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Full Length Research Paper

Association of 15 candidate genes with meat quality traits in Czech Large White pigs

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Meat quality traits are a crucial factor in efficient pork production. In this work, we studied the influence of fifteen genes (*MC4R*, *LPIN1*, *SERCA1*, *H-FABP*, *TNNI2*, *LCAT*, *HMGCR*, *FTO*, *SERPINE1*, *PLIN1*, *EDG4*, *CSRP3*, *PRKAG3*, *CTSZ* and *TCF7L2*) on important meat quality parameters: intramuscular fat, cholesterol level, fatty acid composition (palmitic, stearic, oleic and linoleic), drip loss, ultimate pH, ultimate electrical conductivity and colour. In total, 88 Czech Large White (sire line) sows were tested for previously described polymorphisms by PCR-RFLP. *SERCA1* was genotyped by sequencing. Two new polymorphisms were found in *SERCA1*: c.686A>G and c.810C>T (accession number ENSSSCT00000008553). In our research, association analysis showed *LPIN1*, *LCAT*, *SERPINE1*, *PLIN* and *TCF7L2* to have significant influences on plasma cholesterol level. *HMGCR* was significantly associated with IMF and palmitic acid content. *LCAT* was associated with linoleic acid content. *EDG4* exhibited significant influence on drip loss. None of the tested genes had a significant effect on meat colour.

Key words: Large White, intramuscular fat, fatty acids, drip loss, meat colour, gene association.

INTRODUCTION

Pork production efficiency is strongly dependent on meat quality traits. A sufficient quality of meat is essential in ensuring the demand for pork.

Genes associated with intramuscular fat, cholesterol, fatty acids

A sufficient level of intramuscular fat (IMF), which strongly affects the sensory characteristics, is required to ensure consumer acceptability of pork (Fernandez et al., 1999). High cholesterol concentrations in plasma (hypercholesterolemia) carry a strong risk of cardiovascular diseases (Stapleton et al., 2010). Fatty acid composition affects the nutritional value, tenderness, flavor and taste of the meat. Fatty acids are major components of the fats that have a positive effect on metabolism, provided that they are consumed in optimal concentrations (saturated/unsaturated) (Wood et al., 2003). *MC4R* (melanocortin-4 receptor) influences back fat thickness, growth rate and feed intake (Kim et al., 2000) and is a candidate gene for IMF content (Schwab et al., 2009). *LPIN1* (lipin-1) is important for adipocyte differentiation and induces transcription of the adipogenic gene. This gene is associated with the percentage of leaf fat and IMF (He et al., 2009). *SERCA1* (sarcoendoplasmic reticulum Ca^{2+}-ATPase 1) plays a role in skeletal muscle relaxation via pumping Ca^{2+} from the cytosol to the sarcoplasmic reticulum. It is associated with IMF and water content (Chai et al., 2010). *H-FABP* (heart fatty acid-binding protein) belongs to the *FABP* family and participates in long-chain fatty acid uptake.

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This gene is located on the 6th porcine chromosome and is one of the candidate genes for IMF (Gerbens et al., 1997, 2000). *TNNI2* (troponin I type 2) is a muscle-fiber-type-specific protein, and its expression may affect the composition of muscle fiber, thereby, influencing the meat quality trait (Yang et al., 2010). *LCAT* (lecithin cholesterol acyltransferase) is a soluble enzyme that converts cholesterol and lecithins to cholesterol esters and lysolecithins on the surface of high density lipoprotein (HDL) and is involved in lipoprotein metabolism (Qiao et al., 2010). *HMGCR* (3-hydroxy-3-methylglutaryl-CoA reductase) is a rate-limiting enzyme in the de novo biosynthesis of cholesterol (Friesen and Rodwell, 2004). In pigs, the *HMGCR* gene not only exhibits a relationship to lipid serum traits but also with commercially important meat quality traits (Canovas et al., 2010). The *FTO* (fat mass and obesity-associated) gene encodes a 2-oxoglutarate-dependent nucleic acid demethylase that regulates energy homeostasis, controlling energy expenditure (Grant et al., 2006). In pigs, the mutations within the *FTO* gene were associated with growth rate and fatness (Du et al., 2009; Fan et al., 2010). The *SERPINE1* gene encodes plasminogen activator inhibitor-1 (PAI-1), which is a physiological inhibitor of plasminogen activators. PAI-1 levels were associated with obesity, serum triglyceride and total cholesterol, type 2 diabetes, body mass index, waist circumference, serum triglyceride, total cholesterol, insulin and peritoneal fat in humans (Barbato et al., 2009). *PLIN1* encodes perilipin (PLIN, newly PLIN1; Kimmel et al., 2010) which is a member of the PAT family of proteins that regulate cellular lipid metabolism (Bickel et al., 2009).

