Polymorphism of *SREBP1* is associated with beef fatty acid composition in Simmental bulls

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ABSTRACT. The sterol regulatory element binding factor 1 gene (*SREBP1*) plays an important role in the biosynthesis of fatty acids and cholesterol, and in lipid metabolism. The objective of this study was to investigate the effect of genetic polymorphisms of *SREBP1* on the fatty acid composition of muscle and carcass traits in Simmental bulls and Snow Dragon black cattle. The 84-bp insertion/deletion (indel) in intron 5 of the bovine *SREBP1* gene was genotyped by polymerase chain reaction to investigate its associations with traits. The results showed that the 84-bp indel in intron 5 was significantly associated with palmitoleic acid (C16:1), stearic acid (C18:0), saturated fatty acids (SFA), triglycerides (TAG), and the C16 index in Simmental bulls ($P < 0.05$). Cattle with the LL genotype had higher palmitic acid (C16:1), triglycerides, and C16 index but lower stearic acid (C18:0) and SFA compared to those with the LS genotype ($P < 0.05$). In conclusion, the 84-bp indel of *SREBP1* could be used as a genetic marker for selecting Simmental breeding stock for healthier fatty acid composition.

Key words: *SREBP1* gene; Insertion/deletion mutation; Polymorphism; Fatty acid composition; Simmental bulls; Snow Dragon black cattle

INTRODUCTION

The fatty acid composition of beef is of great research interest owing to its implications for human health. A high intake of saturated fatty acids (SFA) can result in elevated plasma cholesterol, which contributes to cardiovascular disease (Bronte-Stewart et al., 1956). SFA are the main fatty acids found in meat, and approximately 80% of the fatty acid in beef is composed of palmitic (C16:0), stearic (C18:0), and oleic acid (C18:1), while the remaining 20% is distributed among 30 different fatty acids (Whetsell et al., 2003). Among the SFA, lauric (C12:0), myristic (C14:0), and palmitic acid (C16:0) are considered to have the most harmful cardiovascular effects (Mozaffarian et al., 2005), whereas stearic acid is not detrimental to human health (Bonanome and Grundy, 1988). Conversely, monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids increase hepatic low-density lipoprotein (LDL) receptor activity, thereby decreasing the circulating concentration of LDL cholesterol (Woollett et al., 1992). In addition to marbling, the fatty acid composition is the main factor defining meat quality parameters, such as texture and taste, and can be improved by an increased MUFA to SFA ratio (Yang et al., 1999). Recent studies with animal models showed that one of the trans fatty acid isomers also found in beef, vaccenic acid (C18:1), may also have a number of potential health benefits (Wang et al., 2008; Bassett et al., 2010). Therefore, increasing the concentrations of beneficial fatty acids of beef would add value to beef products.

Unlike that of non-ruminants, the fatty acid composition of beef is much less dependent on diet. The sterol regulatory element binding factor 1 gene (*SREBP1*) plays an important role in determining the fatty acid composition of beef. *SREBP1* is a member of the basic helix-loop-helix-leucine zipper family of transcription factors that is involved in adipocyte differentiation, biosynthesis of cholesterol and fatty acids (Brown and Goldstein, 1997), as well as playing an essential role in energy homeostasis. In humans, this gene family consists of two genes: one is *SREBP1*, which has been mapped to chromosome 17 (Hua et al., 1995) and contributes to fat synthesis (Shimano et al., 1997), and *SREBP2* is on chromosome 22 (Miserez et al., 1997) and is related with cholesterol synthesis (Horton et al., 1998). The objective of this study was to investigate the genetic polymorphisms of *SREBP1*, and to evaluate their effects on fatty acid composition of muscle and carcass traits in Simmental bulls and Snow Dragon black cattle.

