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Polymorphism of the retinol-binding protein 4 gene (*RBP4*) and its association with carcass and meat quality traits in swine

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Abstract: To investigate the influence of the retinol-binding protein 4 gene (*RBP4*) on the carcass and meat quality traits of swine, polymorphism was observed by PCR-SSCP in four Chinese native pig breeds (Huoshouhei, Anqingliubai, Wannanhei, and Wei), that were carefully selected for economic traits. The results revealed one SNP (A>G) of the *RBP4* gene in these breeds, excluding Huoshouhei. The AA genotype was the predominant genotype and allele A was the predominant allele with higher frequencies. A further analysis of SNP genotypes associated with carcass and meat quality traits including slaughter rate, average back-fat thickness, eye muscle area, lean percentage, meat color, L* value, a* value, b* value, pH_1, pH_{24}, drip weight loss, intramuscular fat (IMF) content, and shear force was carried out in three pig breeds including Anqingliubai, Wannanhei, and Wei. The results showed that individuals with AA had a higher back-fat thickness and a lower eye muscle area than those with AG and GG. Meanwhile, individuals with AA had a higher a* value than those with AG and GG. However, differences of other traits such as lean percentage, pH, drip weight loss, IMF content, and shear force among different genotypes were irregular. In conclusion, the SNP (A>G) in the porcine *RBP4* gene may be a potential genetic marker for back-fat thickness, eye muscle area, and meat color a* value selection in pigs.

Key words: *RBP4*, carcass traits, meat quality traits, Chinese native pig

1. Introduction

Marker-assisted selection by genetic markers is a tool to improve swine productivity. Genes such as estrogen receptor (*ESR*) for litter size, growth hormone receptor (*GHR*) for growth, and insulin-like growth factor 1 (*IGF1*) for meat quality have been identified in pigs as being associated with economic traits (1,2). The gene encoding retinol-binding protein 4 (*RBP4*) is a member of the *RBP* gene family. The porcine *RBP4* gene has been physically mapped to chromosome 14q25-26; it is 6721 bp in length, it consists of six exons and four introns, and its mRNA is 937 bp long and encodes 201 amino acids (3). In swine, a restriction enzyme cutting site of *Msp*I for the *RBP4* gene has been associated with significant differences in litter size (4). In terms of the function of *RBP4*, a recent study suggested that this protein significantly suppresses the differentiation of porcine preadipocytes into adipocytes by inhibiting the activation of insulin signaling pathways (5). To our knowledge, studies on polymorphism of the *RBP4* gene and the associated genetic effects on porcine carcass and meat quality traits are scarce. Therefore, the present study was conducted to identify SNPs in the *RBP4* gene and to determine their association with carcass and meat quality traits in four Chinese native pig breeds, with the aim of ascertaining effective genetic markers of carcass and meat quality traits.

2. Materials and methods

2.1. Animals

The Anhui Agricultural University Animal Ethics Committee approved the collection of ear tissue from the animals used in this study. Ear tissue samples were randomly collected from 436 adult pigs including 20 barrows and 416 gilts belonging to four Chinese native pig breeds, namely Anqingliubai (n = 110, ♂ = 5), Huoshouhei (n = 105, ♂ = 5), Wannanhei (n = 118, ♂ = 5), and Wei (n = 103, ♂ = 5), taken from native pig farms in the Anhui province of China. The four breeds are independent of each other, without any degree of crosses. The samples were then placed in a centrifuge tube containing 70%

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alcohol and transported to the laboratory in an ice box and stored at –20 °C for DNA extraction.

