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QTL analyses of general compound, color, and pH traits in breast and thigh muscles in Korean native chicken

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ABSTRACT

Meat quality is one important selection criterium to consumers. In Asian countries, demands for native chicken breeds with better meat quality-related traits are increasing. In this study, 13 meat quality related traits in Korean native chicken were collected to identify QTLs that could affect the traits. A total of 20 novel QTLs, including 6 for general meat compounds (GC), 7 for the meat color (MC), and 7 for pH were identified. Significant QTLs (i.e., 1% chromosome wide significance) for crude protein contents in thigh and breast muscles were identified. Other QTLs were also identified with suggestive significance levels (i.e., 5% level of chromosome wide significance). Results presented here could provide useful information to find causal variants to improve meat quality traits in chicken.

1. Introduction

Chickens provide excellent protein sources for human. They are also useful animal models for biological researches. Chicken genome has been sequenced and used for various genetic and genomic studies (Wong et al., 2004). Most economically important traits (e.g. meat quality and growth related traits) are quantitative traits. They normally have continuous variations. These quantitative variations are mainly affected by multiple genetic and environmental factors. Thus, it is very difficult to identify causal genes and variants that affect quantitative traits (Lander and Schork, 1994; Abasht et al., 2006).

Recently, genome-wide mapping technologies such as genome sequencing and high- density array-based genotyping methods have been used to identify quantitative trait locus (QTL). In animal QTLdb (http://www.animalgenome.org/cgi-bin/QTLdb/index), 4,379 QTLs for 206 different traits have been reported from 210 papers in chicken. Of these, 10 traits (i.e., b color, breast pH, drip loss, meat color, muscle dry matter content, muscle fiber cross-sectional area, muscle fiber density, muscle fiber diameter, muscle fiber number and muscle protein content) are meat quality-related traits in chicken. Based on consumers' perspective, these meat quality-related traits are very important. Hence, meat quality-related traits have excellent economic value. These traits can be investigated by analyzing general meat components (Berri et al., 2001). When consumers select meats in the market, their first selection standard is the meat color (Mancini and Hunt, 2005). Water holding capacity (WHC) is another important selection standard because meat WHC can show good texture to consumers. Crude fat, crude protein, and crude ash have sensory and functional importance. In previous research studies, hydrogen ion concentration (pH) has been used as an important criterion to evaluate the meat quality (Allen et al., 1997; Huff- Lonergan and Lonergan, 2005; Barbut et al., 2008). Lower meat pH can generally result in pale meat color and lower WHC. Therefore, pH is another important criterion for meat quality.

Korean native chicken (KNC) is an indigenous purebred in Korea (DAD-IS; http://dad.fao.org/). Based on their plumage colors, there are five lines of KNC: White, Black, Yellow, Gray, and Red. As the most indigenous chicken breed, KNC shows low growth rate and low feed efficiency. However, this breed has excellent and unique meat quality such as particular texture, which is because of

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the higher chewiness and cohesiveness, and different content of fatty acids compared with commercial broilers (Choe et al., 2010; Jeon et al., 2010). However, very limited research has been focused on the identification of genetic factors that affect the meat quality traits in KNC. Therefore, the objective of this study was to identify QTLs of meat quality related traits in KNC thigh and breast muscles in order to identify their causative variations that might be for future breeding purposes.

2. Materials and methods

2.1. Experimental animals

Two-generation nuclear pedigree KNC consisting of 83 G0 founders (i.e., 15 sires and 68 dams) and 597 G1 progeny were established to investigate genetic factors within Korean native chicken breed. No specific production related trait has been used for selection criterion during the establishment of KNC founder generation (G0). Three sires were mated with 4–5 dams within each line to produce G1 birds. Based on their plumage colors, the 597 G1 progeny were classified into the following five lines: Gray (G) ($n=110$), Black (L) ($n=90$), Red (R) ($n=135$), White (W) ($n=126$), and 136 Yellow (Y) ($n=136$). This resource population consisted of 68 full-sib families ranging from 3 to 20 birds (average 10.6). In terms of half-sib family, the population comprised of 15 half-sib families ranging from 28 to 59 birds (average 44.5). All animals were reared with the standard breeding and maintenance procedures established by the National Institute of Animal Science (NIAS) of Korea. This study was conducted strictly in accordance with "The Guide for the Care and Use of Laboratory Animals" published by the institutional Animal Care and Use Committee of NIAS, Korea.