MATERIAL AND METHODS

Animals and sample collection

The experiment was carried out with 442 animals - 314 Simmental bulls and 128 Snow Dragon black cattle. For genomic DNA extraction to estimate the gene frequencies of *SREBP1*, blood samples of Simmental bulls were collected from the JinWei FuRen Breeding Farm, Inner Mongolia Autonomous Region, and muscle samples of Snow Dragon black cattle were collected from the Snow Dragon Beef Company, Dalian, Liaoning Province. Their feeding conditions, slaughter age, foraging concentration and intake, and fattening period were tightly controlled. Carcass and meat quality traits were measured according to the criterion GB/T17238-1998 of the Cutting Standard of Fresh and Chilled Beef in China (China Standard Publishing House). Samples of the longissimus muscle of the back were collected from the left side of the carcasses between the 12th and 13th ribs (approximately 11 cm thick) at 24 h post-

harvest. The marbling score for quality grade was evaluated on a cross section of the longissimus muscle at the 12 to 13 rib interface, which was scored on a scale of 1-6. Fatty acid components were measured from muscle tissues by a hydrolytic extraction method according to Sukhita and Palmquist (1998) using a gas chromatograph (GC-2014C, Shimadzu). Fatty acid components were measured according to the criterion GB/T22223-2008 Fat (total, saturated, and unsaturated) in Food, using the hydrolytic extraction gas chromatography method. All experimental protocols and animal care were performed according to authorization granted by the Chinese Ministry of Agriculture.

Genotyping

We applied polymerase chain reaction (PCR) amplification to detect the 84-bp insertion/deletion (indel) in intron 5 of the bovine *SREBP1* gene. The following primers were used: forward, 5'-CCACAACGCCATCGAGAAACGCTAC-3'; reverse, 5'-GGCCTTCCCTGACCNC CCAACTTAG-3'. PCR was performed in 25- μ L reaction volumes with 50 ng genomic DNA as a template, 2.5 μ L 10X PCR buffer (100 mM Tris-HCl, 15 mM MgCl₂, 500 mM KCl, pH 8.6), 2.0 μ L 2 mM dNTP mix, 0.6 μ L 10 pM each primer, and 0.4 U Taq polymerase (Takara Biotechnology, Japan). The thermal cycling conditions were as follows: 94°C for 10 min for initial denaturation, 35 cycles at 94°C for 30 s, 30 s annealing at 63.9°C, 30 s extension at 72°C, and a final extension for 10 min at 72°C. The resulting fragments were analyzed on 3% agarose gel with ethidium bromide in 1X Tris-borate-ethylenediaminetetraacetic acid (TBE) buffer.

Statistical analysis

Genotype and allele frequencies were calculated according to Falconer and Mackay (1996). A chi square test was performed to test for Hardy-Weinberg equilibrium (HWE) at each locus by comparing expected and observed genotype frequencies (Falconer and Mackay, 1996). For each animal, 22 traits were considered, including total lipids, individual fatty acids, the sum of SFA, MUFA, PUFA, together with the Cn index = Cn:1 / (Cn:0 + Cn:1), where N = 14, 16, or 18, the total desaturation index, estimated as MUFA / (MUFA + SFA), marbling, fat color, back fat thickness, and the health index (HI), which was calculated as the inverse of the atherogenic index proposed by Ulbricht and Southgate (1991) as shown below:

$$HI = \frac{\sum MUFA + \sum PUFA}{4 \times C14:0 + C16:0} \quad (\text{Equation 1})$$

Associations between individual single nucleotide polymorphisms (SNPs) and fatty acid measurements were evaluated using the GLM Mode of SAS for windows 9.1.3. The linear model used was as follows:

$$y_{ijm} = \mu + Y_i + M_j + G_m + W_{ijm} + e_{ijm} \quad (\text{Equation 2})$$

where y_{ijm} is the observation of the fatty acid measurement traits; μ is the overall mean, Y_i is the effect of year of calving, M_j is the effect of month of calving, G_m is the effect of genotype, and e_{ijm} is the random residual effect.