Genes associated with drip loss, ultimate pH and ultimate electrical conductivity

Technological meat quality traits (for example, drip loss and water binding capacity) are important because of the increased consumption of whole meat products (Sevón-Aimonen et al., 2007). Poor water binding capacity is unfavorable because of weight loss during storage. The extent of drip loss in the postrigour state is affected inter alia by the rate and extent of the drop in pH. Rapid pH drop and low water binding capacity is a sign of the PSE defect, while high ultimate pH and over-binding capacity accompanies DFD meat (Fischer, 2007). Electrical conductivity is a relevant technological parameter, where a higher value indicates a lower water-holding capacity. Pre-slaughter stress increases electrical conductivity (Hambrecht et al., 2005).

EDG4 (endothelial cell differentiation gene 4) is identified as a cellular receptor for lysophosphatidic acid (LPA), belonging to the endothelial cell differentiation gene (EDG) family of G protein-coupled receptors (GPCR) (Contos et al., 2000). *CSRP3* (cysteine and glycine-rich protein 3) is the muscle-specific form of the cysteine and glycine-rich protein family and takes part in myofiber differentiation. Cytoplasmic CSRP3 plays a role as a scaffold protein, interacts and co-localizes with alpha-actinin, beta-spectrin and telethonin (T-cap) overlying the Z- and M-lines of myofibrils (Xu et al., 2010). The *PRKAG3* (protein kinase adenosine monophosphate-activated, gamma 3 subunit) gene encodes a muscle-specific isoform of the regulatory γ-subunit of the adenosine monophosphate-activated protein kinase, an enzyme that participates in energy metabolism regulation (Škrlep et al., 2009). The porcine *PRKAG3* gene affects the glycogen content, ultimate pH and meat colour (Ciobanu et al., 2001).

Genes associated with meat colour

Another indicator of meat quality is colour (Mancini and Hunt, 2005). One of the factors affecting the colour of meat is a group of lysosomal proteinases – cathepsins, with a broad spectrum of functions. High cathepsin activities of porcine skeletal muscle have been correlated to defects with excessive meat softness or dark colour (Russo et al., 2008). The *CTSZ* (cathepsin Z) gene is located in the QTL for meat quality on SSC17. This gene affects meat colour (Fan et al., 2010). *TCF7L2* (transcription factor 7-like 2) has been implicated in glucose homeostasis via the regulation of pro-glucagon gene expression and encodes glucagon-like peptide 1 in intestinal cells (Shu et al., 2008). The *TCF7L2* gene is located on porcine chromosome 14 and *TCF7L2* mutations were associated with back fat or meat colour traits (Du et al., 2009, Fan et al., 2010). This study is focused on the influence of the fifteen potential candidate genes on significant meat quality parameters: intramuscular fat (IMF), cholesterol, fatty acids, drip loss, ultimate pH, ultimate electrical conductivity and colour.

MATERIALS AND METHODS

Genetic material

In total, 88 Czech Large White (sire line) randomly selected pure bred sows from the same herd were tested. Pigs were kept in the same conditions and fed the same diet. Animals were slaughtered at an average live weight of 102.2 kg (SD = 10.4 kg). Pigs were slaughtered over a period of 3 months (7 sampling dates) in 2010. Peripheral blood was collected immediately after slaughtering. Blood was collected in tubes containing EDTA (for DNA purification) and in tubes containing heparin (for plasma separation and cholesterol level determination). For further analysis, an approximately 350 g chop with bone (M. longissimus lumborum and thoracis) was removed. DNA was purified automatically in a QIAcube® (Qiagen, Hilden, Germany) using a QIAmp DNA Mini Kit (Qiagen, Hilden, Germany).

Genotyping

Polymorphisms were tested according to PCR-RFLP methods as previously described (Table 1) or with minor modification.

Fragments of the *MC4R*, *LPIN1*, *HMGCR*, *TCF7L2*, *CSPR3*, *PRKAG3*, *LCAT* and *H-FABP* genes were amplified using *Taq* DNA Unis polymerase (Top-Bio, Prague, Czech Republic); *CTSZ*, *FTO*, *EDG4*, *TNNI2* and *SERPINE1* using LA DNA polymerase (Top-Bio, Prague, Czech Republic); *SERCA1* (genotyped by sequencing) and *PLIN* using HS *Taq* polymerase (Qiagen, Hilden, Germany).

SERCA1

The PCR product (339 bp) was sequenced using primer F (Chai et al., 2010) and a BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA) according to the standard protocol. The sequencing reaction was performed in a GeneAmp® PCR System 9700 thermal cycler (Applied Biosystems, Foster City, CA) under the following cycling conditions: 96 °C/1 m in, 25 × (96°C/10 s, 50°C/5 s and 60°C/4 min). The reaction wa s purified using the BigDye® XTerminator™ Purification Kit (Appl ied Biosystems, Foster City, CA). Sequencing was performed using an ABI PRISM® 3100-Avant (Applied Biosystems, Foster City, CA).

