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REVIEW ARTICLE

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Development of DNA markers for improvement of meat quality in a Japanese Black cattle population in Hyogo Prefecture

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Abstract

The polymorphisms associated with economic traits in livestock animals provide useful information as genetic indicators for breeding improvement. Over the last two decades, several DNA markers have been developed in Japanese Black cattle; however, the effect of these markers differs across populations due to differences in their genetic structures and backgrounds. As such, there is a need to verify the effectiveness of these markers in each population. This review summarizes the effectiveness of previously reported markers on carcass traits and the development of novel DNA markers in a Japanese Black cattle population in Hyogo Prefecture. As result of genome wide association studies and resequencing analyses, two novel significant markers associated with meat quality-related traits (beef marbling and fatty acid composition) were developed. These findings will lead to the identification of responsible genes and polymorphisms and contribute to the development of novel DNA markers for numerous traits in various cattle populations.

KEYWORDS
beef marbling, DNA marker, fatty acid composition, Hyogo Prefecture, Japanese Black cattle

1 | INTRODUCTION

In recent years, due to biotechnology developments easing DNA analysis, researchers have attempted to identify genes that affect certain traits in a number of animal species. Many studies have focused on the relationship between economically important traits and gene polymorphisms in domestic animals, which can lead to the identification of the responsible genes and polymorphisms and the development of DNA markers that are useful for breeding.

Cattle are among the most studied livestock species; their whole-genome sequence has been determined, and many gene polymorphisms related to economic traits (e.g., milk and carcass traits) have been identified. Most research has focused on milk traits such as yield and components, and carcass traits such as carcass weight, marbling, and fatty acid composition. Identification of the genetic factors involved in economic-related cattle traits supports improvement since the use of DNA markers allows for more accurate and efficient breeding. Marker-assisted selection, which is based on this concept, is an effective measure for the genetic improvement of livestock animals.

DNA analysis of Japanese Black cattle, the main beef cattle in Japan, has been actively conducted since around 2000, with the continuous identification of numerous gene polymorphisms associated with economic traits (Table 1). Among these polymorphisms, the *EDG1* gene polymorphism, which affects beef marbling, has been one of the main focuses of carcass trait studies (Yamada et al., 2009). Additionally, polymorphisms in the *SCD* gene (Taniguchi et al., 2004), *SREBP1* gene

TABLE 1 The previously-reported gene polymorphisms related to carcass traits in Japanese Black cattle

Gene	Location	Polymorphism	Trait	Reference
EDG1	Promotor	g.1471620G > T	Beef marbling	Yamada et al. (2009)
SCD	Exon 5	A293V	Fatty acid composition	Taniguchi et al. (2004)
SREBP1	Intron 5	84 bp indel	Fatty acid composition	Hoashi et al. (2007)
FASN	Exon 34	T1950A W1955R	Fatty acid composition	Abe et al. (2009)
	5′UTR	g.841G > C	Fatty acid composition	Hayakawa et al. (2015)
PLAG1	3′UTR	rs109231213	Carcass yield	Nishimura et al. (2012)
NCAPG	Exon 23	I442M	Carcass yield	Setoguchi et al. (2009)
GH	Exon 5	L127V	Carcass yield	Oka et al. (2007)
DGAT1	Exon 8	K232A	Subcutaneous fat thickness	Narukami et al. (2011)
NT5E	Exon 7 Exon 8	H440Y V492E	Inosine 5′-monophosphate	Uemoto et al. (2017)

(Hoashi et al., 2007), and *FASN* gene (Abe et al., 2009; Hayakawa et al., 2015) are related to fatty acid composition, whereas polymorphisms in the *PLAG1* gene (Nishimura et al., 2012), the *NCAPG* gene (Setoguchi et al., 2009), and the *GH* gene (Oka et al., 2007) are related to carcass weight, and polymorphisms in the *DGAT1* gene are related to subcutaneous fat thickness (Narukami et al., 2011). Furthermore, in addition to the general carcass traits described above, research has recently begun to focus on various traits that meet consumer needs with respect to beef characteristics. For example, the *NT5E* gene polymorphism is involved with Inosine 5′-monophosphate content, which contributes to the umami taste in beef (Uemoto et al., 2017).