RESULTS

DNA polymorphism identification and genotyping

We identified the 84-bp indel in *SREBP1* in Simmental bulls and Snow Dragon black cattle. The 84-bp polymorphism in intron 5 of the *SREBP1* gene was detected directly from amplified products. Genotyping was carried out based on the different lengths of PCR products in which the S (deletion/short type, 348 bp) and L (insertion/long type, 432 bp) types were detected (Figure 1). In the 314 Simmental bulls, the genotype frequencies were 0.675 (LL type), 0.316 (LS type), and 0.010 (SS type), and the estimated allele frequencies were 0.832 and 0.168 for L and S alleles, respectively. We also investigated 128 Snow Dragon black cattle to determine the frequency of minor alleles, which was 0.039 (Table 1). The genotype frequencies of the two breeds were all in agreement with HWE for each polymorphism ($P > 0.05$).

Figure 1. Genotyping of the *SREBP1* indel polymorphism in intron 5. The arrowheads show the size of DNA fragment (bp). These DNA fragments were fractionated using 3% agarose gel.

Table 1. Genotype and allele frequencies of the *SREBP1* gene in Simmental bulls and Snow Dragon black cattle.

Breed	Gene	N	Genotype frequency			Allele frequency		H_e	PIC
			LL	LS	SS	L	S		
Simmental bulls	SREBP 84-bp indel	314	0.675 (212)	0.316 (99)	0.010 (3)	0.832	0.168	0.279	0.240
Snow Dragon black cattle	SREBP 84-bp indel	128	0.617 (79)	0.344 (44)	0.039 (5)	0.789	0.211	0.333	0.278

Association analysis with fatty acid composition and carcass traits

The indel genotyping was performed on 314 samples of Simmental bulls, and a general linear model was used to estimate the association between the genotypes and fatty acid composition. The 84-bp length polymorphism in *SREBP1* was investigated for associations with beef fatty acid composition. The *SREBP1* genotypes were associated with palmitoleic acid (C16:1), stearic acid (C18:0), SFA, triglycerides, and the C16 index in Simmental bulls (Table 2). Levels of palmitoleic acid (C16:1), triglycerides, and C16 index were higher in cattle with genotype LL than those with genotype LS ($P < 0.05$). The concentration of stearic acid (C18:0)

and the SFA content were 26.1% and 1.19% lower in the LL genotype compared to the LS genotype, respectively ($P < 0.05$). Because only three individuals with the SS genotype were found, we here only compare individuals with LL and LS genotypes. Moreover, significant differences were observed between the *SREBP1* genotypes and C14:0, C14:1, C16:0, C17:0, C18:3, 18:1, 18:2, MUFA, PUFA, C14 index, C18 index, total index and HI.

Table 2. Effect of 84-bp indel in intron 5 of the *SREBP1* gene on fatty acid composition in Simmental bulls.

Trait	84-bp indel			P
	LL	LS	SS	
Myristic acid (C14:0)	2.11 ± 0.08	1.91 ± 0.15	1.78 ± 0.58	0.5276
Tetradecylenic acid (C14:1)	0.06 ± 0.03	0.06 ± 0.05	0.06 ± 0.2	0.979
Palmitic acid (C16:0)	32.2 ± 1.29	35.08 ± 2.33	50.08 ± 9.07	0.1287
Palmitoleic acid (C16:1)	2.08 ± 0.19	0.47 ± 0.34	1.79 ± 1.35	0.0160*
Daturic acid (C17:0)	0.79 ± 0.10	1.04 ± 0.20	1.40 ± 0.80	0.4980
Stearic acid (C18:0)	27.58 ± 1.81	37.34 ± 3.28	50.61 ± 12.75	0.0429*
Oleic acid (18:1)	21.77 ± 1.66	12.77 ± 3.0	13.521 ± 1.68	0.1182
Linoleic acid (18:2)	7.48 ± 0.90	4.72 ± 1.64	0.70 ± 6.38	0.3131
γ-Linoleic acid (C18:3)	0.41 ± 0.16	0.63 ± 0.29	0.41 ± 1.13	0.877
SFA	62.69 ± 2.60	76.11 ± 4.90	104.94 ± 18.6	0.0399*
MUFA	23.90 ± 1.79	13.36 ± 3.25	21.39 ± 12.76	0.1091
PUFA	8.54 ± 1.20	6.13 ± 2.18	7.00 ± 8.49	0.7382
TAG	0.98 ± 0.07	0.59 ± 0.13	0.37 ± 0.54	0.0181*
C14 index	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.09	0.9760
C16 index	0.07 ± 0.01	0.02 ± 0.01	0.01 ± 0.05	0.0168*
C18 index	0.45 ± 0.03	0.25 ± 0.06	0.31 ± 0.24	0.1405
Total index	0.28 ± 0.02	0.16 ± 0.04	0.22 ± 0.16	0.1509
HI	0.89 ± 0.09	0.59 ± 0.16	0.48 ± 0.65	0.4003