2.2. Genotype analysis

Previously, a total of 128 microsatellite (MS) and 8 SNP markers spanning 26 autosomes were used for constructing the 1st version of KNC genetic linkage map with a size of 2729.4 cM (Seo et al., 2015). For the current QTL analysis, we reconstructed the KNC genetic linkage map with additional 30 SNP markers. The newly incorporated SNP markers were genotyped by Fluidigm Genotyping Technology (Fluidigm, USA). The genetic marker order and genetic distance of the new map were determined using CRIMAP program version 2.4 (Green, 1992). The total autosomal map length was 2921.4 cM with average genetic distance between markers of 17.5 cM.

2.3. Phenotype analysis

After slaughtering, phenotypic data for meat quality traits were collected from breast and thigh muscles of 597 G1 birds. The pH value at 15 min post-slaughter was measured for the breast and thigh muscles using portable pH meter (SG2-SevenGo, Mettler-Toledo Into Inc., Schewerzenbach, Switzerland). The ultimate pH value was measured from pH of filtrated meat that was filtered with filter paper (No. 4, Whitman Ltd. Kent, UK) and centrifuge at 2090*g* for 15 min (Union 32R, Hanil Co., Ltd, Inchun, Korea) for 1 g of homogenized minced meat with 9 ml of distilled water. Water holding capacity (WHC; %) was measured using 1 g of minced meat sample on a round filter paper (No. 4, Whatman Ltd. Kent, UK). The filter paper with meat was centrifuged (CR 20B2, Hitachi Koki Co., Ltd. Fukuoka, Japan) at 6710*g* for 10 min. Water released from the filter paper was weighted and calculated as percentage of initial moisture in the meat. The moisture content of the meat was investigated by drying 3 g of the sample on an aluminum dish for 15 hour at 104 °C. Meat color for lightness (L^*), redness (a^*), and yellowness (b^*) of minced meat was measured using a colorimeter (CR-300, Minolta Inc., Tokyo, Japan). Two different areas were measured perpendicularly to the sample in quartz cell (3 cm × 1.5 cm). Crude protein (cProtein; %), crude fat (cFat; %), crude ash (cAsh; %), H2O (%), collagen (mg/g), and cooking loss (%) were measured with standard general compound methods as described previously (AOAC, 1995).

Table 1
Descriptive statistics of meat quality-related traits.

Category	Type	Trait	*N*	Mean	SD	Range
General compounds	Br	cFat^S	597	0.828	0.116	0–1.29
	Leg	cFat^S	597	1.115	0.289	0–2.06
	Br	cAsh^S	597	1.186	0.137	0.94–1.73
	Leg	cAsh^S	597	0.208	0.180	−0.27 to 0.78
	Br	Collagen^S	590	2.007	0.473	0.65–3.84
	Leg	Collagen^L	590	2.075	0.314	1.26–3.01
	Br	H2O	597	73.032	0.742	28.64–94.45
	Leg	H2O	597	74.958	1.497	43.2–79.15
	Br	cProtein	597	24.394	0.517	71.26–75.76
	Leg	cProtein	597	21.962	1.701	71.26–78.05
Meat color	Br	L*	597	59.975	2.586	22.64–25.91
	Leg	L*	596	48.729	4.120	18.51–25.91
	Br	a*^{L}	597	1.971	0.248	3.75–28.98
	Leg	a*	596	13.725	1.918	16.19–39.73
	Br	b*	597	21.246	1.587	1.75–1.94
	Leg	b*	596	20.357	1.665	4.7–7.92
pH	Br	WHC	596	64.092	7.655	1.65–1.9
	Leg	WHC	597	62.049	6.163	5.75–6.88
	Br	Cooking loss	597	20.597	2.846	−0.52 to 1.33
	Leg	Cooking loss	589(7)	30.038	3.827	−1.82 to1.58
	Br	pH1^L	594(3)	1.822	0.041	44.65–68.2
	Leg	pH1	597	6.483	0.241	37.62–57.86
	Br	pH2^L	595(2)	1.762	0.033	1.24–2.83
	Leg	pH2	592(5)	6.210	0.162	8.73–18.81
	Br	Delta_pH	595(2)	0.367	0.328	16.83–27.12
	Leg	Delta_pH	597	0.270	0.283	14.97–23.89

