ASSOCIATION OF DIACYLGLYCEROL ACYLTRANSFERASE 1 (*DGAT1*), STEAROYL-COA DESATURASE 1 (*SCD1*), AND STEROL REGULATORY ELEMENT BINDING PROTEIN 1 (*SREBP-1*) GENOTYPES WITH FAT CONTENT AND FATTY ACID COMPOSITION OF SOW COLOSTRUM AND TRANSIENT MILK

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ABSTRACT

Diacylglycerol acyltransferase 1 (DGAT1), stearoyl-CoA desaturase (SCD1), and sterol regulatory element binding protein 1 (SREBP-1) are key enzymes coded by lipogenic genes with important roles in lipid metabolism in the mammary glands of ruminant animals. This study analyzed the association of lipogenic gene markers with fat content and major fatty acids (i.e., palmitic acid C16:0, oleic acid C18:1n-9, and linoleic acid C18:2n-6) in sow colostrum and transient milk. Genotypes for *DGAT1* (AA, AK, and KK), *SCD1* (AA, AV, and VV), and *SREBP-1* (LL, LS, and SS) were determined using DNA extracted from hair follicles of 17 Landrace (LDR), 15 Large White (LRW), and 15 F1 LDR×LRW and 9 R1 LRW×LDR crossbred sows through polymerase chain reaction-restricted fragment length polymorphism (PCR-RFLP). The AA and AK genotypes of the *DGAT1* gene in F1 LDR×LRW and R1 LRW×LDR sows were associated (P<0.05) with higher fat content in colostrum than for the KK genotype. The AA and AV genotypes of the *SCD1* gene in F1 LDR×LRW sows were associated (P<0.05) with higher C16:0 and C18:2n-6 in colostrum and transient milk than for the VV genotype. The LL genotype of the *SREBP-1* gene was associated (P<0.05) with higher C18:2n-6 in colostrum from R1 LRW×LDR sows but lower C18:2 n-6 in colostrum from F1 LDR×LRW sows than for the LS genotype. The LS and SS genotypes of the *SREBP-1* gene in Landrace sows were associated (P<0.05) with higher fat content but lower C18:1n-9 in transient milk than for the LL genotype. Some *DGAT1*, *SCD1*, and *SREBP-1* genotypes can be used in a local marker-assisted selection program to effect changes in fat content and proportion of major fatty acids in sow colostrum and transient for some breeds.

Keywords: Fatty acids, sow colostrum, transient milk, lipogenic genes and genotypes

INTRODUCTION

The fatty acid (FA) composition of colostrum and sow milk substitutes plays an important role in the survival and growth of piglets (Inoue and Tsukuhara, 2021) and may

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also have positive effects on cardiovascular health in humans when used as a functional food ingredient (Luise *et al*., 2018) or nutraceutical (Ceniti *et al.,* 2022).

While the FA profile, as well as some milk components, can be influenced by the stage of lactation and diet (Hurley, 2015), changing the FA-based nutritional properties of sow colostrum and transient milk is possible in a selective program. However, altering milk fat composition by selective breeding has not been studied extensively in pigs, although the fatty acid composition of sow colostrum and transient milk are deemed important especially to optimize suitable milk replacer diets for piglets of highly prolific sows (Inoue and Tsukuhara, 2021) and different sow breeds (Ren *et al.*, 2022). More recently, Bondoc *et al.* (2023) recommended the use of colostrum as milk replacer formulations for piglets (market hogs) that are produced commercially from F1 crossbred dams in multiplier breeding farms. A separate piglet formula may also be developed for purebred sows in the nucleus herds. Nonetheless, the high cost of measuring FA composition is expected to limit the use of selective breeding programs that are commonly based on performance recording and prediction of breeding values.

In ruminant animals, several lipogenic genes coding for key enzymes of lipid metabolism in the mammary glands were found to be associated with the genetic variation in milk fat composition. These genetic polymorphisms can then be used in marker-assisted selection for the genetic improvement of milk fat composition (Conte *et al.*, 2010). The lipogenic genes and their important roles include diacylglycerol acyltransferase 1 (*DGAT1*) for triacylglycerol synthesis (Grisart *et al.,* 2004); stearoyl-CoA desaturase (*SCD1*) for the desaturation of several FAs in the cis-Δ9 position (Mele *et al.,* 2007); and sterol regulatory element binding protein 1 (*SREBP-1*) for regulating the expression levels of the *SCD1* gene and other genes relevant to lipid and FA metabolism (Rincon *et al.,* 2012).

The aim of this study was to investigate which *DGAT1*, *SCD1*, and *SREBP-1* genotypes might be associated with fat content and major FAs with the highest proportions by weight of total FAs in colostrum and transient milk obtained from Landrace, Large White, and Landrace × Large White crossbred sows.