Meat quality parameter determination

Intramuscular fat and fatty acids determination

Lyophilization of the samples: The samples were frozen in a lyophilisator (Chaist, Alpha 1-2 LD-plus) down to -15°C a nd then - 40°C. The vacuum was applied to reach a residual pres sure of approximately 10 Pa. Each lyophilisation cycle took 48 h. After lyophilisation, the samples were stored in aluminium containers at - 20°C until the lipid extraction (Gaffney, 1996).

Extraction of total lipid from meat: The lyophilized sample was extracted for 5 h with 280 ml of petrol ether (Lachner) using a soxhlet extractor in a 70°C water bath. Petrol ether f rom the bottle was distilled, the rest of the petrol ether was distilled at 45°C in a vacuum chamber (IKA Laboratortechnik, RV 05-ST, Germany), the oil film in the bottle was dried with nitrogen (purity 4.0, Linde), and stored at -20°C (Gomez-Brandon et al., 2008).

Fatty acid determination: The fatty acid composition of the meat fat was determined by gas chromatography as fatty acid methyl esters (FAMEs). FAMEs were prepared by saponification/methylation with BF3 and natrium methanolate (SIGMA-ALDRICH GmbH, Steinheim, Germany) in methanol (Merck, Darmstadt, Germany) according to the method of Komprda et al. (2005). A chromatographic analysis was performed in an MFC 800 gas chromatograph (Fisons Instruments, San Carlos, USA) using a Capital Analytical RH-1ms+ capillary column (30 m length, 0.25 mm i.d., 0.25 µm film thickness) equipped with a flame ionization detector. The carrier gas was nitrogen, the flow rate 1 ml/min, the column temperature 140/240°C. The rate o f heating was 4°C/min; the injector and detector temperatures w ere 260°C (injection 1 µl, split 1:100). Fatty acids were identified by comparing their retention times with standards of the compounds: palmitic (C16: 0), stearic (C18: 0), oleic (C18: 1), linoleic (C18: 2), and linolenic (18: 3) (SIGMA-ALDRICH GmbH, Steinheim, Germany). Each fatty acid was expressed as the percentage of the total fatty acid peak areas (Komprda et al., 2005).

Plasma cholesterol level determination

Blood was collected into tubes containing heparin and centrifuged. Plasma was collected into separate tubes and frozen until analysis. Cholesterol level was determined using a Thermo Scientific Konelab 20XT Clinical Chemistry Analyzer (Thermo Scientific, Bremen, Germany).

Drip loss of the meat

An approximately 150 g sample was cut out of the piece of pork. After weighing (0.0001 g accuracy), the samples were stored for 24 h in a fridge at 5°C. The samples were then dried an d weighed again. Drying was carried out until constant weight and the percentage of meat juice obtained by draining was calculated (Faucitano et al., 2010).

Meat pH_{ult} and EC_{ult} determination

Meat pH_{ult} and EC_{ult} were measured 24 h *post mortem* in the laboratory after transport from the slaughterhouse and storage at 4 to 8°C. Each sample was measured in duplicate and t he mean value was calculated.

Colour evaluation of raw pork meat

The colour measurement of raw pork was then determined using a CIE L*a*b* system with a Konica Minolta CM-3500d spectrophotometer (Konica Minolta, Tokio, Japan). The mean value was calculated from three measurements.

Association analysis

Association analysis was performed using SAS (Version 9.1.4, SAS Institute, Cary, NC, USA) with a linear model using the GLM procedure with the Bonferroni method of multiple comparisons of simultaneous confidence intervals for mean differences. For each group of traits, a separate equation was used with fixed effects of the genes and sampling date. The linear model for intramuscular fat, cholesterol and fatty acids included the fixed effects of *MC4R*, *LPIN1*, *SERCA1* c.686A>G, *SERCA1* c.696C>T, *SERCA1* c.810C>T, *H-FABP Hinf*I, *H-FABP Hae*III, *TNNI2*, *LCAT*, *HMGCR*, *FTO*, *SERPINE1*, *PLIN Nla*IV, and *TCF7L2*, for drip loss, pH_{ult} and EC_{ult} the effects of *SERCA1* c.686A>G, *SERCA1* c.696C>T, *SERCA1* c.810C>T, *TNNI2*, *EDG4*, *CSRP3*, and *PRKAG3*, and for meat colour the effects of *TNNI2*, *PRKAG3*, *CTSZ* and *TCF7L2*. Other effects were not included because of group uniformity.

RESULTS AND DISCUSSION

In this study, we examined the association between polymorphisms in 15 candidate genes and meat quality traits. Allele and genotype frequencies were calculated (Table 2). Specifically, we studied the association between 11 candidate genes and cholesterol level, IMF, palmitic, stearic, oleic and linoleic acid content (Table 3); 5 genes were included in the analysis of drip loss, ultimate pH and ultimate EC (Table 4); 4 genes were included in the analysis of colour – lightness, redness and yellowness (Table 5). The A>G Mutation in *MC4R* has been previously reported to have an impact on obesity-related traits in pigs (Kim et al., 2000). In a later study, Piórkowska et al. (2010) described the influence

Table 1. Description of studied genes and SNPs.