2.2. DNA extraction, PCR-SSCP, and sequencing

DNA was extracted using the phenol-chloroform method, as described by Sambrook (6), and it was preserved at –20 °C for subsequent experiments. Genotyping was conducted using polymerase chain reaction-single strand conformational polymorphism (PCR-SSCP), as described elsewhere (7). Briefly, DNA extracted from the ear tissue samples was used as the PCR template. Using Primer 5.0 software (8), a pair of primers (forward 5'-CATCAAACCCTGGTCTCCTC-3'; reverse 5'-CAGCGATTTGGCGAGGTG -3') covering 503-bp fragments of exon 3, intron 3, and exon 4 was designed according to the genomic sequence of the *Sus scrofa RBP4* gene in the NCBI (NC_010456.4). PCR amplifications were performed in a 15-μL volume containing 7.5 μL of 2X reaction mix, 0.2 μL of 10 μmol/L upstream primers, 0.2 μL of 10 μmol/L downstream primers, 1 μL of 50 ng/μL template DNA, 0.15 μL of 2.5 U/μL Golden DNA Polymerase (TaKaRa, Dalian, China), and 5.95 μL of ultrapure water. The PCR protocol was as follows: 95 °C for 5 min; 35 cycles of 94 °C for 30 s, 54.5 °C for 30 s, and 72 °C for 30 s; and final extension at 72 °C for 8 min. The PCR products were loaded onto 2% agarose gel, resolved by gel electrophoresis, and visualized using a gel imaging system. For SSCP analysis, 2-μL aliquots of the PCR products were mixed with 8 μL of loading buffer, heated for 10 min at 98 °C, and chilled on ice for 10 min. The denatured DNA was subjected to 10% polyacrylamide gel electrophoresis in 1X TBE buffer and constant voltage (180 V) for 12 h at a constant temperature of 4 °C, and gels were then stained with 0.1% silver nitrate. The PCR products of different genotypes were immediately sequenced by Shanghai Sangon Biological Engineering Technology Engineering Service Co., Ltd. (Shanghai, China).

2.3. Measurements of carcass and meat quality traits

After genotyping, ten gilts of each genotype within breeds were slaughtered for carcass and meat quality traits testing according to genotype (9–11). Ultimately, a total of 90 pigs of three genotypes within three pig breeds were slaughtered. The slaughtered pigs were almost 12 months old and of almost the same body weight and were slaughtered on the same day. Carcass traits were determined as follows: 1) slaughter rate: slaughter rate = carcass weight/live weight × 100%; 2) average back-fat thickness = average back-fat thickness of three points, namely, the shoulder, 6th–7th thorax, and lumbosacral junction; 3) eye muscle area (cm^2) = height of the longissimus dorsi muscle (cm) × width of the longissimus dorsi muscle (cm) × 0.7; 4) lean percentage: the tissues were stripped off the left half of the carcass and divided into bone, skin, fat, and muscle. The lean percentage of the total tissue was then calculated as follows: carcass muscle rate or total lean percentage (%) = muscle weight/(muscle weight + fat weight + skin weight + bone weight) × 100%.

Meat quality traits were determined as follows. Meat color was examined as follows: at 1–2 h after slaughter, samples of the longissimus dorsi muscle were taken from the left side of the transverse area of the 6th–7th thorax under normal indoor daytime light (the meat color was not examined under direct sunlight or in the dark). Meat color was then assessed using a colorimetric plate (American NPPC Shade Guide, 1991 edition; Satake, Texas, USA). There are 5 muscle cross-sectional color score levels from shallow to deep for quantitative assessment of meat color, which allows a maximum of 5 points: 1 point, gray color (abnormally pale, soft, and exudative [PSE] color); 2 points, light gray (indicating a tendency toward anomaly or proneness to red PSE color); 3 points, normal; 4 points, normal crimson (slightly dark red); 5 points, dark (abnormal color). Meat color (L*, a*, and b*) was determined 45 min postmortem from an average of four random measurements performed with an ADCI-WSI whiteness colorimeter from Chentaike Experiment Instrument and Technology Co. Ltd. (Beijing, China). The pH values were measured at 1 and 24 h postmortem (pH_1 and pH_{24}, respectively) using an HI-9025 pH meter from Hanna Instruments Co. Ltd. (Beijing, China).

Drip weight loss was evaluated according to the technique described by Gill et al. (12). Intramuscular fat (IMF) content was measured by international methods as described by Feldsine et al. (13). Shear force was determined in a C-LM3 Tenderness Analyzer from Tenovo international Co. Ltd. (Beijing, China) from an average of 10 random measurements (14).