MATERIALS AND METHODS

Colostrum/milk and hair follicle samples

Fifty-six sows [i.e., 17 Landrace (LDR), 15 Large White (LRW), 15 F1 LDR×LRW crosses, and 9 R1 LRW×LDR crosses] raised under identical conditions and fed with the same commercial diet at the INFARMCO swine nucleus breeding farm in Cabuyao City, Laguna, Philippines were used in the study.

A total of 52 colostrum and 40 transient milk samples were collected by hand within the day after parturition and 48–72 h after farrowing, respectively. About 40–50 ml of each colostrum and transient milk sample was placed in conical tubes with screw cap and immediately stored at –20°C prior to fat content and FA analysis.

Phenotypes

Based on Fourier-transformed infrared spectroscopy, the MilkoScan Mars (FOSS Analytical A/S, Hillerod, Denmark) was used in measuring the fat content of the colostrum and transient milk samples.

Eighteen (18) fatty acids were analyzed as a percentage of total FAs (g/100 g of

total fatty acids), including seven saturated fatty acids (SFA), i.e., C12:0 (lauric acid), C14:0 (myristic acid), C16:0 (palmitic acid), C17:0 (margaric acid), C18:0 (stearic acid), C20:0 (arachidic acid), C22:0 (behenic acid); six monounsaturated fatty acids (MUFA), i.e., C14:1 n-5 (myristoleic acid), C16:1 n-7 (palmitoleic acid), C18:1 n-9 (oleic acid), C18:1 n-7 (trans-vaccenic acid), C20:1 n-11 (eicosenoic acid), and C22:1 n-9 (erucic acid); and five polyunsaturated fatty acids (PUFA) i.e., C18:2 c9tll (conjugated linoleic acid or CLA), C18:2 n-6 (linoleic acid or LA), C18:3 n-3 (alpha α-linolenic acid or ALA), C20:4 n-6 (arachidonic acid or AA), and C22:6 n-3 (docosahexaenoic acid or DHA).

Fat was extracted following the method presented by Folche *et al.* (1957). Following the rapid methanolysis/methylation procedure that uses concentrated HCl of Ichihara and Fukubayashi (2010), the fatty acid methyl esters (FAMEs) were prepared and then quantified using a Shimadzu GC 2010 Plus - Capillary Gas Chromatograph System (Shimadzu Corporation, Kyoto, Japan). The Shimadzu GC system is equipped with a Flame Ionization Detector (FID) and AOC-20i autosampler and used a FAMEWax (USP G16) capillary column (30 m, 0.32 mm ID, and 0.25 μm film thickness, Restek Corporation, U.S.). The injector port and FID temperatures were set to 125 °C and then increased to 240 °C at 3 °C min^{-1} and maintained for 5 min. Hydrogen was used as a carrier gas at 40 mL min^{-1}, while nitrogen was used as a makeup gas at 30 mL min^{-1}. The fatty acids were identified based on their retention times as compared with known FAME standards obtained from Sigma Aldrich. The LabSolutions software was used in data analysis (in triplicates).

The nutritional content of the lactation feed concentrates is comprised of 10.23% moisture, 15.21% crude protein, 4.91% crude fat, 5.00% crude fiber, 7.85% ash, and 2,440.0 kcal/kg net energy. The lactation feeds contained 47.83% SFA [i.e., C12:0 (4.89%), C14:0 (3.91%), C16:0 (31.50%), C18:0 (5.77%), C20:0 (1.23%), and C22:0 (0.53%)]; 20.62% MUFA [i.e., C16:1 n-7 (0.34%) and C18:1n9c (20.28%)]; and 25.47% PUFA [i.e., C18:2 n-6 (25.14%) and C18:3 n-3 (0.33%)].

Data regarding breed, parity number, date of birth, and farrowing date were recorded for each sow.

DNA extraction

Hair follicle samples were hand-plucked from the midback area of each animal and placed in an airtight resealable plastic bag stored at room temperature.

The NucleoSpin® Tissue Genomic DNA Extraction kit (Machery-Nagel, Germany) was used in extracting high-quality DNA from clean hair follicles (roots) which were cut and placed in a 1.5 mL microcentrifuge tube. It was added with 180 μL Buffer T1 containing chaotrope, and then frozen with liquid nitrogen. The samples were freeze-thawed repeatedly (4 times) in a water bath set to 56°C before adding 25 μL of the proteinase K solution. After incubated overnight at 56°C, the sample was mixed with 200 μL Buffer B3 containing guanidine hydrochloride, and incubated at 70°C for 10 min. Ethanol (210 μL) was then added to the hair follicle sample and transferred in a NucleoSpin® Tissue Column and centrifuged at 11,000 × g for 1 min. The flow-through (supernatant) was removed, and the residual fluid was vortexed and then mixed with 500 μL Buffer BW (extraction solution containing guanidine hydrochloride and isopropanol) and centrifuged at 11,000 × g for 1 min. After the flow-through was discarded, 600 μL Wash Buffer B5 (Tris-EDTA buffer added with ethanol) was added to the sample column and centrifuged at 11,000 × g for 1 min. The sample column was centrifuged again at 11,000 × g for 5 min to remove the residual ethanol.

