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Association between *ADSL*, *GARS-AIRS-GART*, *DGAT1*, and *DECR1* expression levels and pork meat quality traits

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ABSTRACT. In this study, meat quality traits were compared between Chinese lard- and European lean-type pigs. The association between expression of four genes (*ADSL*, *GARS-AIRS-GART*, *DGAT1*, and *DECR1*) and meat quality traits was also investigated. Meat quality traits were found to differ significantly between pig breeds. Meat color parameter values (a* and b*) and intramuscular fat content in Anqingliubai were significantly higher than those in Landrace ($P < 0.01$). Meat pH at 1 and 24 h following slaughter was significantly higher in Landrace than in Wei pigs, and meat inosine monophosphate (IMP) content was significantly higher in Landrace than in Wei and Anqingliubai pigs (both $P < 0.01$). Expression levels of *ADSL*, *GARS-AIRS-GART*, and *DGAT1* were higher in longissimus lumborum muscle than in heart or liver tissues. *ADSL* and *GARS-AIRS-GART* expression levels were correlated with meat IMP content and pH levels. The results of this study will contribute to the understanding of meat quality traits in Chinese lard- and European lean-type pigs.

Key words: Meat color; Intramuscular fat; *ADSL*; Meat quality; Pig

INTRODUCTION

There is high consumer demand for high quality pork, particularly lean meat (Hermesch et al., 2000a,b,c; Ma et al., 2014). In China, lard-type breeds are the predominant pig. Crosses between lard- and lean-type pig breeds may improve pork flavor. Pork meat quality is determined by meat color, pH, shear force, and intramuscular fat (IMF) content, and is affected by pig breed, nutrition, and environment (Bowker, 2013; Gatta et al., 2013; Shen et al., 2014).

There has been increasing interest in the study of genes involved in pork meat quality. Single nucleotide polymorphisms in *ADSL*, a gene that codes for adenylosuccinate lyase, and in *GARS-AIRS-GART*, a gene that codes for glycinamide ribonucleotide-aminoimidazole ribonucleotide synthetase-glycinamide ribonucleotide transformylase, affect muscle inosine monophosphate (IMP) content in chickens (Shu et al., 2007, 2009; Ye et al., 2010). The gene *DGAT1*, which affects IMP content by increasing triglyceride levels in pig muscle (Nonneman and Rohrer, 2002), is associated with improved meat quality in Landrace swine. The gene *DECR1* plays a role in isocitrate dehydrogenase activity, and muscle pH and redness (Amills et al., 2005). Differences in allele frequencies of *DECR1* have been reported in pigs with different phenotypes for glycolytic potential and drip loss (Kaminski et al., 2010), which suggests that this gene may have pleiotropic effects.

Few studies have focused on the relationship between gene expression levels and pork meat quality traits. Anqingliubai and Wei, two Chinese lard-type pig breeds, have high fecundity rates and good meat quality. Landrace, a European lean-type pig breed, has high growth rates. In this study, we compared meat quality between Anqingliubai, Wei, and Landrace pig breeds and performed a correlation analysis between the genes *ADSL*, *GARS-AIRS-GART*, *DGAT1*, and *DECR1*, and pork meat quality traits. The objectives of the study were to identify meat quality differences among breeds, and evaluate the role of these four genes on meat quality traits.

MATERIAL AND METHODS

Animals and ethics statement

Sixty pigs were used in the study; 20 lean-type European Landrace pigs, and two lard-type Chinese indigenous breeds (Wei and Anqingliubai, both N = 20). Pigs were of marketing age and were housed in standard indoor conditions at the experimental farm of the College of Animal Science and Technology, at Anhui Agricultural University. Experiments were approved by the Animal Ethics Committee of Anhui Agricultural University. Pigs had *ad libitum* access to feed and water and were humanely euthanized at the end of the study.

Heart and liver tissues, and longissimus lumborum (LL) muscle samples (5 g each) were collected post mortem, immersed in liquid nitrogen, and stored at -80°C for total RNA extraction. Additionally, 500 g LL was collected for measurement of meat quality traits.