This review outlines the results of gene analyses related to carcass traits in Japanese Black cattle in Hyogo Prefecture. It also discusses future breeding prospects based on the current situation of the population, compared with other Japanese Black cattle populations.

2 | VERIFICATION OF THE EFFECT OF PREVIOUSLY-REPORTED DNA MARKERS IN HYOGO POPULATION

As described above, several DNA markers that are responsible for certain traits or that are in linkage disequilibrium with these polymorphisms have been described in Japanese Black cattle; understanding the genetic structure and verifying the effects of these markers within a specific population can provide useful information for developing a breeding scheme for the population. Ookura et al. (2013) genotyped six DNA markers, the *EDG1*, *SCD*, *SREBP1*, *FASN*, and *NCAPG* genes, in 539 Japanese Black cattle from a single population in Hyogo Prefecture to report their genetic frequency and effect on carcass traits. The minor allele frequency of each gene polymorphism was 0.265 for *EDG1*, 0.04 for *SCD*, 0.32 for *SREBP1*, 0.09 for *FASN* W1955R, and 0.007 for *NCAPG*. On the other hand, *FASN* g.841 was completely fixed to the G allele (Table 2). Apart from *NCAPG*, which was removed from further analysis due to its markedly biased frequency, the effects of the other four markers on each trait were investigated using ANOVA. The *EDG1* marker did not have a significant effect on the Beef Marbling Standard ($p = 0.9183$). In terms of fatty acid composition, *SCD*, *SREBP1*, and *FASN* each had significant effects on any of the fatty acids. *SCD* had a significant effect on C14:0, C14:1, C18:0, C18:1, C18:2, MUFA, PUFA, and SFA. *SREBP1* had a significant effect on C14:0, C16:0, C16:1, C18:0, C18:1, MUFA, and SFA. *FASN* W1955R had a significant effect on C18:2 and PUFA ($p < 0.05$). Next, the effect of each genotype on each fatty acid was investigated using Tukey's HSD analysis (Table 3). In *SCD*, animals with the AA genotype had a higher percentage of C14:1, C18:1, and C18:2 unsaturated fatty acids, compared to those with the AV genotype, indicating that the A allele was favorable for the trait. In *SREBP1*, the L allele appeared to be favorable because LL animals had a higher percentage of C16:1 and C18:1 unsaturated fatty acids. In *FASN* W1955R, the W allele was favorable for C18:2 and PUFA.

Among the genes involved in fatty acid composition, *SCD* and *FASN* showed extremely high favorable allele frequencies (>0.90). In a previous report examining a different Japanese Black cattle population, the frequency of favorable alleles was 0.594 in *SCD* (Taniguchi et al., 2004) and 0.670 in *FASN* W1955R (Abe et al., 2009). These results indicate that the frequency of favorable alleles was higher in the Hyogo Prefecture population than in other populations, suggesting that the Hyogo population have been under stronger selection pressure for this trait. In Hyogo Prefecture, there have been no clear or direct selection indicators of fatty acid composition improvement, but selection for beef quality, such as fat flavor and a good melting point, may have indirectly affected the frequency of these genes. On the other hand, the frequency of favorable alleles was 0.678 in *SREBP1*, indicating that it was less affected by selection, compared to *SCD* and *FASN*. Nonetheless, a previous study using 234 Japanese Black cattle, which were as part of the progeny testing performed by the Wagyu Registry Association of Japan from 2002 to 2006, reported that the S allele is a favorable allele that increases unsaturated fatty acid content (Hoashi et al., 2007), demonstrating an opposite effect compared to that in the current study by Ookura et al. (2013). The *SREBP1* polymorphism is an insertion/deletion polymorphism in an intron, and it is not thought to be directly responsible for fatty acid composition; in other words, the *SREBP1* polymorphism is thought to be in linkage disequilibrium with

TABLE 2 Genetic frequency of DNA markers in a Japanese Black cattle population in Hyogo prefecture