Gene	SNP	Position	Primer pairs (5´- 3´); F;R	Restriction enzyme	References	Anneal temp. (°C)
MC4R	A>G	exon 3	TACCCTGACCATCTTGATTG ATAGCAACAGATGATCTCTTTG	*Taq*I	Kim et al. (2000)	58
LPIN1	C>T	exon 2	GTTTGTCACCGTGAAGGA AAGCCACAGTAATCAGAACA	*Taq*I	He et al. (2009)	58
SERCA1	C>T	exon 8	CAAGGGGCATCACCCGACT CTGGAATTGCAGCCACAGC	–	(Chai et al., 2010)	56
H-FABP	G>C	exon1	GGACCCAAGATGCCTACGCCG CTGCATCTTTGACCAAGAGG	*Hin*fI	Gerbens et al. (1997)	62
	G>C	intron 2	ATTGCTTCGGTGTGTTTGAG TCAGGAATGGGAGTTATTGG	*Hae*III	Gerbens et al. (1997)	62
TNNI2	C>T	intron 3	GGGTGGGACTTCGAAGGGA AGAGGAGACAGAGTCAGGGC	*Sma*I	(Yang et al., 2010)	64
LCAT	C>G	intron 1	GCTCCTCAATGTGCTCTTC CATCTAGCGTGGCTTTCC	*PVu*II	Qiao et al. (2009)	63
HMGCR	A>G	exon 9	CAAATCCTGTTACTCAGAGAG CAGGAGCATAGCGTGTTATG	*Hha*I	Canovas et al. (2010)	56
FTO	T>G	intron 3,4	ACAGGCCCTGAAGAGGAAAG AGTAACCTGGAGTTCCTGTGG	*Tai*I	Fontanesi et al. (2010)	64
SERPINE1	G>A	intron 3	AGCATCCTCTTCTCCATAG TCCTTCCTCTCTCTCTCTT	*Mbi*I	Weisz et al. (2010)	59
PLIN	G>A	exon 2	TAGCTCATCAGACTCCAGGGA CTCTTCCTTCCCCCATCAGT	*Hinc*II	Vykoukalová et al. (2009)	56
	A>G	exon 3	CCAGAAGACCTACACCAGCAC TCTGGATGCCCTTCTCGTAA	*Hin*1I	Vykoukalová et al. (2009)	58
	T>C	exon 6	GATCTGCTCTCCTTCCCTCC CTGTTTCAGAGCGCGAGAC	*Nla*IV	Vykoukalová et al. (2009)	64
EDG4	C>T	exon 2	GCCAGTGCTACTACAATGAG CCCAGAATGATGACAACAG	*Mbo*I	Shan et al. (2009)	59
CSRP3	C>T	intron 3	GGTACTGTTCGCCAAGGAGA TCCAGGAAAGTGGGTGAAGA	*Taq*I	Xu et al. (2010)	60
PRKAG3	A>G	I199V	GGAGCAAATGTGCAGACAAG CCCACGAAGCTCTGCTTCTT	*Bsa*HI	Milan et al. (2000)	57
CTSZ	A>G	exon 2	GGCATTTGGGGCATCTGGG ACTGGGGGATGTGCTGGTT	*Alw*NI	Ramos et al. (2009)	66
TCF7L2	A>G	intron 10	AGAAAGGAAAGGGTGCAGGT GCGATAACTTGTCAGCACGA	*Bsr*I	Fan et al. (2010)	61

Table 2. Allele and genotype frequencies.