Values are reported as LSM ± SE. Fatty acid contents are reported as g/100 g total fatty acids. SFA = total saturated fatty acids; MVFA = total monounsaturated fatty acids; PUFA = total polyunsaturated fatty acids; TAG = triglycerides; HI = health index. * $P < 0.05$.

We also investigated the polymorphisms' associations with carcass traits in Simmental bulls and Snow Dragon black cattle (Table 3). Back fat thickness in Snow Dragon black cattle with the SS genotype was 19.89 and 21.94% higher than those of the LL and LS genotypes, respectively ($P < 0.05$). No significant differences were observed between the *SREBP1* genotypes and other traits in Snow Dragon black cattle and Simmental bulls.

Table 3. Effect of 84-bp indel in intron 5 of the *SREBP1* gene on carcass traits on Simmental bulls and Snow Dragon black cattle.

Trait	Simmental bulls				Snow Dragon black cattle			
	LL	LS	SS	P	LL	LS	SS	P
Marbling	5.07 ± 0.14	5.35 ± 0.25	5.07 ± 1.0	0.978	2.66 ± 0.21	2.93 ± 0.27	2.65 ± 0.62	0.164
Fat color	2.05 ± 0.10	1.94 ± 0.14	2.12 ± 0.75	0.897	3.44 ± 0.19	3.47 ± 0.25	3.49 ± 0.57	0.217
Backfat thickness	0.18 ± 0.01	0.20 ± 0.01	0.10 ± 0.06	0.415	1.57 ± 0.19	1.53 ± 0.17	1.96 ± 0.41	0.022*

Values are reported as LSM ± SE. * $P < 0.05$.

DISCUSSION

At present, breeding goals are changing from high yield to high meat quality traits (van Wijk et al., 2005), and are increasingly associated with human health. Performing asso-

ciation studies with a candidate gene is a step toward better comprehension of the genetic basis of productive traits (Óvilo et al., 2006). *SREBP1* is an important candidate gene for selecting carcass and meat quality traits in cattle breeding research. However, few studies on this gene have been conducted to date in cattle. In the present study, *SREBP1* polymorphisms were detected by PCR in Simmental bulls and Snow Dragon black cattle.

SREBP1 belongs to the family of basic helix-loop-helix-leucine zipper transcription factors that bind to the sterol regulatory element (DNA sequence TCACNCCAC), and acts as a key regulatory element for fatty acid biosynthesis and cholesterol homeostasis (Felder et al., 2005). In humans, a precursor of *SREBP* is organized into three domains: 1) transactivation domain in the NH₂ terminal with a serine/proline-rich bHLH-LZ region; 2) transmembrane-spanning segments bound to the lumen of the endoplasmic reticula; 3) regulatory domain in the COOH terminal (Brown and Goldstein, 1999; Shimano, 2001; Eberlé et al., 2004). The three domains in the bovine *SREBP1* protein have also been confirmed based on comparison of amino acid sequences between bovine and human *SREBP1*.