Br: breast muscle; Leg: thigh muscle; cFat: crude fat content (%); cAsh: crude ash content (%); H_2O: crude moisture (%); cProtein: crude Protein; L^*: CIE lightness value; a^*: CIE redness value; b^*: CIE yellowness; WHC; water holding capacity (%); pH1: after slaughter 15 min pH; pH2: ultimate pH; ^{L}Data transformed using natural log; ^{S}Data transformed using square root; For no. of animals (*n*), values in parenthesis are the number of animals omitted based on ascertainment of normality.

2.4. Statistical and QTL analyses

Before performing QTL analysis, basic descriptive statistics were obtained and normal distribution of the phenotype data were verified. If putative outliers were found, they were omitted based on normality ascertainment using Ryan–Joiner method implemented in Minitab software (Minitab, USA). The RJ score ≥ 0.99 was employed for the ascertainment of normality. Several meat quality related traits showed significant departure from normality. Therefore, they were transformed with natural logarithm or square root to eliminate their skewness (Table 1). A general linear model (GLM) was performed using the Minitab software (version 14, Minitab Inc. USA) to identify factors affecting phenotypic variation.

QTL mapping was conducted using two different methods: half-sib QTL analysis based on linear regression and full-sib QTL analysis based on variance components. Phenotypic values used for half-sib QTL analysis were pre-adjusted for fixed effects of sex, batch, line, and carcass weight. A half-sib QTL analysis was performed with GridQTL program using paternal half-sib families (Seaton et al., 2006). The conditional probability of alternative QTL genotypes of given marker genotypes was computed at 1-cM intervals within and across the half-sib families. The pre-adjusted