The sample column was transferred into a fresh 1.5 mL microcentrifuge tube for elution. About 50 µL Buffer BE (elution buffer preheated to 70°C) was added directly to the sample column. After 1 min of incubation at room temperature, the tube was centrifuged at 1,100 × g for 1 min. This procedure was repeated to collect the purified DNA.

The quantity and quality of the extracted gDNA were confirmed using UV spectrophotometry (Abs_{260}/Abs_{280}) and agarose gel electrophoresis (1% agarose at 100 volts), respectively. Extracted gDNA of good quality (i.e., absorbance quotient value of 1.8 < ratio (R) < 2.0) were stored at –20 °C for further analysis.

Genotyping

Genotypes for the DGAT1, SCD1, and SREBP-1 were analyzed using the procedures described by Syndler-Nedz *et al.* (2015) for Polish Landrace and Large White sows, Lim *et al.* (2015) for Berkshire pigs in South Korea, and Renaville *et al.* (2010) for country ham production in the U.S., respectively. The primers used in the amplification of DGAT1, SCD1, and SREBP-1 genes and corresponding restriction enzymes (AvaII, MspI, and NlaIII, respectively) are listed in Table 1. The polymerase chain reaction - restricted fragment length polymorphism (PCR-RFLP) was carried out using a Veriti 96-well thermal cycler with thermal profiles used for each primer pair. The digestion products were separated by electrophoresis on 2% agarose gel for 30-45 min and visualized under UV transillumination (Bio-Rad Gel Doc™ XR+ Systems).

To further validate the genotypes, samples were sent to private laboratories for Sanger nucleotide sequencing. Sequence similarities with the corresponding regions of other pig breeds were determined using the Basic Local Alignment Search Tool (BLAST) in the NCBI database. Genotypes were determined by identifying the absence and presence of the recognition site of the restriction enzyme using Vector NTI and FinchTV.

Statistical analysis

Differences in the FA composition of colostrum and transient milk across sow breeds were initially determined using ANOVA (SAS Ver. 9.2, 2009) and adjusted for the age at farrowing, parity, and fat content.

Chi-square tests were used to test significant differences in gene and genotypic frequencies as well as Hardy-Weinberg equilibrium (HWE) in Landrace, Large White, and F1 LDR×LRW and R1 LRW×LDR crossbred sows. Polymorphic information content (PIC) was estimated to measure the ability of the molecular marker to detect polymorphisms (Botstein *et al.*, 1980), while heterozygosity (H) was used to determine the average frequency of heterozygous individuals (Nei and Roychoudhury, 1974) in each breed group.

The association analyses between lipogenic genotypes and fat content and FA composition (separately for colostrum and transient milk) were performed through PROC GLM of SAS 9.2 software for unbalanced data using the following model:

$$y_{ijklmn} = \mu + Breed_i + (Breed \times DGAT1)_{ij} + (Breed \times SCD1)_{ik} + (Breed \times SREBP\text{-}1)_{il} + Parity_m + e_{ijklmn}$$

where y_{ijklmn} is the dependent variable (fat content and individual FA in colostrum and transient milk FA, g/100 g of total FAs), µ is overall mean, $Breed_i$ is fixed effect of i^{th} breed (Landrace, Large White, F1 LDR×LRW cross, R1 LRW×LDR cross), (Breed ×

Table 1. List of primers and restriction enzymes used in the analysis of *DGAT1*, *SCD1*, and *SREBP-1* genes.

Gene	Forward Primer	Reverse Primer	Product Size (bp)	Restriction Enzyme	Recognition Site	Chromo-some (location)/ Reference sequence	Position of SNP poly-morphism	Reference
*DGAT***1**	GCA TCC TGA ATT GGT GTG TG	GGC CAT TCA GAA CAG	257	*Ava*II	5'…G^GWCC…3' 3'…CCWG^G…5'	4 (Intron 2)/ AY116586	3,184	Syndler-Nedz *et al.* (2015)
SCD1	AGC TTC CTC TCC CAC AGT CA	GTC TTG GCC TCT TGT GCT TC	425	*Msp*I	5'…C^CGG…3' 3'…GGC^C…5'	14 (Exon 6' (3'-UTR))/ AY487830.1	16,663	Lim *et al.* (2015)
SREBP-1	ATG CCT GCC TGC CCT AAC	GCC ATC TGT CCT CTT TGC TG	503	*Nla*III	5'…CATG^…3' 3'…^GTAC…5'	12 (Intron 3)/ AB686492	13,336	Renaville *et al.* (2010)

DGAT1)$_{ij}$ is the interaction effect between the i^{th} breed and j^{th} *DGAT1* genotype (AA, AK, and KK), (Breed × SCD1)$_{ik}$ is the interaction effect between the i^{th} breed and k^{th} *SCD1* genotype (AA, AV, and VV), (Breed × SREBP-1)$_{il}$ is the interaction effect between the i^{th} breed and l^{th} *SREBP-1* genotype (LL, LS, and SS), Parity$_m$ is the effect of m^{th} parity (number of farrowing), and e_{ijklmn} is random error ~NID (0, e^2).