Our study of the 84-bp indel in Simmental bulls and Snow Dragon black cattle identified three different genotypes, which are in accordance with previous results reported by Hoashi et al. (2007) in Japanese Black cattle. Furthermore, in a study of five different breeds, this polymorphism was only found in the Limousine breed, suggesting that it might be a breed-specific phenomenon and may not be segregating widely in different cattle populations (Bhuiyan et al., 2009). In the present study, Snow Dragon black cattle showed a slightly higher frequency of the SS genotype compared to Simmental bulls, which may be due to its long history of selective breeding.

The present study also showed that the genotype LL of *SREBP1* resulted in an increase in C16 and a decrease in C18 and SFA proportion in the muscle. In contrast, the stearic acid concentration was 6.30% lower in the SS genotype compared to the LL genotype ($P < 0.05$), but the linoleic and PUFA contents were 11.06 and 12.20% higher in SS compared to LL (Bhuiyan et al., 2009). Several studies have reported associations between *SREBP1* and fatty acid composition and carcass traits. The S type contributed to a 1.3% increase in the MUFA proportion and a 1.6°C lower melting point of intramuscular fat (Hoashi et al., 2007). Steers with the LL genotype had a 23.0% higher concentration of C17:1 than that of steers with the LS genotypes ($P = 0.013$) (Han et al., 2013).

Because the 84-bp indel exists in intron 5 of the bovine *SREBP1* gene, it may affect the translation efficiency of *SREBP1* itself. This suggests that the indel might indirectly contribute to fat-quality characteristics in cattle. Previous studies have reported associations between intron regions of the tumor necrosis factor receptor gene and the lipoprotein lipase gene with adipocyte metabolism (Benjafield et al., 2001; Pasalic et al., 2001). The inserted 84-nucleotide fragment might function like a microRNA in regulating transcription levels of its downstream genes, which would indirectly affect fatty acid traits.

Previous studies in humans have shown that *SREBP1a* gene polymorphisms were related to risks of cardiovascular disease and hyperlipoproteinemia (Miserez et al., 2001; Védie et al., 2001). As in other mammals, there were no splice variants detected in the bovine *SREBP1* gene, and it shows the most similarity with the human *SREBP1a* sequence (Hoashi et al., 2007). Human *SREBP1a* is a higher potential transcriptional activator than the other isoform, *SREBP1c*, due to its longer NH₂-terminal trans-activation domain (Shimano et al., 1997).

Stearoyl-CoA desaturase gene (SCD1) is a rate-limiting enzyme responsible for the conversion of SFA into MUFA. This enzyme, located in the endoplasmic reticulum, inserts a double bond between carbons 9 and 10 of the fatty acyl chain, so affecting the fatty acid composition of membrane phospholipids, triglycerides and cholesterol esters (Ntambi and Miyazaki, 2004). Our previous study showed that up-regulation of the *SREBP1* gene in bovine fetal fibroblasts results in an expression of SCD mRNA. This result indicates that as a member of the family of transcription factors, *SREBP1* also affects the *SCD* gene (Xu et al., 2013).

The present study is the first to determine the full-length coding sequence of the *SREBP1* gene in our resource population of Simmental, and to detect genetic polymorphisms in the genomic region. In this study, we demonstrated that the bovine *SREBP1* polymorphism is associated with proportions of C16:0, C18:0, SFA, and TAG in the fat composition. This result indicates that genotyping of *SREBP1* is a useful method for the selection of favorably flavored beef, as well as contributing SCD genotype information for the beef industry, which is relevant in controlling human lipid metabolism disease. Since the association was low due to the relatively small sample size, further research will be necessary to study these SNPs in larger populations and in other breeds. Furthermore, the effects should be investigated at the cellular level to better clarify the role of *SREBP1* on fatty acid composition and carcass traits.

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