshire.

Trait		Means ± SE	Minimum	Maximum
Carcass weight (kg)		85.068 ± 0.32	71.00	105.00
Backfat thickness (mm)		24.408 ± 0.26	12.00	37.00
post-mortem pH_{45min}		5.992 ± 0.01	5,34	6.90
post-mortem pH_{24hr}		5.882 ± 0.01	5.40	6.72
Meat color	CIE L*	48.355 ± 0.16	38.01	57.68
	CIE a*	6.19 ± 0.06	3.40	9.86
	CIE b*	2.767 ± 0.05	0.78	6.15
Water holding capacity (%)		58.056±0.13	52.85	64.97
Chemical composition (%)	Collagen	0.893±0.00	0.53	1.27
	Fat	2.878±0.06	0.67	10.15
	Moisture	75.498±0.04	70.44	77.57
	Protein	23.74±0.03	21.46	25.44
Drip loss (%)		4.329±0.10	0.75	14.38
Cooking loss (%)		28.198±0.17	15.22	39.02
Warner-Bratzler shear force (kg)		2.784±0.03	1.47	4.83

CIE L*, a* and b* represent meat color lightness, redness and yellowness, respectively.

Table 3. Summary of four SNP genotyping analyses.

Gene name	Genotype			Allele		[a]MAF	[b]HWE	Call rate (%)
	Major homo	Hetero	Minor homo	Major	Minor			
KIAA1717	AA	AB	BB	A	B	0.2399	0.8778	100.00
HUMMLC2B	AA	AB	BB	A	B	0.3096	0.8001	100.00
DECR1	BB	AB	AA	B	A	0.2415	0.0939	100.00
FTO	BB	AB	AA	B	A	0.3096	0.8001	100.00

[a]MAF indicates a minor allele frequency; [b]HWE represents a permutation-based Chi-square test for Hardy-Weinberg equilibrium.

Table 4. Association between *KIAA1717* genotypes and meat quality traits.

Trait		AA (n = 187)	AB (n = 117)	BB (n = 19)	P value
Meat color	CIE L	48.657 ± 3.005	48.065 ± 2.982	47.176 ± 2.225	0.049
	CIE a	6.223 ± 1.155	6.195 ± 1.042	5.836 ± 0.931	0.347
	CIE b	2.766 ± 1.007	2.791 ± 0.986	2.635 ± 0.751	0.815
Cooking loss (%)		28.242 ± 2.943	28.205 ± 3.338	27.734 ± 3.569	0.797
Drip loss (%)		4.459 ± 1.913	4.284 ± 1.760	3.333 ± 1.325	0.037
Backfat thickness (mm)		23.824 ± 4.522	25.103 ± 4.836	25.895 ± 5.646	0.027

Table 4. continues

Chemical composition (%)	Collagen	0.891 ± 0.140	0.903 ± 0.127	0.862 ± 0.093	0.427
	Fat	2.862 ± 1.281	2.891 ± 1.196	2.961 ± 1.056	0.938
	Moisture	75.493 ± 0.922	75.505 ± 0.868	75.509 ± 0.783	0.992
	Protein	23.754 ± 0.729	23.725 ± 0.699	23.693 ± 0.629	0.901
Warner-Bratzler shear force (kg)		2.757 ± 0.589	2.828 ± 0.631	2.785 ± 0.652	0.618
Water holding capacity (%)		57.820 ± 2.261	58.232 ± 2.373	59.303 ± 2.751	0.019
Post-mortem pH_{24hr}		5.855 ± 0.205	5.912 ± 0.221	5.965 ± 0.178*	0.015

CIE L, a and b represent meat color lightness, redness and yellowness, respectively.

Table 5. Association between *HUMMLC2B* genotypes and meat quality traits.

Trait		AA (n = 155)	AB (n = 136)	BB (n = 32)	P value
Meat color	CIE L	48.134 ± 2.944	48.443 ± 2.894	49.061 ± 3.426	0.251
	CIE a	6.174 ± 1.125	6.219 ± 1.121	6.144 ± 0.942	0.914
	CIE b	2.750 ± 0.994	2.836 ± 1.028	2.559 ± 0.704	0.345
Cooking loss (%)		27.937 ± 3.157	28.634 ± 2.998	27.611 ± 3.316	0.087
Drip loss (%)		4.065 ± 1.595	4.667 ± 2.020	4.177 ± 2.004	0.018
Backfat thickness (mm)		24.690 ± 4.869	24.250 ± 4.593	23.719 ± 4.828	0.504
Chemical composition (%)	Collagen	0.877 ± 0.128	0.924 ± 0.131	0.842 ± 0.138	0.001
	Fat	2.890 ± 1.137	2.918 ± 1.383	2.654 ± 1.021	0.548
	Moisture	75.496 ± 0.829	75.487 ± 1.018	75.554 ± 0.585	0.930
	Protein	23.727 ± 0.694	23.701 ± 0.739	23.972 ± 0.648	0.145
Warner-Bratzler shear force (kg)		2.782 ± 0.625	2.844 ± 0.571	2.545 ± 0.631	0.043
Water holding capacity (%)		58.049 ± 2.328	58.093 ± 2.399	57.942 ± 2.350	0.947
Post-mortem pH_{24hr}		5.921 ± 0.213	5.845 ± 0.192	5.853 ± 0.254	0.006

CIE L, a and b represent meat color lightness, redness and yellowness, respectively.