Results of the three genotype effects on fat content and major FAs with the highest proportions by weight of total FAs were presented as least squares means ± standard errors and compared between sow breeds, separately for colostrum and transient milk. Differences are considered significant at P value less than 0.05.

RESULTS AND DISCUSSION

The fat content and FA profiles of colostrum and transient milk across sow breeds are presented in Table 2. The fat percentage was similar in colostrum (6.49%) and transient milk (6.51%). The major FAs with the highest proportions were oleic acid (C18:1 n-9), linoleic acid (C18:2 n-6), and palmitic acid (C16:0). Oleic acid was higher in transient milk (35.8%) than in colostrum (32.8%). Linoleic acid and palmitic acid were both higher in colostrum (24.6% and 20.4%, respectively) than in transient milk (19.0% and 18.9%, respectively). The proportion of other FAs used in the study was less than five percent. In particular, the proportions of C12:0, C17:0, C20:0, C14:1 n-5, C20:1 n-11, C22:1 n-9; C18:2 c9 t11, C18:3 n-3, and C22-6 n-3 were less than one percent.

Gene and genotype frequency distribution

The lipogenic gene markers were generally polymorphic for all breed groups, except for the *SCD1* gene which was monomorphic in Large White sows (Table 3). The polymorphic information content (PIC) and heterozygosity (H) values were similar for all lipogenic gene markers, and consistently higher (i.e., more informative) in the Landrace breed (i.e., PIC = 0.35–0.37, H = 0.46–0.50). The PIC and H values for the SCD1 gene were nil in Large White and particularly low in R1 LRW×LDR crossbred sows.

***DGAT1* locus**. The *DGAT1* genotypes in Landrace and the *SREBP-1* in Large White, F1 LDR×LRW cross, and R1 LRW×LDR cross were in Hardy-Weinberg equilibrium (P<0.06), suggesting that observed allelic and genotypic frequencies in these breeds were as per the expectation. The frequency of A allele in *DGAT1* was highest in Large White (0.80), followed by F1 LDR×LRW cross (0.67), Landrace (0.50), and lowest in R1 LRW×LDR crossbred sows (0.44).

***SCD1* locus.** The distribution of *SCD1* genotypes in all breeds was not in Hardy-Weinberg equilibrium (P>0.05). The frequency of the A allele in *SCD1* was highest in R1 LRW×LDR cross (0.89), followed by F1 LDR×LRW cross (0.70), and lowest in Landrace sows (0.35). The *SCD1* gene was found only in Large White sows with the AA genotype, suggesting that the *SCD1* gene may be used to discriminate purebred Large White pigs (with erect ears) from the Landrace (with drooping ears), and the Landrace × Large White crossbred pigs (with erect or drooping ears). Crossbred gilts/sows (F1 LDR×LRW or R1 LRW×LDR) are commonly used as the specialized dam line to produce market hogs in commercial breeding farms. More data, however, would be required to support this finding.

***SREBP-1* locus.** The *SREBP-1* genotypes in all breed groups were in Hardy-Weinberg equilibrium (P<0.05). The frequency of the L allele in *SREBP-1* was highest in F1

Table 2. Mean and standard deviations of fat percentage and the proportion of fatty acids (g/100 g of total fatty acids) in sow colostrum and transient milk.

	Sow Colostrum	Transient milk
Fat percentage	6.49 ± 2.68	6.51± 4.03
Saturated FAs		
C12:0	0.26 ± 0.10	0.23 ± 0.13
C14:0	2.03 ± 0.47	1.73 ± 0.48
C15:0	n.d.	n.d.
C16:0	20.44 ± 3.08	18.88 ± 3.28
C17:0	0.19 ± 0.04	0.16± 0.04
C18:0	4.56 ± 0.83	4.79 ± 0.89
C20:0	0.90 ± 0.03[a]	0.77 ± 0.19
C22:0	4.12 ± 4.92	4.00 ± 4.90
Monounsaturated FAs		
C14:1 n-5	0.04 ± 0.03	n.d.
C16:1 n-7	2.29 ± 0.78	2.79 ± 0.92
C18:1 n-9	32.85 ± 5.70	35.77 ± 7.02
C18:1 n-7	1.56 ± 0.73	2.14 ± 0.44
C20:1 n-11	0.14 ± 0.05	0.12 ± 0.04
C22:1 n-9	0.06 ± 0.03	n.d.
Polyunsaturated FAs		
C18:2 c9 t11, CLA	0.04 ± 0.01	n.d.
C18:2 n-6, LA	24.64 ± 6.71	18.99 ± 3.80
C18:3 n-3, ALA	0.24 ± 0.09	0.35 ± 0.09
C20:4 n-6, AA	1.14 ± 0.35	0.81 ± 0.29
C22:6 n-3, DHA	0.11 ± 0.04	0.10 ± 0.01

n.d. – not detected.