Gene	Allele frequency				Genotype frequency					
MC4R	*A*	0.70	*G*	0.30	*AA*	0.48	*AG*	0.43	*GG*	0.09
LPIN1	*C*	0.80	*T*	0.20	*CC*	0.63	*CT*	0.33	*TT*	0.03
SERCA1 c.686A>G	*A*	0.11	*G*	0.89	*AA*	0.01	*AG*	0.20	*GG*	0.78
SERCA1 c.696C>T	*C*	0.86	*T*	0.14	*CC*	0.74	*CT*	0.24	*TT*	0.02
SERCA1 c.810C>T	*C*	0.72	*T*	0.28	*CC*	0.48	*CT*	0.49	*TT*	0.03
H-FABP HinfI	*h*	0.63	*H*	0.38	*hh*	0.61	*Hh*	0.02	*HH*	0.36
H-FABP HaeII	*D*	0.40	*d*	0.60	*DD*	0.15	*Dd*	0.50	*dd*	0.35
TNNI2	*C*	0.88	*T*	0.12	*CC*	0.76	*CT*	0.24	*TT*	0.00
LCAT	*C*	0.94	*G*	0.05	*CC*	0.90	*GC*	0.10	*GG*	0.00
HMGCR	*A*	0.67	*C*	0.33	*AA*	0.41	*AC*	0.51	*CC*	0.08
FTO	*T*	0.65	*G*	0.35	*TT*	0.35	*GT*	0.59	*GG*	0.06
SERPINE1	*A*	0.64	*G*	0.36	*AA*	0.36	*AG*	0.55	*GG*	0.09
PLIN HincII	*G*	1.00	*A*	0.00	*GG*	1.00	*GA*	0.00	*AA*	0.00
PLIN Hin1I	*A*	0.64	*G*	0.36	*AA*	0.39	*AG*	0.49	*GG*	0.11
PLIN NlaIV	*C*	0.35	*T*	0.65	*CC*	0.11	*CT*	0.49	*TT*	0.4
EDG4	*C*	0.79	*T*	0.21	*CC*	0.61	*CT*	0.35	*TT*	0.03
CSRP3	*C*	0.88	*T*	0.12	*CC*	0.78	*CT*	0.19	*TT*	0.02
PRKAG3	*A*	0.83	*G*	0.17	*AA*	0.66	*AG*	0.34	*GG*	0.00
CTSZ	*A*	0.47	*G*	0.53	*AA*	0.13	*AG*	0.69	*GG*	0.18
TCF7L2	*A*	0.43	*G*	0.57	*AA*	0.14	*AG*	0.58	*GG*	0.28

of MC4R on IMF percentage. We found no association between *MC4R* genotypes and IMF. Moreover, no association has been found between *MC4R* and cholesterol and fatty acids composition.

The polymorphism C>T in the *LPIN1* gene was found to have an impact on IMF. Pigs with the genotype *CT* had a higher IMF content than those with *CC* (He et al., 2009). We observed lower plasma cholesterol content in pigs with the *TT* genotype than those with *CT* ($P < 0.05$). In addition to the previously described C>T substitution at the 66 bp of exon 8 in *SERCA1* (Chai et al., 2010), and the C>T at position 20 in AY027798 (Ciobanu et al., 2002) (corresponds to c.696C>T in our study), two new polymorphisms were detected in exon 8 of *SERCA1*: c.686A>G and c.810C>T (accession number ENSSSCT00000008553). Chai et al. (2010) described the effect of the *CC* genotype (*SERCA1* c.696C>T) on the IMF and water content. The *CC* genotype was associated with a lower IMF and higher water content than *CT* and *TT* ($P < 0.05$). Our results did not confirm these findings. No association was found between *SERCA1* c.696C>T and IMF and drip loss or any of the other traits studied. Moreover, new polymorphisms c.686A>G and c.810C>T were not associated with any of the studied traits.

The results of the *H-FABP* analysis remained inconsistent. *H-FABP* was previously described as the gene influencing IMF content (Árnyasi et al., 2006; Pang et al., 2006; Li et al., 2010). On the other hand, no association with IMF was found by Nechtelberger et al. (2001) and Chmurzynska et al. (2007). Urban et al. (2002) found a close to significant ($P = 0.06$) difference between the *HH* and *Hh* genotypes (*Hinf*I). In our study, *H-FABP Hae*III had a non-significant influence on IMF content, even though the difference between genotypes *Dd* and *dd* is very close to significant ($P = 0.0557$). No association was found between *H-FABP Hinf*I polymorphism and IMF, cholesterol and fatty acid composition.

Polymorphism C>T in *TNNI2* was previously associated with pH, colour, marbling score and intramuscular fat (Yang et al., 2010). No associations were found between *TNNI2* and IMF, cholesterol level, fatty acids composition, drip loss, pH_{ult}, EC_{ult} and colour.

The C>G polymorphism in *LCAT* was previously reported to have an influence on several carcass traits: ratio of lean to fat, caul fat weight, leaf fat weight, carcass length and bone percentage (Qiao et al., 2009). We studied the relationship between *LCAT* and cholesterol level, IMF and fatty acid composition. We noticed a higher cholesterol level ($P < 0.01$) and higher linoleic acid content ($P < 0.05$) in animals with the *GC* genotype than those with *CC*.

HMGCR was described as a gene influencing total serum cholesterol, LDL/HDL ratio, triglyceride level, IMF and oleic and linoleic acid content (Canovas et al., 2010). No correlation was found between *HMGCR* and total serum cholesterol, but we observed an influence of A>C polymorphism on IMF ($P < 0.05$); the *CC* genotype was associated with higher IMF than *AC* and *AA*. We found

Table 3. Association analysis of intramuscular fat, cholesterol and fatty acids content.