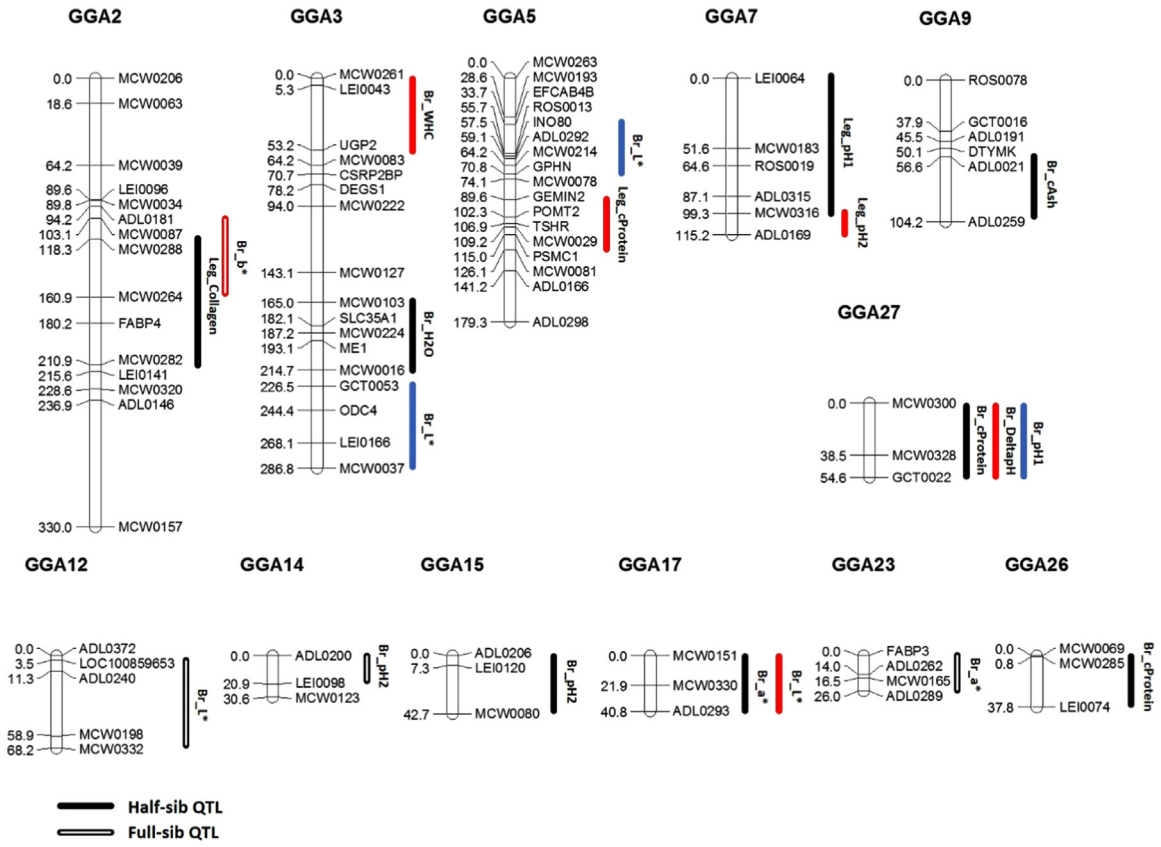

Fig. 1. Schematic overview of quantitative trait loci (QTLs) for meat quality-related traits in KNC. Confidence intervals of identified QTLs from half-sib and full-sib analyses are presented together with the KNC genetic linkage map.

phenotypic data of progeny were then regressed onto the probability of QTL genotype to evaluate the significant effect of allele substitution using the following formula:

$$y_{ij} = m_i + a_i x_{ij} + e_{ij} \text{(Model·1)}$$

where, y_{ij} was the phenotypic value of the *j*th animal, originating from the *i*th sire; m_i was the average effect for the *i*th half-sib family; a_i was the allelic substitution effect for a putative QTL within the *i*th sire; x_{ij} was the conditional probability for *j*th individual that could transmit a given allele from the *i*th sire; e_{ij} was the residual effect. To address multiple testing issues in the half-sib QTL analysis, chromosome-wide significance thresholds (i.e., 1% for significant threshold, 5% for suggestive threshold) were computed by 1000 permutations (Churchill and Doerge, 1994).

A multi-point variance component QTL mapping was conducted with SOLAR program using full-sib families (Almasy and Blangero, 2010). First, the identical-by-decent (IBD) matrix was estimated based on the markers, the genetic linkage map, and the pedigree information at each putative position along the autosomes. The estimated IBD matrix was then used to model a QTL using the following full linear mixed model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wq} + \mathbf{e} \text{(Model·2)}$$

where, **y** was a vector of the phenotypic observations for meat quality related traits; **b** was a vector of fixed effects including sex, line, batch, and carcass weight; **u** was a vector of random additive polygenic effects; **q** was a vector of random additive QTL effect; **e** was a vector of residual effects; **X**, **Z**, **W** were incidence matrices for **b**, **u**, and **q**, respectively. The mean and variance for random additive polygenic effects was defined as: $\mathbf{u} \sim N(0, \mathbf{A}\sigma_a^2)$, where **A** was the additive genetic relationship matrix computed from the resource pedigree in this study and $\sigma_a{}^2$ was the additive polygenic variance component. The mean and variance for additive QTL effects were defined as: $\mathbf{q} \sim N(0, \mathbf{G}\sigma_q^2)$, where **G** was the IBD matrix and σ_q^2 was the QTL effect variance component, **e** was a vector of residual effects with a distribution of $N(0, \mathbf{I}\sigma_e{}^2)$, where **I** was the identity matrix and $\sigma_e{}^2$ was the residual variance component. The reduced linear mixed model used for the null hypothesis was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \text{(Model·3)}$$

Model 3 used the same variable definitions as in model 2. Likelihood ratio (LR) for a given genomic position was computed by comparing log likelihood of the two models. Under null hypothesis, the LR value asymptotically followed Chi-square distribution with one degree of freedom. To address multiple testing issues in the variance component of QTL analysis, chromosome-wide significance thresholds (i.e., 1% for significant threshold, 5% for suggestive threshold) were computed by a numerical method as described previously (Piepho, 2001). The 1-LOD (logarithm of odds) drop method was employed to estimate the confidence intervals for the identified QTL by half-sib and full-sib QTL analyses (Lander and Botstein, 1989).