Measurements of meat quality traits

Meat color (based on the parameters L*, a*, and b*) was determined 45 min post mortem from an average of four random measurements performed using an ADCI-WSI whiteness colorimeter (Chentaike Experiment Instrument and Technology, Beijing, China). Meat pH values were measured at 1 and 24 h post mortem, using an HI-9025 pHmeter (Hanna Instruments, Beijing, China). Mean shear force was determined using a C-LM3 Tenderness Analyzer (Tenovo International, Beijing,

China) from 10 random measurements (Zhang et al., 2014a). Inosine monophosphate content was determined using the method reported by Shu et al. (2007); IMF content was measured using AOAC (Association of Official Analytical Chemists) methods (Feldsine et al., 2002).

q-PCR

Total RNA was extracted different tissues using TRIzol reagent (Invitrogen, Carlsbad, CA, USA). The quality of RNA was assessed using 0.8% agarose (w/v) gel electrophoresis, stained with 0.5 µg/mL ethidium bromide. Total RNA (2 µg) from each tissue was reverse-transcribed into cDNA, using a PrimerScript RT Reagent Kit (TaKaRa, Osaka, Japan). Following incubation at 37°C for 1 h and deactivation at 95°C for 10 min, cDNA was used for q-PCR, which was performed in an ABI 9700 DNA Thermal Cycler (ABI, Foster City, CA, USA). The 25 µL reaction mixture contained: 2 µL cDNA; 12.5 µL 2X SYBR Green SuperReal PreMix (Tiangen, Beijing, China); 1 µL of each primer; and 8.5 µL RNase-free H_2O. The thermocycling program consisted of an amplification reaction of 95°C for 2 min; then 40 cycles at 95°C for 10 s, 58.5 to 62.5°C for 20 s, and 72°C for 15 s. Amplification reactions were performed in triplicate for each gene. Gene-specific primers are shown in Table 1.

Table 1. Primers used in q-PCR.

Gene	Sequence accession No.	Primer sequences (5'-3')	PCR Tm (°C)	Fragment size (bp)
ADSL	NM-001130733.1	F-GCCAACCGACGTATCTGTTT R-ATTTTCTCGTGGCAATCCTG	58.5	206
GARS-AIR S-GART	XM-003358935.1	F-ATTGCCCAGCAGTGCCATA R-CGATTCCAGCCACAACAGC	61.5	163
DGAT1	397118	F-AAGGACGGACACGACGATG R-ATGCCACGGTAGTTGCTGAA	60.0	107
DECR1	503544	F-AAGACTCTCTCCTAATGCCTG R-TACCACAAAACCTGACCCA	62.5	161
β-actin	XM-003124280.2	F-CTCTTCCAGCCCTCCTTCC R-GGTCCTTGCGGATGTCG	60.0	97

Statistical analyses

A cycle threshold was obtained from each PCR, and the expression level of each gene relative to that of β-actin was evaluated by $2^{-\Delta\Delta Ct}$. One-way ANOVA and bivariate correlation analyses were performed using SPSS version 17.0 (Weaver and Wuensch, 2013). Data are reported as means ± SE. Statistical significance was set to $P < 0.05$.

RESULTS

Meat quality traits of different pig breeds

Anqingliubai pigs had the highest meat color parameters (L*, a*, and b*; Table 2), and significantly higher a* and b* values compared to Landrace pigs ($P < 0.01$). Meat pH at 1 and 24 h was significantly higher for Anqingliubai and Landrace, compared to Wei pigs ($P < 0.01$). Meat shear force values were significantly higher in Anqingliubai than in Landrace and Wei pigs ($P < 0.01$). Wei and Anqingliubai had significantly higher IMF content than Landrace pigs (Table 2); however, Landrace had significantly higher IMP content ($P < 0.01$).

Table 2. Meat quality traits in different pig breeds.

Traits	Wei N = 20	Anqingliubai N = 20	Landrace N = 20
a*	11.52 ± 2.58^{A}	12.95 ± 2.74^{A}	6.18 ± 1.35^{B}
b*	5.95 ± 0.34^{A}	14.51 ± 0.32^{B}	7.48 ± 0.17^{A}
L*	35.12 ± 5.45^{A}	40.08 ± 7.12^{B}	38.85 ± 4.37^{B}
pH 1 h	5.89 ± 0.53^{A}	6.31 ± 0.71^{B}	6.37 ± 0.75^{B}
pH 24 h	5.40 ± 0.48^{A}	5.71 ± 0.64^{B}	5.78 ± 0.67^{B}
Shear force (N)	22.38 ± 2.45^{B}	51.56 ± 3.63^{A}	23.45 ± 2.83^{B}
IMF (%)	3.18 ± 0.36^{A}	3.46 ± 0.20^{A}	1.54 ± 0.11^{B}
IMP (mg/g)	2.34 ± 0.63^{A}	2.22 ± 0.20^{A}	2.76 ± 0.41^{B}

a*, b*, and L* are meat color parameters; IMP, inosine monophosphate; IMF, intramuscular fat. Within each row, different uppercase letters represent significant differences between samples ($P < 0.01$).