2.4. Statistical analysis

Genetic characteristics such as gene frequency, genotype frequency, homozygosity, heterozygosity, effective number of alleles, and polymorphism information content were calculated by PopGene 1.31 software (15). Using the general linear mixed effects model in SPSS 19.0 (16), the genetic effects of the different genotypes on carcass and meat quality traits were analyzed. The model applied was as follows:

$$Y_{ij} = \mu + G_j + e_{ij},$$

where Y_{ij} is the phenotypic value of the carcass or meat quality trait; μ is the overall mean, G_j is the j genotype effect, and e_{ij} is the random error. Significance was accepted at $P < 0.05$ unless otherwise indicated.

3. Results

3.1. Genotyping and sequencing results

Three genotypes (AA, AG, and GG) were detected in the Anqingliubai, Wannanhei, and Wei pig breeds by PCR-SSCP method (Figure 1a). After directly sequencing of

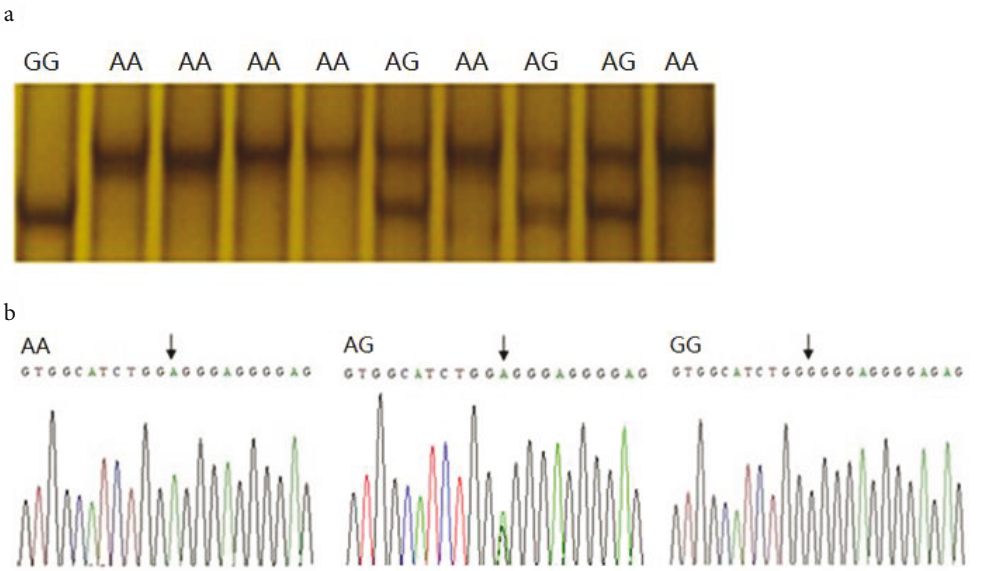

Figure 1. SSCP detection and sequences of different genotypes of the porcine *RBP4* gene. **a)** Genotypes are indicated at the top of the lanes; **b)** sequence comparison of AA, AG, and GG genotypes. The arrow indicates A>G transition at that position.

the PCR products, one SNP (A>G) was detected in the amplification sequence of the *RBP4* gene (Figure 1b). The genotypes and allele frequencies of the identified SNP in four different pig breeds are presented in Table 1. Genotype AA had higher frequencies than genotype GG and allele A had higher frequencies than allele G in the Anqingliubai, Wannanhei, and Wei pig breeds, which indicated that the AA genotype was the predominant genotype and allele A was the predominant allele. However, no mutation was found in the Huoshouhei pig breed, which had one genotype (AA). In the Anqingliubai, Wannanhei, and Wei pig breeds, the polymorphism information content (PIC) indicated moderate polymorphisms in the *RBP4* gene (0.25 < PIC < 0.50). The chi-square test showed that the allelic and genotypic frequencies reached Hardy–Weinberg equilibrium in these three pig breeds (Table 1).

3.2. Genetic effects on carcass traits in different genotypes

In the Anqingliubai breed, the AA genotype showed a higher average back-fat thickness than the GG genotype ($P < 0.05$). The AA genotype showed a lower eye muscle area than the GG genotype ($P < 0.05$), although no significant differences were found in the slaughter rate and lean percentage. In the Wannanhei breed, the AA genotype showed a higher average back-fat thickness than the GG genotype ($P < 0.05$), but there were no significant differences in slaughter rate, eye muscle area, or lean percentage between these genotypes. In the Wei breed, no significant differences were found among the genotypes in terms of slaughter rate, average back-fat thickness, eye muscle area, or lean percentage (Table 2).