3. Results and discussion

A total of 13 meat quality related traits were measured in both breast and thigh muscles to identify QTLs in KNC (Table 1). In this study, meat quality related traits were classified based on general compounds (GCs), pH, and meat color (MC). GCs are very important nutritional factors, including crude protein (cProtein), crude fat (cFat), crude ash (cAsh), collagen, and crude moisture (H2O) used in this study. MC was measured as one of the sensory preference factors in meat, including L* (Lightness), a* (redness), and b* (yellowness) values. The hydrogen ion concentration (pH) is a crucial meat quality trait because pH can affect meat color and meat tenderness. The pH values were measured twice [i.e., after

slaughter 15 min later (pH1) and homogenized samples in the laboratory (pH2)]. In addition, delta pH indicating the difference between the two points of measurements was also calculated. Water holding capacity (WHC) and cooking loss (CL) traits were also grouped into pH due to the fact that pH could affect WHC and CL (Allen et al., 1997; Huff- Lonergan and Lonergan, 2005) (Table 1). To identify QTL that could influence meat quality related traits, we performed both half-sib and full-sib analyses in this study.

3.1. Linkage map

The genetic linkage map was re-constructed using additional 30 SNP marker information based on the 1st version of KNC linkage map (Seo et al., 2015). We performed a preliminary QTL analysis for quantitative economic traits (e.g. meat quality) using the 1st version of genetic linkage map (Data not shown). Based on the identified QTL from the previous QTL analysis and our massive parallel sequencing data of KNC (Seo et al., 2015), we selected 30 informative SNPs within the positional candidate genes of initially detected QTL. For the 2nd version of linkage map construction, we used a total of 166 DNA markers consisting of 128 microsatellite (MS) markers and 38 SNP markers that covered 26 autosomes (Fig. 1). The length of the genetic distances was 2921.4 centi-Morgan (cM). The average distance between markers was calculated as 17.49 cM. This genetic linkage map using KNC showed similar genetic distances and same marker orders compared to the chicken consensus linkage map (Groenen et al., 2000).

3.2. QTL for general compounds (GCs)

GCs include various types of nutritional factors in meats that are important selection criteria for consumers. Based on the half-sib QTL mapping, we identified the following four QTLs with suggestive threshold: breast cAsh (GGA9), thigh collagen (GGA2), breast cProtein (GGA27), and breast H2O (GGA3) (Table 2). Especially, significant (i.e., 1% chromosome wide threshold) QTL that could affect cProtein in breast and thigh muscles were identified on GGA 26 and GGA5, respectively (Table 2). In chicken QTLdb, six significant associations regarding the contents of protein in the muscle were reported in different genomic positions. Nie et al. (2010) reported positive associations of *GHSR* (*growth hormone secretagogue receptor* on GGA9 and *GHRL* (*ghrelin/obestatin prepropeptide*) on GGA12 with protein contents in meats using F2 intercross population between Xinghua and White Recessive Rock chicken. Zeng et al. (2011) also performed an association study using SNP markers in a candidate gene (i.e., *G0S2*) within the same population as used in Nie et al. (2010). The full name of *G0S2* gene is *G0/G1 switch gene2*. It was initially thought to be involved in mediate re-entry of cell from G0 phase to G1 phase of cellular cycle. However, it is also implicated in regulating metabolism (Heckmann et al., 2013). They also reported a positive association between *G0S2* gene and cProtein in thigh meat. This gene is located within the confidence interval of QTL that affect cProtein in breast meat. However, results of the muscle type was different from that of previous studies. It might be worthy to investigate the association of *G0S2* with cProtein in KNC. In addition, *SLC35A1* (*solute carrier family 35*, *member A1*) and *ME1* (*malic enzyme 1*) are found within the confidence interval of breast H2O QTL on GGA3, while *POMT2* (*Protein-O-mannosyl transferase 2*) is located within the leg cProtein QTL region on GGA5 (Fig. 1).