Gene		Genotype (N)	Cholesterol (mmol/L)	IMF (%)	Palmitic acid (%)	Stearic acid (%)	Oleic acid (%)	Linoleic acid (%)
MC4R		*AA (41)*	1.92 ± 0.42	3.62 ± 0.48	27.28 ± 0.69	15.42 ± 0.82	50.06 ± 1.28	7.22 ± 0.84
		AG (35)	1.81 ± 0.43	3.66 ± 0.50	27.55 ± 0.72	15.60 ± 0.84	49.36 ± 1.32	7.43 ± 0.86
		GG (6)	1.42 ± 0.46	4.07 ± 0.53	27.26 ± 0.76	15.17 ± 0.90	50.84 ± 1.41	6.69 ± 0.92
LPIN		*CC (52)*	2.08 ± 0.36	3.83 ± 0.41	27.39 ± 0.59	15.63 ± 0.70	50.25 ± 1.10	6.71 ± 0.72
		CT (27)	2.14 ± 0.39^{a}	3.70 ± 0.45	27.52 ± 0.65	15.75 ± 0.76	49.59 ± 1.20	7.06 ± 0.78
		TT (3)	0.92 ± 0.61^{a}	3.82 ± 0.71	27.19 ± 1.02	14.81 ± 1.21	50.41 ± 1.90	7.58 ± 1.24
SERCA1	c.686A>G	*AG (16)*	1.60 ± 0.47	3.87 ± 0.54	27.67 ± 0.78	15.43 ± 0.92	50.02 ± 1.44	6.84 ± 0.94
		GG (66)	1.83 ± 0.37	3.69 ± 0.43	27.06 ± 0.62	15.36 ± 0.73	50.15 ± 1.15	7.39 ± 0.75
	c.696C>T	*CC (62)*	1.67 ± 0.35	3.54 ± 0.41	27.36 ± 0.58	15.60 ± 0.69	50.45 ± 1.08	6.57 ± 0.70
		CT (18)	1.45 ± 0.40	3.78 ± 0.47	27.55 ± 0.67	15.64 ± 0.79	50.60 ± 1.24	6.20 ± 0.81
		TT (2)	2.01 ± 0.62	4.03 ± 0.72	27.19 ± 1.04	14.94 ± 1.22	49.20 ± 1.92	8.58 ± 1.25
	c.810C>T	*CC (39)*	1.88 ± 0.37	3.93 ± 0.43	27.21 ± 0.61	15.17 ± 0.72	50.59 ± 1.14	6.98 ± 0.74
		CT (40)	1.82 ± 0.40	4.02 ± 0.46	27.40 ± 0.67	15.10 ± 0.78	50.52 ± 1.23	6.94 ± 0.80
		TT (3)	1.45 ± 0.56	3.40 ± 0.65	27.49 ± 0.94	15.92 ± 1.11	49.14 ± 1.74	7.43 ± 1.13
H-FABP	*Hinf*I	*hh (49)*	1.94 ± 0.36	3.64 ± 0.42	27.61 ± 0.60	15.04 ± 0.70	50.16 ± 1.10	7.15 ± 0.72
		Hh (2)	1.32 ± 0.64	3.99 ± 0.74	26.95 ± 1.06	16.00 ± 1.25	50.05 ± 1.97	6.96 ± 1.28
		HH (31)	1.89 ± 0.39	3.72 ± 0.45	27.53 ± 0.65	15.15 ± 0.76	50.05 ± 1.20	7.23 ± 0.78
	*Hae*III	*DD (12)*	1.58 ± 0.45	3.52 ± 0.52	27.09 ± 0.74	15.38 ± 0.88	50.22 ± 1.38	7.26 ± 0.90
		Dd (42)	1.85 ± 0.42	3.66 ± 0.48	27.52 ± 0.69	15.50 ± 0.82	49.67 ± 1.28	7.27 ± 0.84
		dd (28)	1.72 ± 0.42	4.17 ± 0.49	27.48 ± 0.71	15.31 ± 0.83	50.37 ± 1.31	6.81 ± 0.85
TNNI2		*CC (62)*	1.77 ± 0.40	3.92 ± 0.47	27.28 ± 0.67	15.37 ± 0.79	50.30 ± 1.25	7.03 ± 0.81
		CT (20)	1.66 ± 0.44	3.65 ± 0.51	27.45 ± 0.73	15.43 ± 0.86	49.87 ± 1.34	7.20 ± 0.88
LCAT		*CC (75)*	1.33 ± 0.39^{A}	3.86 ± 0.46	27.68 ± 0.66	15.47 ± 0.78	50.24 ± 1.22	6.56 ± 0.79^{a}
		GC (7)	2.10 ± 0.46 ^{A}	3.71 ± 0.53	27.05 ± 0.76	15.32 ± 0.90	49.93 ± 1.41	7.67 ± 0.92^{a}
HMGCR		*AA (33)*	1.72 ± 0.45	3.44 ± 0.52^{b}	26.76 ± 0.75^{A}	15.30 ± 0.88	50.21 ± 1.39	7.69 ± 0.91
		AC (42)	1.64 ± 0.43	3.50 ± 0.50^{a}	26.85 ± 0.72^{B}	15.29 ± 0.84	50.30 ± 1.32	7.54 ± 0.86
		CC (7)	1.80 ± 0.43	4.41 ± 0.50^{ab}	28.48 ± 0.72^{AB}	15.60 ± 0.85	49.74 ± 1.33	6.11 ± 0.87
FTO		*GG (5)*	1.35 ± 0.55	3.85 ± 0.64	26.83 ± 0.92	15.86 ± 1.08	49.93 ± 1.70	7.31 ± 1.11
		GT (48)	1.89 ± 0.36	3.80 ± 0.42	27.48 ± 0.61	15.21 ± 0.71	50.35 ± 1.12	6.93 ± 0.73

Table 3. Contd.