LDR×LRW cross (0.60), followed by Landrace (0.56) and R1 LRW×LDR cross (0.56), and lowest in Large White (0.40).

Association of lipogenic genotypes with fat content and with FA composition

Colostrum

DGAT1 genotypes were not related (P>0.05) to the proportion of palmitic acid, oleic acid, and linoleic acid in colostrum from all sow breeds. However, *DGAT1* genotypes were significantly associated (P<0.05) with fat content of colostrum obtained from Landrace sows, F1 LDR×LRW and R1 LRW×LDR crossbred sows (Table 4 and 5). In Landrace sows, fat content was higher in the homozygous AA and KK genotypes (5.0%) than in the AK genotype (0.7%). For F1 LDR×LRW crosses, fat content was highest in the AA genotype (9.0%), followed by the AK genotype (7.1%) and KK genotype (3.4%). For R1 LRW×LDR

Table 3. Gene and genotypic frequencies and measures of polymorphism of *DGAT1*, *SCD1*, and *SREBP-1* genes in Landrace, Large White, and Landrace × Large White crossbred sows.

Breed	**n**	**Genotype frequency**			**Gene frequency**		**HWE**		**Polymorphism**	
DGAT1										
	n	AA	AK	KK	A	K	χ^2	P value	PIC	H
Landrace	17	0.41	0.18	0.41	0.50	0.50	7.118	0.028	0.3750	0.5000
Large White	15	0.67	0.27	0.07	0.80	0.20	0.417	0.812	0.2688	0.3200
F1 LDR×LRW	15	0.40	0.53	0.07	0.67	0.33	0.600	0.741	0.3457	0.4444
R1 LRW×LDR	9	0.00	0.89	0.11	0.44	0.56	5.760	0.056	0.3719	0.4938
Total	56	0.41	0.41	0.18	0.62	0.38	0.972	0.615	0.3612	0.4731
SCD1										
	n	AA	AV	VV	A	V	χ^2	P value	PIC	H
Landrace	17	0.12	0.47	0.41	0.35	0.65	0.157	0.992	0.3524	0.4567
Large White	15	1.00	0.00	0.00	1.00	0.00	-	-	-	-
F1 LDR×LRW	15	0.47	0.47	0.07	0.70	0.30	0.185	0.912	0.3318	0.4200
R1 LRW×LDR	9	0.78	0.22	0.00	0.89	0.11	0.141	0.932	0.1780	0.1975
Total	56	0.55	0.30	0.14	0.71	0.29	4.071	0.130	0.3293	0.4157
SREBP-1										
	n	LL	LS	SS	L	S	$\chi 2$	P value	PIC	H
Landrace	17	0.29	0.53	0.18	0.56	0.44	0.092	0.955	0.3715	0.4931
Large White	15	0.00	0.80	0.20	0.40	0.60	6.667	0.036	0.3648	0.4800
F1 LDR×LRW	15	0.20	0.80	0.00	0.60	0.40	6.667	0.036	0.3648	0.4800
R1 LRW×LDR	9	0.11	0.89	0.00	0.56	0.44	5.760	0.056	0.3719	0.4938
Total	56	0.16	0.73	0.11	0.53	0.47	12.292	0.002	0.3743	0.4986

HWE – Hardy-Weinberg equilibrium; χ^2 – Chi-square value; PIC – Polymorphic information content; H – Heterozygosity

Table 4. Least-square means of percent fat and the proportion of major fatty acids (g/100 g of total fatty acids) for *DGAT1*, *SCD1*, and *SREBP-1* genotypes in **colostrum** from Landrace and Large White sows.