Marker	Genotype frequency			Allele frequency	
EDG1 g.1471620G > T	G/G ($n = 295$)	T/G ($n = 202$)	T/T ($n = 42$)	G	T
	0.55	0.37	0.08	0.735	0.265
SCD A293V	A/A ($n = 496$)	A/V ($n = 43$)	V/V ($n = 0$)	A	V
	0.92	0.08	0.00	0.96	0.04
SREBP1 84 bp indel	L/L[a] ($n = 256$)	S/L[a] ($n = 219$)	S/S[a] ($n = 64$)	L	S
	0.47	0.41	0.12	0.68	0.32
FASN W1955R	W/W ($n = 450$)	W/R ($n = 81$)	R/R ($n = 8$)	W	R
	0.83	0.15	0.02	0.91	0.09
FASN g.841G > C	G/G ($n = 45$)	G/C ($n = 0$)	C/C ($n = 0$)	G	C
	1.00	0.00	0.00	1.00	0.00
NCAPG I442M	I/I ($n = 533$)	M/I ($n = 5$)	M/M ($n = 1$)	I	M
	0.99	0.01	0.00	0.993	0.007

[a]L:long; S:short.

TABLE 3 Effects of *SCD*, *SREBP1* and *FASN* genotypes on fatty acid composition in a Japanese Black cattle population in Hyogo prefecture

	SCD		*SREBP1*			*FASN* W1955R	
Fatty acid composition	A/A ($n = 496$)	A/V ($n = 43$)	S/S ($n = 64$)	S/L ($n = 219$)	L/L ($n = 256$)	W/W ($n = 450$)	W/R ($n = 81$)
C14:0	1.89 ± 0.04^{b}	2.10 ± 0.07^{a}	2.04 ± 0.06	2.01 ± 0.05	1.94 ± 0.05	1.99 ± 0.06	2.01 ± 0.05
C14:1	0.94 ± 0.03^{a}	0.82 ± 0.05^{b}	0.84 ± 0.04	0.90 ± 0.03	0.90 ± 0.03	089 ± 0.03	0.88 ± 0.04
C16:0	21.40 ± 0.26	21.97 ± 0.42	22.22 ± 0.40^{a}	21.65 ± 0.31^{ab}	21.18 ± 0.30^{b}	21.90 ± 0.28	21.47 ± 0.38
C16:1	4.33 ± 0.09	4.38 ± 0.14	4.18 ± 0.13^{b}	4.44 ± 0.11^{a}	4.46 ± 0.10^{a}	4.37 ± 0.09	4.34 ± 0.13
C18:0	11.05 ± 0.23^{b}	11.83 ± 0.37^{a}	11.94 ± 0.35^{a}	11.26 ± 0.28^{b}	11.11 ± 0.27^{b}	11.41 ± 0.25	11.47 ± 0.33
C18:1	55.27 ± 0.36^{a}	53.98 ± 0.57^{b}	53.74 ± 0.55^{b}	54.74 ± 0.43^{b}	55.39 ± 0.41^{a}	54.30 ± 0.38	54.95 ± 0.52
C18:2	2.14 ± 0.06^{a}	1.98 ± 0.09^{b}	2.10 ± 0.09	2.04 ± 0.07	2.05 ± 0.06	2.14 ± 0.06^{a}	1.98 ± 0.08^{b}
MUFA	61.90 ± 0.41^{a}	60.50 ± 0.66^{b}	60.05 ± 0.64^{b}	61.43 ± 0.50^{a}	62.13 ± 0.48^{a}	60.90 ± 0.45	61.51 ± 0.60
PUFA	2.23 ± 0.06^{a}	2.07 ± 0.09^{b}	2.20 ± 0.09	2.13 ± 0.07	2.14 ± 0.07	2.24 ± 0.06^{a}	2.07 ± 0.08^{b}
SFA	35.86 ± 0.42^{b}	37.42 ± 0.66^{a}	37.75 ± 0.64^{a}	36.44 ± 0.50^{b}	35.73 ± 0.48^{b}	36.87 ± 0.45	36.42 ± 0.60

Note: a, b: Means with different superscripts within same trait and gene differ significantly at $p < 0.05$ (Tukey's HSD analysis).

the responsible polymorphism, and the favorable allele would be reversed between the Hyogo population and the other populations due to recombination between the two polymorphisms. In the future, the responsible polymorphism should be identified such that it can be used as an indicator for improvement in the Hyogo population.