Table 1. Genotype frequencies, gene frequencies, and population genetics parameters of the A>G site of the porcine *RBP4* gene.

Breeds	N	Genotypic frequency (%)			Allelic frequency (%)		Population genetics parameters			
		AA	AG	GG	A	G	PIC	He	Ne	χ^2
Anqingliubai	110	53.64	37.27	9.09	72.27	27.73	0.3205	0.4008	1.6689	0.5391
Wannanhei	118	66.10	28.81	5.09	80.51	19.49	0.2646	0.3138	1.4574	0.7919
Wei	103	57.28	31.07	11.65	72.82	27.18	0.3175	0.3959	1.6553	4.7717
Huoshouhei	105	105	0	0	105	0	—	—	—	—

PIC: Polymorphism information content; He: heterozygosity; Ne: effective number of alleles; $\chi^2_{0.05} = 5.991$, $\chi^2_{0.01} = 9.21$.

Table 2. Comparison of carcass traits among the different genotypes of the A>G mutation.

Carcass trait	Genotypes	Mean ± SD		
		Anqingliubai	Wannanhei	Wei
Slaughter rate (%)	AA	73.90 ± 2.50	72.82 ± 2.40	73.53 ± 2.64
	AG	72.73 ± 1.75	73.51 ± 2.24	74.97 ± 1.56
	GG	71.05 ± 2.96	76.14 ± 0.87	73.97 ± 2.98
Average back-fat thickness (mm)	AA	48.62 ± 2.27 [a]	38.69 ± 2.10 [a]	37.32 ± 2.74
	AG	45.25 ± 2.62 [ab]	36.43 ± 1.72 [ab]	35.99 ± 3.84
	GG	41.75 ± 2.18 [b]	35.82 ± 1.86 [b]	35.00 ± 3.51
Eye muscle area (cm^2)	AA	25.04 ± 1.60 [a]	24.38 ± 1.94	25.17 ± 0.47
	AG	25.56 ± 0.75 [a]	24.76 ± 2.48	25.24 ± 1.38
	GG	27.75 ± 0.75 [b]	26.83 ± 2.71	26.46 ± 1.75
Lean percentage (%)	AA	45.88 ± 2.16	46.65 ± 2.22	45.20 ± 0.82
	AG	45.85 ± 1.05	46.50 ± 1.92	45.30 ± 2.51
	GG	46.15 ± 6.21	43.86 ± 3.05	47.28 ± 2.58

In the same traits among different genes, the same letter implies no significant difference ($P > 0.05$) and different lowercase letters indicate significant differences ($P < 0.05$). The same applies below.

3.3. Genetic effects on meat quality traits in different genotypes

In the Anqingliubai breed, the AA genotype had a higher a* value than the GG genotype ($P < 0.05$). Furthermore, the AG genotype showed a higher IMF content than the GG genotype ($P < 0.05$), although there were no significant differences in other traits between them. In the Wannanhei breed, the AG genotype had a higher b* value than the GG genotype ($P < 0.05$), although there were no significant differences in other traits between them. In the Wei breed, the AA genotype showed a higher a* value than the AG genotype ($P < 0.05$), but there were no significant differences in other traits between them (Table 3).

4. Discussion

The results of the present study showed that the new SNP (A>G) appeared in the AA, AG, and GG genotypes of the Anqingliubai, Wannanhei, and Wei pig breeds but only in the AA genotype in the Huoshouhei pig breed. This may be due to the sample size being smaller and the locus being conservative in the Huoshouhei breed (17). The genotypic frequency of AA exceeded 50% in the Anqingliubai, Wannanhei, and Wei populations, and the PIC values of different sites in the *RBP4* gene ranged between 0.25 and 0.5, indicating moderate polymorphism and a high probability of genetic variation. In addition, the genotypic and allelic frequencies in these three breeds reached Hardy–Weinberg equilibrium, implying that after long-term evolution and natural or artificial selection, population genetic variation and flow in native pigs tend to stabilize, making them more adaptable (18).