	Percent fat	**C16:0 Palmitic acid**	**C18:1 n-9 Oleic acid**	**C18:2 n-6 Linoleic acid**
Landrace (LDR), N=17				
DGAT1				
- AA (7)	5.05 ± 2.22^{a}	19.99 ± 1.31	28.74 ± 2.37	23.97 ± 2.65
- AK (3)	0.67 ± 2.45^{b}	17.85 ± 2.10	27.46 ± 3.80	18.45 ± 4.26
- KK (7)	5.04 ± 1.32^{a}	18.42 ± 1.14	29.24 ± 2.06	23.11 ± 2.31
SCD1				
- AA (2)	0.11 ± 3.39^{b}	16.39 ± 2.36^{b}	26.01 ± 4.26	20.09 ± 4.78^{b}
- AV (8)	4.55 ± 1.84^{a}	18.65 ± 1.29^{ab}	28.90 ± 2.33	18.67 ± 2.61^{b}
- VV (7)	6.11 ± 1.22^{a}	21.22 ± 1.13^{a}	30.53 ± 2.05	26.77 ± 2.30^{a}
SREBP-1				
- LL (5)	1.60 ± 2.88	18.55 ± 1.90	31.25 ± 3.43	22.54 ± 3.85
- LS (9)	4.88 ± 1.16	19.85 ± 0.95	26.84 ± 1.71	21.63 ± 1.91
- SS (3)	4.28 ± 2.26	17.86 ± 1.76	27.35 ± 3.18	21.37 ± 3.56
Large White (LRW), N=15				
DGAT1				
- AA (11)	6.37 ± 0.91	20.28 ± 0.88	30.26 ± 1.62	23.40 ± 1.78
- AK (3)	4.87 ± 1.77	20.28 ± 1.75	30.87 ± 3.17	18.17 ± 3.54
- KK (1)	6.55 ± 2.72	22.98 ± 2.73	30.58 ± 4.94	18.57 ± 5.52
SCD1				
- AA (15)	5.93 ± 1.25	21.18 ± 1.25	30.57 ± 2.26	20.05 ± 2.53
- AV (0)	-	-	-	-
- VV (0)	-	-	-	-
SREBP-1				
- LL (0)	-	-	-	-
- LS (12)	6.98 ± 1.06	20.38 ± 1.07	33.26 ± 1.94	22.42 ± 2.16
- SS (3)	4.88 ± 1.96	21.98 ± 1.93	27.88 ± 3.50	17.67 ± 3.90

Least-squares means with different superscript letters within a column for a particular gene are significantly different ($P<0.05$). Figures in parentheses indicate the number of animals.

Table 5. Least-square means of percent fat and the proportion of major fatty acids (g/100 g of total fatty acids) for *DGAT1*, *SCD1*, and *SREBP-1* genotypes in **colostrum** from Landrace × Large White crossbred sows.

	Percent fat	**C16:0 Palmitic acid**	**C18:1 n-9 Oleic acid**	**C18:2 n-6 Linoleic acid**
F1 LDR×LRW cross, N=13				
DGAT1				
- AA (4)	9.02 ± 2.25^{a}	17.86 ± 2.27	33.03 ± 4.10	21.27 ± 4.60
- AK (8)	7.12 ± 1.22a^{ab}	17.14 ± 1.17	29.42 ± 2.11	19.32 ± 2.37
- KK (1)	3.41 ± 3.56^{b}	19.23 ± 3.65	36.87 ± 6.60	25.69 ± 7.39
SCD1				
- AA (5)	7.36 ± 2.70	22.41 ± 1.30^{a}	38.95 ± 2.35^{a}	29.08 ± 2.63^{a}
- AV (7)	5.67 ± 1.33	22.10 ± 2.10^{a}	39.45 ± 3.79^{a}	28.45 ± 4.25^{a}
- VV (1)	6.17 ± 0.00	9.71 ± 3.63^{b}	20.92 ± 6.55^{b}	8.74 ± 7.34^{b}
SREBP-1				
- LL (3)	8.23 ± 2.40	17.88 ± 2.90	35.72 ± 5.24	16.12 ± 5.87^{b}
- LS (10)	6.91 ± 2.61	18.27 ± 1.33	30.50 ± 2.41	28.06 ± 2.70^{a}
- SS (0)	-	-	-	-
R1 LRW×LDR cross, N=7				
DGAT1				
- AA (0)	-	-	-	-
- AK (6)	5.16 ± 1.40^{a}	21.54 ± 1.45	33.25 ± 2.62	27.45 ± 2.88
- KK (1)	0.84 ± 2.93^{b}	22.66 ± 2.95	25.48 ± 5.34	20.68 ± 5.91
SCD1				
- AA (5)	5.76 ± 3.31	23.33 ± 2.32	31.11 ± 4.20	27.29 ± 4.70
- AV (2)	3.47 ± 0.00	20.87 ± 2.33	27.61 ± 4.21	21.02 ± 4.71
- VV (0)	-	-	-	-
SREBP-1				
- LL (1)	3.47 ± 0.00	23.74 ± 3.16	29.11 ± 5.71	30.30 ± 6.40^{a}
- LS (6)	5.76 ± 3.32	20.46 ± 1.83	29.61 ± 3.30	18.01 ± 3.69^{b}
- SS (0)	-	-	-	-

Least-squares means with different superscript letters within a column for a particular gene are significantly different ($P<0.05$). Figures in parentheses indicate the number of animals.

crossbred sows, fat content was higher in the AK genotype (5.2%) than in the KK genotype (0.8%). This may imply that the A allele was associated with a higher fat content of colostrum from crossbred sows.