The *EDG1* polymorphism has been reported to affect beef marbling. In the Hyogo population, the frequency of the favorable allele did not show significant bias (0.265), and there was no observed effect on beef marbling. This result suggests that past improvements in beef marbling within the Hyogo population were not due to the *EDG1* gene, and that the *EDG1* marker will not be effective in future breeding. In *NCAPG*, the frequency of the favorable allele was extremely low (0.007). Nishimaki et al. (2016) investigated the genetic frequency of the *NCAPG* marker in Japanese Black cattle populations from eight prefectures, and noted that the frequency of the favorable allele ranged from 0.01 to 0.48, with it varying greatly depending on the population. Compared with these populations, the frequency of the favorable allele was extremely low in the Hyogo population; it is possible that the ancestral population had little to no favorable allele, or that it was caused by restrictions on carcass weight that might have been conducted in the Hyogo population for prioritizing meat quality. On the other hand, the low frequency of the favorable allele indicates that the DNA marker may be highly effective for improvement. To date, carcass weight has not been positively improved in the Hyogo

population, and conservation of individuals with the favorable allele may be important for future breeding efforts.

As described above, the genetic frequencies and gene effects in Japanese Black cattle were different in the Hyogo population, compared to other prefecture populations. This discrepancy suggests that the Hyogo population has a different genetic structure.

3 | THE SEARCH FOR NOVEL POLYMORPHISMS ASSOCIATED WITH MEAT QUALITY IN THE HYOGO POPULATION

Recent advances in molecular biology have led to the development of large-scale analysis tools of gene function and genetic variation, particularly DNA chips capable of comprehensively genotyping many SNPs. The development of SNP chips has supported the development of a novel QTL search method: genome wide association studies (GWAS). GWAS search for the association between a huge number of SNPs and a specific trait using linkage disequilibrium (LD) throughout the genome. The advantages of GWAS include the ability to detect narrower candidate regions than can be detected through linkage analysis, and the ability to perform analysis using general populations instead of family populations. GWAS were originally used for investigating human genetic diseases, with many reports identifying responsible genes. Furthermore, in cattle, since the entire bovine genome sequence and the positioning of SNP information have been completed, GWAS also became available for QTL analysis, such as the study of economic traits. To date, GWAS have been used to identify the responsible genes and mutations for various traits in cattle (Buzanskas et al., 2014; Crispim et al., 2015; Freebern et al., 2020; Ishii et al., 2013).

In the previous section, effects in the Hyogo population were verified using the DNA markers that are effective in other Japanese Black cattle populations; however, the alleles are almost fixed in the Hyogo population due to breed improvement. Therefore, future breeding requires the identification of genetic variation specific to the Hyogo population. To conduct a novel QTL search, GWAS was performed in the fat area ratio to rib eye area (FAR; Nakajima et al., 2018), which is highly correlated with beef marbling, and oleic acid percentage (C18:1; Kawaguchi et al., 2018). From a group of 1836 animals, 100 animals with high or low values were selected based on the corrected phenotype of FAR and C18:1, then pooled into high and low groups, respectively. DNA pool-based GWAS were performed using Illumina BovineSNP50 BeadChip v2 with three replicate assays for each pooled sample. As a result, candidate regions for both traits were identified (Figure 1). In terms of FAR, the most significant candidate region was located on BTA7; this is consistent with past QTL reports using another Japanese Black cattle population (Hirano et al., 2007), suggesting that the major locus that controls beef marbling in the Hyogo population may be similar to that in other Japanese Black cattle populations. On the other hand, the QTL regions identified on BTA9 and 14 for C18:1had not yet been reported in any Japanese Black cattle, suggesting that it is a novel QTL specific to the Hyogo population. Further research will enable the development of DNA markers for these traits.

4 | DEVELOPMENT OF A NOVEL DNA MARKER FOR THE FAT AREA RATIO TO RIB EYE AREA

As a result of GWAS analyses, SNPs showing a significant association with FAR were detected in BTA7 (Nakajima et al., 2018). Next, a search for effective polymorphisms was conducted to develop DNA markers for FAR in this region (Sasazaki et al., 2020). The area around the significant SNPs (10–30 Mb) was selected as the candidate region. Of the 200 individuals used for pooling GWAS, four steers with the GG genotype of the most significant SNP (No.1 SNP) from the top 100 individuals, and four steers with the AA genotype from the bottom 100 individuals were selected. The entire genome sequence of the candidate region was determined for a total of eight individuals, and all polymorphisms were comprehensively detected via comparisons.