3.3. QTL for meat colors

Meat color is one of the economically important sensory traits to consumers. When consumers buy fresh meat from the market, meat color is the first standard of selection. Therefore, good preference of meat color can be a valuable trait. In the KNC resource population, we identified the following four QTLs based on half-sib analysis: QTL for a* on GGA17, and on GGA3, and on GGA5 for breast muscle, and GGA17 for leg muscle (Table 2). Additionally, three QTLs were revealed based on full-sib analysis. The QTLs that could affect lightness (L*), redness (a*), and yellowness (b*) of breast muscles were on GGA12, GGA23, and GGA2, respectively (Table 2). For b* trait, no QTL was identified using half-sib QTL analysis. Only full-sib analysis mapped QTL on GGA2 for b*. All QTLs that could affect meat color related traits based on half- and full-sib analyses were identified with suggestive significances in the KNC resource population. Lack of concordance between half-sib analysis based on regression and full-sib QTL analysis based on

Table 2
QTLs identified from half-sib and full-sib analyses in Korean native chicken.

Category	Phenotype		Half-sib QTLs						Full-sib QTLs					
			GGA	*F-ratio*	*P-value*	Position (cM)	[a]Flanking Markers		GGA	LOD	*P-value*	Position (cM)	[a]Flanking Markers	
General Compounds	Br	cAsh	9	2.15*	0.0070	91	*ADL0021*	*ADL0259*	–	–	–		–	–
	Leg	Collagen	2	2.23*	0.0049	169	*MCW0288*	*MCW0282*	–	–	–		–	–
	Br	cProtein	26	2.42**	0.0020	31	*MCW0069*	*LEI0074*	–	–	–		–	–
	Br	cProtein	27	2.01*	0.0131	39	*MCW0300*	*GCT0022*	–	–	–		–	–
	Leg	cProtein	5	2.98**	0.0001	109	*GEMIN2*	*PSMC1*	–	–	–		–	–
	Br	H2O	3	2.52*	0.0013	182	*MCW0103*	*MCW0016*	–	–	–		–	–
Meat Color	Br	a*	17	2.17*	0.0064	4	*MCW0151*	*ADL0293*	23	1.34*	0.013	6	*FABP3*	*ADL0289*
	Br	b*	–	–	–	–	–	–	2	2.13*	0.002	132	*MCW0087*	*MCW0264*
	Br	L*	3	2.23*	0.0049	254	*GCT0053*	*MCW0037*	12	1.62*	0.006	59	*LOC10042*	*MCW0332*
	Br	L*	5	2.22*	0.0051	53	*EFCAB4B*	*GPHN*	–	–	–		–	–
	Leg	L*	17	2.01*	0.0131	5	*MCW0151*	*ADL0293*	–	–	–		–	–
pH	Br	Delta pH	27	2.31*	0.0034	4	*MCW0300*	*GCT0022*	–	–	–		–	–
	Br	pH1	27	2.22*	0.0051	0	*MCW0300*	*GCT0022*	–	–	–		–	–
	Leg	pH1	7	2.19*	0.0059	38	*LEI0064*	*MCW0316*	–	–	–		–	–
	Br	pH2	15	2.13*	0.0077	42	*ADL0206*	*MCW0080*	14	1.56*	0.007	0	*ADL0200*	*LEI0098*
	Leg	pH2	7	2.23*	0.0049	103	*MCW0316*	*ADL0169*	–	–	–		–	–
	Br	WHC	3	2.32*	0.0033	27	*MCW0261*	*UGP2*	–	–	–		–	–

Br: breast muscle; Leg: thigh muscle; cFat: crude fat content (%); cAsh: crude ash content (%); H_2O: crude moisture (%); cProtein: crude Protein; L*: CIE lightness value; a*: CIE redness value; b*: CIE yellowness; WHC; water holding capacity (%); pH1: after slaughter 15 min pH; pH2: ultimate; '–' sign means not applicable. [a]Flanking markers were used to determine the closest markers using the 1 LOD drop method.