The *SCD1* genotypes were significantly associated (P<0.05) with fat content, palmitic acid, and linoleic acid in colostrum of Landrace sows. Fat content was higher in the AV and VV genotypes (4.6–6.1%) than in the AA genotype (0.1%). The proportion of palmitic acid was also higher in the AV and VV genotypes (18.6–21.2%) than in the AA genotype (16.4%). Linoleic acid was higher in the VV genotype (26.8%) than in the AA and AV genotypes (18.6–20.1%). The *SCD1* genotypes were also significantly associated (P<0.05) with palmitic acid, oleic acid, and linoleic acid in colostrum of F1 LDR×LRW crossbred sows. Both AA and AV genotypes had higher values than the VV genotype in terms of palmitic acid (22.1–22.4% vs 9.7%), and linoleic acid (28.4–29.1% vs 8.7%). This may suggest that the V allele was associated with higher fat content and a higher proportion of palmitic acid and linoleic acid of colostrum from Landrace and F1 LDR×LRW crossbred sows. The AA and AV genotypes also had higher oleic acid (38.9–39.4%) than the VV genotype (20.9%).

The *SREBP-1* genotypes were significantly associated (P<0.05) with linoleic acid in colostrum from F1 LDR×LRW and R1 LRW×LDR crossbred sows. Linoleic acid was higher in the LS genotype (28.1%) than in the LL genotype (16.1%) in F1 LDR×LRW crosses. In contrast, linoleic acid was higher in the LL genotype (30.3%) than in the LS genotype (18.0%) in R1 LRW×LDR crossbred sows. This may indicate that the S allele was associated with a higher proportion of linoleic acid in F1 LDR×LRW sows, while the L allele was associated with more linoleic acid in R1 LRW×LDR crossbred sows.

Transient milk

DGAT 1 genotypes were not related (P>0.05) to fat content and the proportion of palmitic acid, oleic acid, and linoleic acid in transient milk from all sow breeds (Tables 6 and 7). In contrast, Schennink *et al.* (2007) reported a significant association of DGAT1 K-allele with a higher proportion of palmitic acid and lower proportions of myristic, unsaturated C18, and conjugated linoleic acid in milk fat from Holstein cattle in the Netherlands. Conte *et al.* (2010) also reported that *DGAT1* polymorphism was highly associated with milk FA composition, which validated the important role of *DGAT1* in lipid metabolism of the mammary gland.

For *SCD1* genotypes, both the AA and AV genotypes compared to the VV genotype had significantly (P<0.05) higher fat content (10.9–13.2% vs 2.8%), palmitic acid (20.2–21.7% vs 10.8%), and linoleic acid (18.12–20.1% vs 9.5%) of transient milk from F1 LDR×LRW crossbred sows. Oleic acid of transient milk was significantly higher (P<0.05) in both AA and AV genotypes than in the VV genotype (i.e., 38.6–41.94% vs 18.4%) in Landrace sows. For R1 LRW×LDR crossbred sows, however, oleic acid was significantly higher (P<0.05) in the AA genotype than in the AV genotype (i.e., 44.0% vs 33.7%).

For *SREBP-1* genotypes of Landrace sows, both LS and SS genotypes had significantly higher fat content of transient milk (P<0.05) than in the LL genotype (i.e., 5.0% vs 0.6%). Oleic acid, however, was higher in the LL genotype (47.3%) than in both LS and SS genotypes (31.5–35.3%). It seems that the S allele was associated with a higher fat content, while the L allele was associated with a higher proportion of oleic acid in transient milk from Landrace sows.

Table 6. Least-square means of percent fat and the proportion of major fatty acids (g/100 g of total fatty acids) for *DGAT1*, *SCD1*, and *SREBP-1* genotypes in **transient milk** from Landrace and Large White sows.