Genome resequencing revealed a total of 127,090 polymorphisms in the candidate region. Of these polymorphisms, 31,945 polymorphisms were intragenic. Furthermore, these polymorphisms were classified based on the degree of LD with the No.1 SNP, and were further

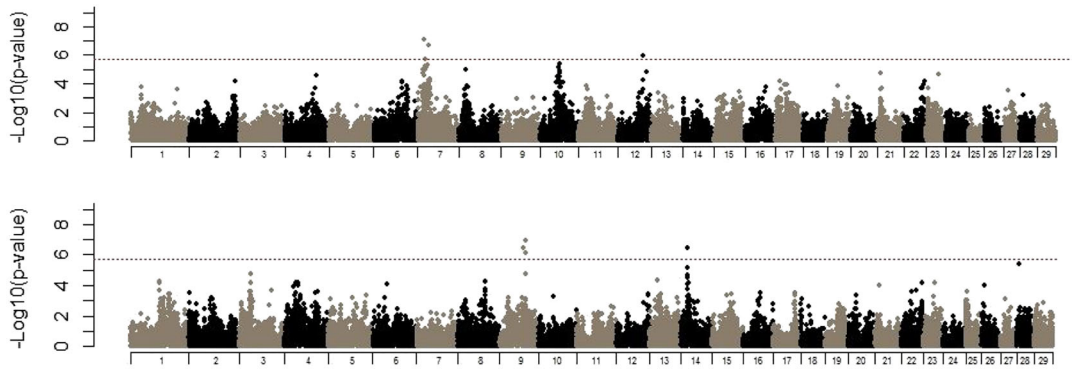

FIGURE 1 Genome-wide plots of −log10 (*p* value) for an association of loci with fat area ratio to rib eye area (above) and oleic acid percentage (below)

narrowed to 6044 polymorphisms with higher LD with the No.1 SNP. Gene function was subsequently investigated on the 179 genes in which these polymorphisms were located, such that 170 polymorphisms within eight genes were finally selected. Among these 170 polymorphisms, since only the K81M polymorphism (BTA7: 26,329,353) in the *SLC27A6* gene was an amino acid substitution, it was the most promising candidate polymorphism.

The effect on FAR was verified using a Japanese Black cattle population from Hyogo Prefecture ($n = 904$). The genotype of this K81M polymorphism was determined using the TaqMan method, and the effect was calculated via ANOVA and a Tukey Kramer's HSD test (Table 4). The frequencies of the KK, KM, and MM genotypes were 0.059, 0.402, and 0.540, respectively, and the frequencies of the K and M alleles were 0.259 and 0.741, respectively. The p value of *SLC27A6* K81M was 0.0009, indicating that *SLC27A6* K81M had a highly significant effect on FAR. Moreover, *SLC27A6* K81M showed a lower p-value than No.1 SNP ($p = 0.0049$), suggesting that *SLC27A6* K81M may be the responsible polymorphism. Upon comparison of the least square means of each genotype, the FAR of the KK genotype was significantly higher than that of the MM genotype. Considering that the K allele is a minor allele and the proportion of additive genetic variance was relatively high (5.79%), this polymorphism is an effective marker with a very high effect on FAR within the Hyogo population.

5 | DEVELOPMENT OF A NOVEL DNA MARKER FOR OLEIC ACID PERCENTAGE

Using GWAS, candidate regions for C18:1 percentage were identified on BTA9 and 14. Since these QTLs had not previously been reported in any cattle populations, the identification of novel responsible genes for fatty acid composition was expected within the Hyogo population (Kawaguchi et al., 2018). Thus, all polymorphisms were detected around the QTLs by whole-genome sequencing to identify candidate polymorphisms (Kawaguchi et al., 2019). In the whole-genome sequencing analysis, we selected four animals with a higher percentage of oleic acid and four animals with a lower percentage of oleic acid, in the same manner as in the search for FAR candidates.