* 5% chromosome wide significant.
** 1% chromosome wide significant.

variance components was found in the QTL results for meat color traits. Rowe et al. (2006) and De Koning et al. (2003) also reported the discrepancy between the QTL results based on the two methods. The discordance in the QTL mapping results between the two methods is mainly due to the fact that the half-sib model uses only the inheritance of paternal alleles, while the full-sib model utilize the transmission of both paternal and maternal alleles for calculating identical-by-decent probabilities to map QTLs. These systemic differences in the procedure of QTL mapping can cause the discrepancy between the two methods.

Several studies have reported the QTLs that could affect breast MC in various regions in chicken genome. Nadaf et al. (2007) reported QTL that could affect breast a* on GGA11 and breast b* on GGA1 and GGA11 using intercross between high and low growth lines. Le Bihan-Duval et al. (2011) identified similar QTL on GGA 11 compared to the QTL results of Nadaf et al. (2007) in the same intercross. They found *BCMO1* (*beta,beta-carotene 15,15-monooxygenase*) as a positional candidate gene of the QTL on GGA11. On the other hand, Yoshida et al. (2013) reported various QTLs that could influence breast a* (GGA1, 2, 7, and 24), breast b* (GGA3, and 24), and thigh b* (GGA1, and 2). In comparison with other QTL studies for MC, the QTLs for MC identified in this study are novel QTLs.

3.4. QTL for pH

The hydrogen ion concentration (pH) is considered as one of the important meat quality related trait because pH can affect water holding capacity (WHC) and drip loss (cooking loss) in meats. Moreover, many studies have reported the relationship of meat color with pH traits due to dark or pale meat depending on pH concentrations. Therefore, pH in meats is one of the economically important traits for meat sensory quality. In this KNC resource population, half-sib QTL analysis identified suggestive QTL for pH1 on GGA27 and GGA7 in breast and thigh muscles, respectively (Table 2). In addition, QTL for pH2 was identified on GGA15 with suggestive significance. QTL for thigh meat pH2 was also detected on GGA7 (Table 2). The QTL for delta pH was identified only in breast muscle on GGA27 (Table 2). The QTL for breast muscle pH1 and delta pH of affected QTL were detected in the GGA27 micro-chromosome area. QTL for breast WHC was identified on GGA3 (Table 2). Using intercross between White Leghorn and Red Jungle Fowl, Wright et al. (2006) reported a QTL for ultimate pH on GGA2 and two 5% chromosome wide QTLs in GGA7 and GGA20. Using cross lines between high and low growth, Nadaf et al. (2007) reported several QTLs for pH on GGA1, GGA2, GGA4, and GGA12. Of these, QTLs for pH 15 min after slaughter were mapped on GGA1, GGA2, and GGA12. The QTL for ultimate pH was detected on GGA4. These results were found to be different QTL regions compared to our KNC QTL study results.

4. Conclusion

In conclusion, we identified 20 QTLs for meat quality related traits. Most of these QTL regions were novel as meat quality traits (Table 2). A 1% chromosome wide significant QTL for cProtein in thigh and breast muscles was detected. In addition, QTLs were identified with 5% chromosome wide significances. Different QTLs identified in Korean chicken breeds compared to other chicken breeds and commercial broilers represent the unique characteristics of muscle of Korean native chicken breeds. Choe et al. (2010) reported phenotypic differences in meat quality characteristics between commercial Korean native chickens and broilers. Additionally, we could not detect any QTL affecting the breast and leg traits, simultaneously. These results indicated that the genetic structure controlling the two traits are different in muscle fibre type composition of leg (red/slow/oxidative) and breast (white/fast/glycolytic). Even though further study for fine mapping and identification of causative variants are ultimately needed, this study will provide useful information to trace variations in meat quality traits in the KNC population.

Conflict of interest statement

None.

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