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PPARα signal pathway gene expression is associated with fatty acid content in yak and cattle longissimus dorsi muscle

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ABSTRACT. Intramuscular fatty acid (FA) is related to meat qualities such as juiciness, tenderness, palatability, and shear force. PPARα plays an important role in lipid metabolism in the liver and skeletal muscle. This study investigated FA composition in yaks and cattle, in order to ascertain whether a correlation between PPARα signal pathway genes as candidate genes and meat FA composition in yaks and cattle exists. Statistical analyses revealed that levels of monounsaturated fatty acid (MUFA) and polyunsaturated fatty acid (PUFA) in yaks were significantly higher than those in cattle ($P < 0.01$), whereas saturated fatty acid (SFA) levels were significantly lower than those in cattle ($P < 0.05$). The mRNA expression levels of *FABP4* ($P < 0.05$), *SCP2* ($P < 0.05$), and *APOA1* ($P < 0.01$) in yaks were significantly lower than those in cattle. However, *LPL* expression in yaks was significantly higher than that in cattle ($P < 0.05$). In yaks, the expression levels of *FABP3* ($P < 0.05$) and *LPL* ($P < 0.01$) were negatively correlated with MUFA, and those of *FABP4* and *SCD* were positively correlated with PUFA ($P < 0.01$). In cattle, the mRNA level of *PLTP* was positively correlated with SFA ($P < 0.05$), and *LPL* was positively correlated

with MUFA ($P < 0.05$). These results suggest that these genes may participate in the regulation and control of intramuscular FA metabolism in yaks, so they could be used as candidate markers to improve yak meat quality.

Key words: PPARα signal pathway gene; mRNA expression; Yak; Cattle; Fatty acid composition

INTRODUCTION

In recent years, meat quality has become an important component of consumer demand, particularly yak meat, which is low in fat and cholesterol, and high in protein, vitamins, and essential minerals such as copper, zinc, iron, and potassium (Wan et al., 2012). Yak meat is a staple source of animal protein, and the most important component of economic income for Tibetans living between 2500 and 5500 m above sea level. Despite the fact that yak meat is not as tender as cattle meat, the economic value of yak meat is high (Niu et al., 2009).

Intramuscular fatty acid (FA) is an important factor that affects meat quality variables such as juiciness, tenderness, palatability, shear force, and muscle pH value (Goodson et al., 2002; Hausman et al., 2009). Intramuscular FA is composed of 60-70% phospholipids. Several FA groups and single FAs have different physiological effects, and can function as physiological regulators (Cao et al., 2008). The content and composition of intramuscular FA are influenced by several factors, such as breed (Wang et al., 2011), gender, age (Bednárová et al., 2013), and nutrition (Yang et al., 2006).

The content and composition of intramuscular FA are mainly determined by lipid metabolism. Peroxisome proliferator-activated receptors (PPARs), which have three subtypes (PPARα, PPARβ/δ, and PPARγ), are nuclear hormone receptors that are activated by FAs and their derivatives (Takahashi, 2005). PPARα plays a role in the clearance of circulating or cellular lipids by the regulation of gene expression involved in lipid metabolism in the liver and skeletal muscle. The expression of many PPARα signaling pathway genes in the longissimus muscles, including those involved in lipid transport [phospholipid transfer protein (PLTP) and apolipoprotein A-I (APOA1)], lipogenesis [malic enzyme 1 (ME1) and stearoyl-CoA desaturase (SCD)], FA transport [diazepam binding inhibitor (DBI), FA binding protein 3 (FABP3), thrombospondin receptor (CD36), and lipoprotein lipase (LPL)], FA oxidation [sterol carrier protein 2 (SCP2)], and adipocyte differentiation [FA binding protein 4 (FABP4)] may contribute to FA deposition. However, whether the expression of lipid metabolic genes is associated with FA deposition within steers is unknown.

This study was conducted in order to identify PPARα signaling pathway genes that are associated with FA content in the longissimus dorsi muscle of yaks and cattle. The mRNA expression levels of 11 PPARα signaling pathway genes, including those involved in lipid transport, lipogenesis, FA transport, FA oxidation, and adipocyte differentiation were measured. Correlations between gene expression levels and FA content were analyzed, and differences in gene expression levels and FA content between yaks and cattle were investigated.