Based on whole-genome sequencing data, we detected a total of 39,658 polymorphisms within the candidate region on BTA9 (64,956,436–74,956,436) among nine animals, including the reference sequence (bosTau8). Firstly, we selected 10,045 polymorphisms within genes. Secondly, we focused on polymorphisms with more than four allele differences between the high and low percentage groups. As a result of narrowing polymorphisms, 1993 polymorphisms within a total of 23 genes were considered to be candidates; these 23 genes were further narrowed to three candidate genes in terms of their gene function related to fatty acid metabolism, and one candidate polymorphism in each gene was selected. To verify the effects of the three candidate SNPs on C18:1, three SNPs were genotyped in 899 animals from the Hyogo population using the TaqMan method. Of these three SNPs, *CYB5R4* gene polymorphism c.*349G > T (BTA9; 66,377,383) was most effective for fatty acid composition (Table 5). The frequencies of the GG, GT, and TT genotypes were 0.505, 0.446, and 0.049, respectively. The frequencies of the G and T alleles were 0.728 and 0.272, respectively. The ANOVA demonstrated that *CYB5R4* c.*349G > T is strongly associated with C18:1 ($p = 0.0075$). Moreover, the p-value was lower than that of No.1 SNP from the GWAS in the same population ($p = 0.0080$), suggesting that the SNP may be the responsible for the QTL on BTA9. In addition, the

TABLE 4 Genetic frequency of SLC27A6 K81M and least squares mean of corrected phenotype for FAR in a Japanese Black population of Hyogo Prefecture ($n = 904$)

	Genotype frequency					Mean				
Polymorphism	(*n*)			Allele frequency		± SE			*p* value	%VA
SLC27A6 K81M	KK	KM	MM	K	M	KK	KM	MM	0.0009	5.79
	0.059	0.402	0.540	0.259	0.741	0.0068 [a]	0.0011 [a]	−0.0047 [b]		
	(53)	(363)	(488)			±0.0035	±0.0015	±0.0013		

Note: FAR: Fat area ratio to rib eye area. *e*-values: the least square mean of e-values for FAR for each genotype. a, b: means with different superscript are significantly different between genotypes. %VA: the proportion of additive genetic variance explained by the polymorphism.

TABLE 5 Genetic frequency of *CYB5R4* c.*349G > T and least squares mean of corrected phenotype for C18:1 in a Japanese Black population of Hyogo Prefecture ($n = 899$)

	Genotype frequency					Mean				
Polymorphism	(*n*)			Allele frequency		± SE			*p* value	%VA
	GG	GT	TT	G	T	GG	GT	TT	0.0075	4.20
	0.505	0.446	0.049	0.728	0.272	0.056 [a]	−0.261 [b]	−0.636 [b]		
	(454)	(401)	(44)			±0.087	±0.093	±0.279		

Note: C18:1: oleic acid percentage. *e*-values: the least square mean of e-values for C18:1 for each genotype. a, b: means with different superscript are significantly different between genotypes. %VA: the proportion of additive genetic variance explained by the polymorphism.

Tukey Kramer's HSD test revealed that the GG genotype showed a significantly higher C18:1 percentage than the TT genotype, indicating that the frequency of the favorable allele was relatively high (0.728) in the population. Furthermore, the proportion of additive genetic variance was 4.2%. Overall, we conclude that *CYB5R4* c.*349G > T could be an effective marker for improving C18:1 percentage in the Hyogo population.

6 | CONCLUSION AND FUTURE PROSPECTIVES

When improving livestock animals, identification of the genetic factors that control target traits allows for efficient selective breeding and provides important information for future breeding plans. However, the effectiveness of DNA markers differs depending on the population due to factors such as an extremely biased genetic frequency of the polymorphism, even if the effect has been confirmed in another population. In this review, two novel markers that we developed and could be effective for improving meat quality of the Hyogo population are shown. Future results would lead to the identification of the responsible gene and polymorphisms for each trait, and contribute to the development of novel DNA markers for various traits in various cattle populations.

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CONFLICT OF INTEREST

Authors declare no conflict of interest for this article.

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