Correlation between meat pH and color

Correlation analyses revealed that meat pH at 1 h following slaughter was significantly positively correlated with L* and b* (Table 3), and significantly negatively correlated with a* ($P < 0.01$). Meat pH 24 h following slaughter was significantly negatively correlated with a* ($P < 0.01$).

Table 3. Correlation analyses between meat pH and color parameters.

Meat color parameters	Correlation with pH 1 h	Correlationwith pH 24 h
L*	0.374**	0.250
b*	0.340**	0.194
a*	-0.343**	-0.381**

Correlation coefficients in table; **$P < 0.01$; h, hours after slaughter.

Expression levels of *ADSL*, *GARS-AIRS-GART*, *DGAT1*, and *DECR1*

Expression levels of *ADSL* were similar among the three pig breeds. In other of decreasing *ADSL* expression levels, tissues were LL, then heart, and liver. *ADSL* expression levels were higher in LL than in liver of Wei and Landrace ($P < 0.05$; Figure 1A and C) but not significant differently in Anqingliubai (Figure 1B). *GARS-AIRS-GART* expression levels were highest in LL, followed by the liver and heart; however, results were not significant (Figure 1D, E, and F). *DGAT1* expression levels were not significantly different in Wei and Anqingliubai pigs (Figure 1G, and H) but significantly different among LL, heart, and liver in Landrace ($P< 0.01$; Figure 1I). *DECR1* expression levels were not significantly different in Wei and Anqingliubai pigs (Figure 1J, and K) but significantly different among LL, heart, and liver in Landrace ($P< 0.01$; Figure 1L).

Correlation between gene expression levels and meat quality traits

ADSL expression levels were significantly negatively correlated with IMP content in Landrace liver and significantly positively correlated with meat pH 1 h following slaughter, in Anqingliubai and Landrace heart ($P < 0.05$). Expression levels of *GARS-AIRS-GART* were significantly negatively correlated with IMP content in Anqingliubai heart and Wei liver ($P < 0.01$) and significantly positively correlated with meat pH 24 h following slaughter in Anqingliubai heart and LL ($P < 0.05$; Table 4).