($p < 0.05$), shear force ($p < 0.05$), and pH_{24hr} ($p < 0.01$) (Table 5); a SNP in *DECR1* was associated with meat color (*CIE* a and b) ($p < 0.05$) and backfat thickness ($p < 0.05$) (Table 6); and a SNP in *FTO* was associated with meat color (*CIE* L, a and b) ($p < 0.01$ or $p < 0.05$), protein content ($p < 0.01$), drip loss ($p < 0.05$), and water-holding capacity ($p < 0.05$) (Table 7). Interestingly, in addition to meat quality traits reported previously, the SNPs were significantly associated with other meat quality traits as well, indicating that these SNPs have novel associations with multiple meat quality traits in *Berkshire* pigs.

Taken collectively, our results provide a starting point for the understanding of the relationship between genetic effects and *Berkshire*-unique meat qualities. Furthermore, these SNPs may be used for marker-assisted selection as a genetic marker for *Berkshire* meat quality traits.

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Table 6. Association between *DECR1* genotypes and meat quality traits.

Trait		BB (n = 180)	AB (n = 130)	AA (n = 13)	P value
Meat color	CIE L	48.282 ± 3.058	48.528 ± 2.792	47.651 ± 3.689	0.530
	CIE a	6.271 ± 1.064	6.148 ± 1.151	5.489 ± 0.940	0.040
	CIE b	2.841 ± 0.970	2.735 ± 0.999	2.071 ± 0.796	0.021
Cooking loss (%)		28.178 ± 3.130	28.319 ± 3.014	27.282 ± 4.072	0.518
Drip loss (%)		4.334 ± 1.783	4.407 ± 1.947	3.490 ± 1.473	0.232
Backfat thickness (mm)		25.106 ± 4.851	23.515 ± 4.596	23.692 ± 3.119	0.012
Chemical composition (%)	Collagen	0.886 ± 0.134	0.900 ± 0.131	0.921 ± 0.144	0.500
	Fat	3.002 ± 1.282	2.727 ± 1.193	2.679 ± 0.798	0.130
	Moisture	75.435 ± 0.887	75.568 ± 0.903	75.675 ± 0.856	0.330
	Protein	23.697 ± 0.713	23.793 ± 0.733	23.798 ± 0.357	0.481
Warner-Bratzler shear force (kg)		2.784 ± 0.612	2.800 ± 0.622	2.635 ± 0.367	0.651
Water holding capacity (%)		58.131 ± 2.211	57.871 ± 2.466	58.876 ± 3.028	0.278
Post-mortem pH_{24hr}		5.891 ± 0.220	5.862 ± 0.196	5.964 ± 0.236	0.186

CIE L, a and b represent meat color lightness, redness and yellowness, respectively.

Table 7. Association between *FTO* genotypes and meat quality traits.

Trait		BB (n =160)	AB (n=159)	AA (n=4)	P value
Meat color	CIE L	48.523 ± 3.031	48.106 ± 2.878	51.593 ± 3.096	0.041
	CIE a	6.021 ± 1.052	6.340 ± 1.134	6.988 ± 0.848	0.012
	CIE b	2.650 ± 0.962	2.852 ± 0.985	4.088 ± 0.603	0.005
Cooking loss (%)		27.971 ± 2.904	28.406 ± 3.340	29.058 ± 2.285	0.397
Drip loss (%)		4.473 ± 1.901	4.136 ± 1.756	6.275 ± 1.607	0.027
Backfat thickness (mm)		24.456 ± 4.944	24.459 ± 4.489	20.500 ± 6.351	0.254
Chemical composition (%)	Collagen	0.887 ± 0.137	0.899 ± 0.130	0.898 ± 0.132	0.728
	Fat	2.835 ± 1.225	2.922 ± 1.258	2.878 ± 0.933	0.823
	Moisture	75.477 ± 0.837	75.523 ± 0.941	75.368 ± 1.305	0.865
	Protein	23.875 ± 0.736	23.604 ± 0.666	23.770 ± 0.470	0.003
Warner-Bratzler shear force (kg)		2.757 ± 0.627	2.810 ± 0.591	2.853 ± 0.571	0.721
Water holding capacity (%)		58.375 ± 2.658	57.719 ± 1.946	58.763 ± 2.943	0.037
Post-mortem pH_{24hr}		5.904 ± 0.215	5.863 ± 0.209	5.778 ± 0.125	0.140

CIE L, a and b represent meat color lightness, redness and yellowness, respectively.

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