		TT (29)	1.91 ± 0.39	3.70 ± 0.45	27.78 ± 0.64	15.12 ± 0.76	49.97 ± 1.19	7.10 ± 0.78
		AA (28)	1.98 ± 0.43^{a}	3.46 ± 0.50	27.69 ± 0.71	15.29 ± 0.84	49.79 ± 1.32	7.19 ± 0.86
SERPINE1		*AG (46)*	1.47 ± 0.46^{a}	3.64 ± 0.54	27.49 ± 0.77	15.75 ± 0.91	50.08 ± 1.43	6.65 ± 0.93
		GG (8)	1.70 ± 0.42	4.24 ± 0.49	26.92 ± 0.70	15.15 ± 0.83	50.39 ± 1.30	7.51 ± 0.85
		CC (9)	1.37 ± 0.47^{a}	3.71 ± 0.55	27.31 ± 0.79	15.76 ± 0.93	49.83 ± 1.46	7.04 ± 0.95
PLIN	*Nla*IV	*CT (40)*	1.99 ± 0.39^{a}	3.82 ± 0.45	27.45 ± 0.64	15.43 ± 0.76	49.87 ± 1.19	7.22 ± 0.78
		TT (33)	1.78 ± 0.42	3.82 ± 0.49	27.34 ± 0.70	14.99 ± 0.83	50.55 ± 1.30	7.08 ± 0.85
		AA (11)	1.26 ± 0.47^{A}	4.08 ± 0.55	27.82 ± 0.79	15.01 ± 0.93	50.11 ± 1.45	7.03 ± 0.95
TCF7L2		*AG (47)*	2.05 ± 0.42^{A}	3.72 ± 0.48	26.94 ± 0.69	15.66 ± 0.82	50.15 ± 1.28	7.21 ± 0.84
		GG (24)	1.84 ± 0.39	3.55 ± 0.45	27.34 ± 0.65	15.52 ± 0.77	49.99 ± 1.21	7.11 ± 0.79

The same superscripts in a column show significant differences between the genotypes: ^{A,B}, P < 0.01; ^{a,b}, P < 0.05. Least squares means ± standard error; N = 82.

an association between *HMGCR* and palmitic acid content (P < 0.01); the *CC* genotype was associated with higher palmitic acid content than *AC* and *AA*. Moreover, animals with the *CC* genotype had lower linoleic acid content than those with *AC* (P = 0.0574) and *AA* (P = 0.0604).

In previously published studies, *FTO* was associated with obesity-related traits, IMF content and lean meat content (Fontanesi et al., 2010). In this study, no association was found between T>G polymorphism in *FTO* and IMF. Moreover, no association was found between *FTO*, cholesterol level and fatty acids composition.

SERPINE1 could be one of the factors influencing obesity-related traits in humans (Barbato et al., 2009). We observed that *SERPINE1* had an influence on plasma cholesterol level in pigs. *AA*-genotype animals were associated with a higher cholesterol level than those with *AG* (P < 0.05). We studied three polymorphisms in *PLIN1* – *Hinc*II, *Hin*1I and *Nla*IV. In the *Hin*1I and *Nla*IV polymorphisms, according to Vykoukalová et al. (2009), the only genotype combinations detected were *AA-TT*, *AG-TC* and *GG-CC* (apart from one sample with the combination *AG-TT*) and therefore, only *Nla*IV was included in the association analysis. Only the *GG* genotype was detected in *Hinc*II. This finding is consistent with Vykoukalová et al. (2009), who found allele *A* only in Meishan and a Meishan × Piétrain cross. As a result, *Hinc*II was excluded from the association analysis. Vykoukalová et al. (2009) reported a correlation between *PLIN1* and average daily gain and backfat thickness. On the basis of our observations, we found an association between *PLIN1 Nla*IV and cholesterol level. Pigs with the *CT* genotype had a higher cholesterol level than those with *CC* (P < 0.05).