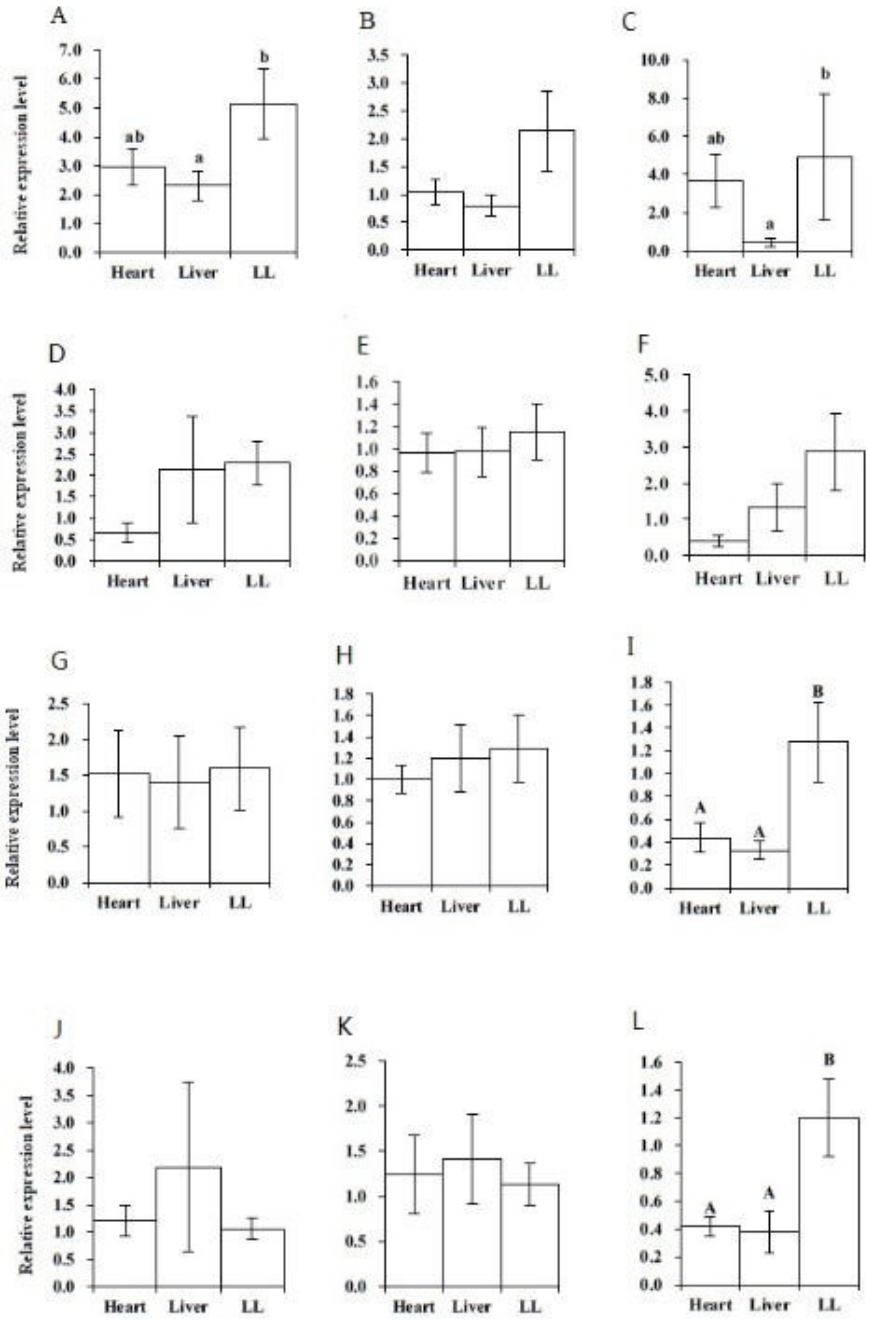

Figure 1. Gene expression levels in three pig breeds Expression of ADSL in Wei (**A**), Anqingliubai (**B**), and Landrace (**C**) pigs; GARS-AIRS-GART [Wei (**D**), Anqingliubai (**E**), Landrace (**F**)]; DGAT1 [Wei (**G**), Anqingliubai (**H**), Landrace (**I**)]; andDECR1 [Wei (**J**), Anqingliubai (**K**), Landrace (**L**)]. Within each horizontal panel, bars labeled with different upper- and lowercase letters represent significant differences in gene expression level sat a value of $P < 0.01$ and $P < 0.05$, respectively. LL, longissimus lumborum muscle.

Table 4. Correlation analyses between gene expression levels and meat quality traits (IMP, pH 1 h, and pH 24 h).

Breed	Gene	Tissue	Correlation with IMP	Correlation with pH 1 h	Correlation with pH 24 h
Wei	*ADSL*	Heart	-0.31	0.028	0.035
		Liver	0.108	-0.175	0.073
		LL	0.495	0.104	0.104
	GARS-AIRS-GART	Heart	0.026	-0.538	0.13
		Liver	-0.735**	0.282	-0.392
		LL	0.16	-0.051	-0.008
Anqingliubai	*ADSL*	Heart	-0.146	0.572*	0.063
		Liver	0.199	0.449	0.264
		LL	0.131	-0.489	0.052
	GARS-AIRS-GART	Heart	-0.806**	0.168	0.643*
		Liver	0.592	0.176	0.138
		LL	0.357	-0.213	0.557*
Landrace	*ADSL*	Heart	-0.592	0.833*	0.039
		Liver	-0.825*	0.195	0.711
		LL	-0.003	-0.607	0.201
	GARS-AIRS-GART	Heart	-0.884	0.844	0.909
		Liver	-0.507	-0.565	-0.585
		LL	-0.44	0.276	0.311

Correlation coefficients in table; *P < 0.05; **P < 0.01; h, hours after slaughter; IMP, inosine monophosphate; LL, longissimus lumborum muscle.