Polymorphisms in the *Msp*I site in exon 4 of the *RBP4* gene have been found in a number of porcine breeds, and these were found to be correlated with reproductive traits (3,19,20). However, studies on polymorphism of the *RBP4* gene and the associated genetic effects on porcine carcass and meat quality traits are scarce. Studies have shown an association between the *RBP4* gene and fat-related features; this gene may be involved in adipocyte differentiation and seems to be associated with adipose tissue development and obesity (21–23). In this study, we found that the A>G mutation in the porcine *RBP4* gene brings about significant differences in traits like average back-fat thickness, eye muscle area, a* value, b* value, and IMF content in the Anqingliubai, Wannanhei, and Wei pig breeds. As reported in a previous study, the results implied that the *RBP4* genotypes had a very significant effect on the back fat thickness, the days to 90 kg, and average daily gain in Berkshire pigs (24). Our results provided a straightforward insight that the *RBP4* gene has effects on back-fat thickness, eye muscle area, and meat color a* value in Chinese native pig breeds and could serve as a genetic marker for carcass and meat quality traits. However, the number of pigs analyzed in our study was restricted, and further investigations are needed to confirm the relationships between the SNPs

Table 3. Comparison of meat quality traits among the different genotypes of the A>G mutation.

Meat quality traits	Genotypes	Mean ± SD		
		Anqingliubai	Wannanhei	Wei
Meat color	AA	4.20 ± 0.27	4.13 ± 0.25	4.25 ± 0.29
	AG	4.13 ± 0.25	4.13 ± 0.25	4.13 ± 0.48
	GG	4.00 ± 0.41	4.25 ± 0.29	4.13 ± 0.25
L* value	AA	40.05 ± 3.06	34.91 ± 1.67	39.36 ± 3.31
	AG	38.06 ± 2.65	34.17 ± 4.43	39.86 ± 2.53
	GG	41.69 ± 3.46	40.94 ± 4.29	39.16 ± 2.65
a* value	AA	13.85 ± 2.30 [a]	12.19 ± 1.87	13.23 ± 1.59 [a]
	AG	12.65 ± 0.91 [ab]	11.76 ± 1.85	12.04 ± 0.68 [b]
	GG	10.80 ± 1.25 [b]	11.72 ± 1.71	13.07 ± 1.12 [ab]
b* value	AA	14.49 ± 0.87	12.53 ± 0.91 [ab]	14.04 ± 0.70
	AG	13.34 ± 1.02	12.92 ± 1.85 [a]	13.92 ± 1.24
	GG	14.03 ± 1.47	11.94 ± 1.42 [b]	13.82 ± 0.66
pH_1	AA	6.25 ± 0.22	6.11 ± 0.28	6.31 ± 0.27
	AG	6.34 ± 0.12	6.28 ± 0.30	6.27 ± 0.17
	GG	6.35 ± 0.29	5.87 ± 0.40	6.18 ± 0.40
pH_{24}	AA	5.76 ± 0.13	5.70 ± 0.31	5.75 ± 0.15
	AG	5.62 ± 0.03	5.81 ± 0.18	5.68 ± 0.21
	GG	5.72 ± 0.30	5.58 ± 0.21	5.73 ± 0.28
Drip weight loss, %	AA	2.08 ± 0.33	3.15 ± 0.64	2.13 ± 0.05
	AG	2.28 ± 0.49	3.23 ± 0.49	2.15 ± 0.44
	GG	2.38 ± 0.74	3.00 ± 0.67	2.55 ± 0.39
IMF, %	AA	3.22 ± 0.22 [ab]	3.37 ± 0.30	3.38 ± 0.47
	AG	3.74 ± 0.60 [a]	3.61 ± 0.29	3.40 ± 0.58
	GG	2.93 ± 0.48 [b]	3.34 ± 0.40	3.11 ± 0.55
Shear force, N	AA	52.82 ± 11.90	54.60 ± 9.38	51.30 ± 11.34
	AG	53.93 ± 18.09	49.58 ± 11.03	50.40 ± 11.50
	GG	43.13 ± 11.85	48.55 ± 9.42	47.91 ± 9.85

and carcass and meat quality traits among other pig populations.

In conclusion, the newly identified SNP (A>G) in the *RBP4* gene is significantly associated with back-fat thickness, eye muscle area, and meat color a* value in Chinese native pig breeds and could be a potential genetic marker in marker-assisted selection of these carcass and meat quality traits in swine.

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