	Percent fat	**C16:0 Palmitic acid**	**C18:1 n-9 Oleic acid**	**C18:2 n-6 Linoleic acid**
Landrace (LDR), N=12				
DGAT1				
- AA (3)	5.64 ± 2.55	17.32 ± 3.06	37.21 ± 4.15	21.34 ± 3.50
- AK (3)	2.68 ± 3.52	17.13 ± 3.60	41.15 ± 4.90	18.32 ± 4.13
- KK (6)	2.28 ± 1.86	18.84 ± 1.97	35.62 ± 2.67	19.19 ± 2.25
SCD1				
- AA (1)	2.11 ± 4.18	15.31 ± 5.04	49.98 ± 6.85^{a}	19.22 ± 5.77
- AV (7)	4.24 ± 2.30	18.29 ± 2.24	38.72 ± 3.04^{b}	18.85 ± 2.56
- VV (4)	4.25 ± 1.98	19.69 ± 2.43	25.28 ± 3.30^{c}	20.77 ± 2.78
SREBP-1				
- LL (3)	0.59 ± 4.51^{b}	17.00 ± 3.41	47.27 ± 4.64^{a}	19.41 ± 3.91
- LS (6)	4.97 ± 1.55^{a}	19.34 ± 1.75	31.42 ± 2.37^{b}	18.55 ± 2.00
- SS (3)	5.03 ± 2.45^{a}	16.94 ± 2.98	35.29 ± 4.05^{b}	20.89 ± 3.41
Large White (LRW), N=12				
DGAT1				
- AA (9)	4.82 ± 1.28	17.15 ± 1.54	32.43 ± 2.09	18.38 ± 1.76
- AK (3)	4.54 ± 2.12	19.47 ± 2.65	34.81 ± 3.60	18.66 ± 3.03
- KK (0)	-	-	-	-
SCD1				
- AA (12)	4.68 ± 1.41	18.31 ± 1.77	33.62 ± 2.41	18.52 ± 2.03
- AV (0)	-	-	-	-
- VV (0)	-	-	-	-
SREBP-1				
- LL (10)	5.21 ± 1.08	20.08 ± 4.39	36.52 ± 1.75	20.21 ± 1.47
- LS (2)	4.14 ± 2.66	20.38 ± 2.53	30.73 ± 4.49	16.83 ± 3.78
- SS (0)	-	-	-	-

Least-squares means with different superscript letters within a column for a particular gene are significantly different ($P<0.05$). Figures in parentheses indicate the number of animals.

Table 7. Least-square means of percent fat and the proportion of major fatty acids (g/100 g of total fatty acids) for *DGAT1*, *SCD1*, and *SREBP-1* genotypes in **transient milk** from Landrace × Large White crossbred sows.

	Percent fat	**C16:0 Palmitic acid**	**C18:1 n-9 Oleic acid**	**C18:2 n-6 Linoleic acid**
F1 LDR×LRW cross, N=8				
DGAT1				
- AA (2)	8.39 ± 3.53	18.89 ± 4.02	32.85 ± 5.46	16.17 ± 4.60
- AK (6)	9.52 ± 1.35	16.27 ± 1.69	33.10 ± 2.29	15.62 ± 1.93
- KK (0)	-	-	-	-
SCD1				
- AA (3)	13.16 ± 2.86[a]	20.23 ± 2.14[a]	41.93 ± 2.91[a]	18.06 ± 2.45[a]
- AV (4)	10.90 ± 2.02[a]	21.70 ± 2.54[a]	38.63 ± 3.46[a]	20.14 ± 2.91[a]
- VV (1)	2.81 ± 4.18[b]	10.82 ± 5.15[b]	18.37 ± 6.99[b]	9.50 ± 5.89[b]
SREBP-1				
- LL (3)	10.07 ± 3.13	18.00 ± 3.94	34.84 ± 5.36	14.84 ± 4.51
- LS (5)	7.84 ± 2.09	17.16 ± 1.83	31.11 ± 2.49	16.96 ± 2.10
- SS (0)	-	-	-	-
R1 LRW×LDR cross, N=7				
DGAT1				
- AA (1)	5.56 ± 2.85	18.73 ± 2.01	40.16 ± 2.73	19.66 ± 2.30
- AK (6)	8.20 ± 3.24	21.73 ± 4.11	37.68 ± 5.58	16.23 ± 4.70
- KK (0)	-	-	-	-
SCD1				
- AA (5)	6.26 ± 2.55	20.91 ± 3.23	43.98 ± 4.39a	15.72 ± 3.70
- AV (2)	3.21 ± 2.54	19.55 ± 3.23	33.72 ± 4.39b	20.17 ± 3.70
- VV (0)	-	-	-	-
SREBP-1				
- LL (1)	2.76 ± 3.48	20.08 ± 4.39	42.93 ± 5.96	16.53 ± 5.02
- LS (6)	2.92 ± 2.01	20.38 ± 2.53	34.77 ± 3.44	19.36 ± 2.90
- SS (0)	-	-	-	-

Least-squares means with different superscript letters within a column for a particular gene are significantly different ($P<0.05$). Figures in parentheses indicate the number of animals.

In this study, the *DGAT1*, *SCD1*, and *SREBP-1* genotypes were not related to the fat content and major FAs in the colostrum and transient milk of Large White sows.

In conclusion, this study revealed new information on *DGAT1*, *SCD1*, and *SREBP-1* gene polymorphisms and the associations of lipogenic genotypes with fat content and proportion of major fatty acids in sow colostrum and transient milk. It seems that the *DGAT1* A-allele was associated with a higher fat content in colostrum of Landrace and crossbred sows, but not related to palmitic acid, oleic acid, and linoleic acid. The *SCD1* V-allele can be a potential candidate marker to increase the fat content and the proportion of palmitic acid, oleic acid, and linoleic acid in colostrum and transient milk obtained from Landrace and F1 LDR×LRW crossbred sows. The *SREBP-1* L-allele may be associated with lower fat content but more oleic acid in transient milk from Landrace sows.

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