DISCUSSION

Meat quality traits of different pig breeds

Meat quality is dependent on genetic, breeding, environmental, stress, and processing factors (Muhlisin et al., 2014). Our results revealed significant differences in meat quality traits among Anqingliubai, Wei, and Landrace pigs. Anqingliubai and Wei were found to have strong triglyceride deposition capacity, while Landrace had high lean meat percentage. Anqingliubai had higher meat color parameter values and IMF content than Landrace and, correspondingly, better appearance and flavor than Landrace. However, meat storage performance of Landrace was superior to that of Chinese pig breeds, because Landrace pig tissues had higher pH values. Recent studies have reported that European commercial pig breeds have high growth rates, lean meat percentage, and feed conversion rates; however, meat quality is poor. On the other hand, Chinese pig breeds have low growth rates but high meat quality (Shen et al., 2014; Zhang et al., 2014b). These previously reported findings are consistent with our results. Pork meat quality would likely improve with crosses between European lean-type pigs (as the sire) and Anqingliubai lard-type pigs (as the dam). Meat pH 1 h after slaughter was significantly correlated with L*, a*, and b* color parameters. Meat pH decreases rapidly with increased myoprotein denaturation, reduced water holding capacity, increased water loss, and gray color formation (Bendall and Swatland, 1988; Page et al., 2001).

Effect of different tissues on gene expression

ADSL and GARS-AIRS-GART are enzymes involved in the biosynthesis of purine nucleotides, which contribute to delicate flavors in muscle tissue (Kan and Moran, 1995; Shu et al., 2009). Recent studies have reported that *ADSL* and *GARS-AIRS-GART* affect IMP content in chickens (Shu et al., 2009; Ye et al., 2010). In this study, *ADSL* and *GARS-AIRS-GART* had high expression levels in LL and low expression levels in heart and liver. Therefore, the purine biosynthetic pathway was mainly active in muscle tissue.

DGAT1 is the only enzyme involved in triglyceride synthesis (Szczerbal et al., 2007; Drosatos-Tampakaki et al., 2014; Liu et al., 2014). Triglyceride synthesis mainly occurs in hepatic cells; however, studies have reported that *DGAT1* has low expression levels in human liver. It is possible that DGAT2 participates in fat metabolic processes (Du et al., 2014). *DGAT1* is ubiquitous in animals and humans; the highest expression levels are present in the small intestine (Cases et al., 1998). *DGAT1* was expressed in the heart, liver, and LL of the three pig breeds in the current study; the highest expression levels were obtained in the muscle tissue. Therefore, triglyceride synthesis can occur in muscle.

DECR1 is involved in the β-oxidation of polyunsaturated fatty acids (PUFAs) and, therefore, in fatty acid balance and energy metabolism. Additionally, the gene has a regulatory effect on fat and protein deposition (Amills et al., 2005; Ursini-Siegel et al., 2007). In Landrace pigs, *DECR1* expression levels were higher in LL than in heart or liver tissues; however, opposite results were seen in Wei and Anqingliubai. These results revealed differences in *DECR1* expression between lean- and lard-type pigs. Lean-type pigs have higher PUFA content, requiring more *DECR1* (Davoli et al., 2002; Amills et al., 2005; Ramirez et al., 2014).

Effect of gene expression levels on meat quality traits

Inosine monophosphate content was significantly negatively correlated with *ADSL* and *GARS-AIRS-GART* expression levels in the three pig breeds; however, there were differences among the breeds (Iwamoto et al., 2009). Among meat quality traits, pH may contribute to abnormal meat characteristics (Bendall and Swatland, 1988). In this study, pH 1 and 24 h following slaughter was positively correlated with *ADSL* and *GARS-AIRS-GART* expressed in the heart and LL of Anqingliubai and Landrace pigs; these results are consistent with the findings of Karol et al. (2010).

Anqingliubai pigs had superior meat color and flavor compared to Landrace and Wei pigs; however, meat storage performance of Landrace was superior to that of Anqingliubai and Wei. *ADSL*, *GARS-AIRS-GART*, *DGAT1*, and *DECR1* were widely expressed in the heart, liver, and LL muscle, but expression levels were highest in the LL of all three pig breeds. *ADSL* and *GARS-AIRS-GART* expression levels significantly affected meat pH and IMP content.

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