The polymorphism A>G in intron 10 of *TCF7L2* was recorded as a mutation influencing backfat and meat colour (Du et al., 2009; Fan et al., 2010). We studied the relationship between *TCF7L2* and cholesterol level, IMF, fatty acid composition and colour. This study found *TCF7L2* to be associated with plasma cholesterol content (the *AA* genotype was associated with a lower level than *AG*; P < 0.01). *EDG4* was associated with drip loss; animals with the *CT* genotype had a higher drip loss than those with *CC* and *TT* (Shan et al., 2009). Similarly in our study, pigs with the *CT* genotype had a higher drip loss than those with *CC* (P < 0.05). *PRKAG3* was previously associated with ultimate pH and colour (Ciobanu et al., 2001; Otto et al., 2007). We tested the effect of *PRKAG3* on drip loss, ultimate pH, ultimate EC and colour, but no correlation was found. Cathepsin Z (*CTSZ*) was associated with meat colour in previously published studies (Fan et al., 2010; Ramos et al., 2009). According to our results, no relationship between *CTSZ* and colour has been proven. An association between *CSRP3*, firmness, lab loin pH, off flavor score and water holding capacity was found by Xu et al. (2010). We studied the influence of *CSRP3* gene on drip loss, ultimate pH and ultimate EC, but did not find any correlation.

Table 4. Association analysis of drip loss, pH_{ult} and EC_{ult}.

Gene		Genotype (N)	Drip loss (%)	pH ultimate	EC ultimate
SERCA1	c.686A>G	*AG (18)*	3.16 ± 0.21	5.57 ± 0.09	6.39 ± 0.93
		GG (69)	3.22 ± 0.18	5.56 ± 0.07	6.28 ± 0.81
	c.696C>T	*CC (64)*	3.11 ± 0.16	5.61 ± 0.06	5.64 ± 0.70
		CT (21)	3.30 ± 0.18	5.57 ± 0.07	5.71± 0.78
		TT (2)	3.15 ± 0.33	5.59 ± 0.13	7.65 ± 1.45
	c.810C>T	*CC (41)*	3.17 ± 0.17	5.64 ± 0.07	5.86 ± 0.77
		CT (43)	3.11 ± 0.18	5.62 ± 0.07	5.56 ± 0.79
		TT (3)	3.29 ± 0.29	5.51 ± 0.12	7.58 ± 1.30
TNNI2		*CC (67)*	3.24 ± 0.19	5.58 ± 0.08	6.55 ± 0.84
		CT (20)	3.14 ± 0.20	5.60 ± 0.08	6.12 ± 0.89
EDG4		*CC (54)*	3.01 ± 0.16[a]	5.60 ± 0.07	5.89 ± 0.71
		CT (30)	3.26 ± 0.19[a]	5.60 ± 0.08	6.56 ± 0.83
		TT (3)	3.30 ± 0.29	5.56 ± 0.12	6.55 ± 1.29
CSRP3		*CC (68)*	3.32 ± 0.17	5.63 ± 0.07	5.97 ± 0.75
		CT (17)	3.22 ± 0.19	5.56 ± 0.08	6.11 ± 0.85
		TT (2)	3.04 ± 0.32	5.57 ± 0.13	6.91 ± 1.41
PRKAG3		*AA (57)*	3.25 ± 0.18	5.60 ± 0.07	6.14 ± 0.78
		AG (30)	3.13 ± 0.21	5.58 ± 0.09	6.53 ± 0.92

The same superscripts in a column show significant differences between the genotypes:[a] $P < 0.05$. Least squares means ± standard error; N = 87.

Table 5. Association analysis of meat colour.

Gene	Genotype (N)	Lightness	Redness	Yellowness
TNNI2	*CC (67)*	55.95 ± 0.70	1.76 ± 0.24	11.19 ± 0.32
	CT (21)	55.45 ± 1.13	1.93 ± 0.40	11.25 ± 0.51
PRKAG3	*AA (58)*	56.37 ± 0.77	1.76 ± 0.27	11.43 ± 0.35
	AG (30)	55.03 ± 1.01	1.92 ± 0.35	11.02 ± 0.46
CTSZ	*AA (11)*	56.60 ± 1.31	1.93 ± 0.46	11.61 ± 0.60
	AG (61)	56.26 ± 0.73	2.13 ± 0.26	11.58 ± 0.33
	GG (16)	54.24 ± 1.20	1.47 ± 0.42	10.48 ± 0.55
TCF7L2	*AA (12)*	54.73 ± 1.29	1.92 ± 0.45	10.95 ± 0.59
	AG (51)	56.85 ± 0.92	1.94 ± 0.33	11.63 ± 0.42
	GG (25)	55.53 ± 0.98	1.67 ± 0.34	11.08 ± 0.45

Least squares means ± standard error; N = 88.

Our research mostly included recent candidate genes, whose effects have not yet been fully explored. Results indicate that SNPs are markers that are in linkage disequilibrium with unknown causative mutations affecting the chosen performance traits. Moreover, the analysis of these quantitative traits could be influenced by an unknown genetic background. Further research on the extended population is needed to confirm these results. These results could be useful for better understanding the given candidate genes and their potential use in

marker-assisted selection and healthy and quality meat production.

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