MATERIAL AND METHODS

Animals

The eight yaks and eight cattle used were 3 years old and from pastoral areas in the Tibetan Autonomous Prefecture of Gannan, Gansu Province, China. Muscle tissue samples were

taken from the right side of the longissimus dorsi muscle at the 12th/13th rib. Samples for RNA extraction were collected after slaughter, immediately frozen in liquid nitrogen, and stored at -80°C. Samples for FA composition analysis were collected 24 h after carcass cooling and maintained at 4°C.

RNA extraction and real-time polymerase chain reaction (PCR)

Total RNA was extracted from the tissues using an RNAprep Pure Kit (For Tissue) (Tiangen), according to the manufacturer instructions. Total RNA was quantified by absorbance at 260 nm, and its integrity was checked by agarose gel electrophoresis and ethidium bromide staining of the 28 and 18S bands. Total RNA was reverse-transcribed into cDNA using a PrimeScript™ RT reagent kit (Takara), according to manufacturer instructions. A real-time PCR was conducted with 12.5 µL SYBR® Premix Ex *Taq*™ II (Takara), 0.2 µL 10 µM primers, 9.5 µL ddH_2O, and a 1-µL total reaction volume that contained 100 ng cDNA. The thermal cycling parameters were as follows: 95°C for 5 s, followed by 40 cycles at 95°C for 30 s and Tm for 30 s. All of the primers were designed using integrated mRNA sequences based on sequences published by the National Center for Biotechnology Information (NCBI) (www.ncbi.nlm.nih.gov; Table 1). The $2^{-\Delta\Delta Ct}$ method was used to determine the relative fold-changes (Schmittgen and Livak, 2008), and all of the data were normalized with the housekeeping glyceraldehyde-3-phosphate dehydrogenase gene.

Table 1. Primer sequences used in the real-time polymerase chain reaction.

Gene name and symbol	GenBank ID	5'→3'	Sequence	Amplicon size (bp)
Glyceraldehyde-3-phosphate dehydrogenase, *GAPDH*	NM_001034034	Forward	ccacgagaagtataacaacacc	120
		Reverse	gtcataagtccctccacgat	
Phospholipid transfer protein, *PLTP*	NM_001035027	Forward	tccatttccagccagacca	102
		Reverse	ccccatcatagaagaaccagtagag	
Fatty acid binding protein 3, *FABP3*	NM_174313	Forward	tgtgcgggagatggttga	146
		Reverse	tgccgagtccaggagtagcc	
Fatty acid binding protein 4, *FABP4*	NM_174314	Forward	caaattgggccaggaatttga	197
		Reverse	tctcataaactctggtggcagtgac	
Lipoprotein lipase, *LPL*	NM_001075120	Forward	acttgccacctcattcctg	119
		Reverse	acccaactctcatacattcctg	
Thrombospondin receptor, *CD36*	NM_174010	Forward	ggtccttacacatacagagttcg	115
		Reverse	atagcgagggttcaaagatgg	
Malic enzyme 1, *ME1*	NM_001144853	Forward	tgctgcgattggtggtgc	191
		Reverse	tcggaagggtaacgggat	
Stearoyl-CoA desaturase, *SCD*	NM_173959	Forward	actgcggtccaagtcgtt	164
		Reverse	cagccttgtctggagtcatc	
Sterol carrier protein 2, *SCP2*	NM_001033990	Forward	tgaactccctttgcctccttt	171
		Reverse	caggttctattcacccagcactt	
Apolipoprotein A-I, *APOA1*	NM_174242	Forward	accgtgtatgtggaagcaatcaag	107
		Reverse	tcccagttgtccaggagtttcag	
Peroxisome proliferator-activated receptor alpha, *PPARα*	NM_001034036	Forward	gaatcggaataagtgcca	156
		Reverse	gtttcggaatcttctaggtc	
Diazepam binding inhibitor, *DBI*	NM_001113321	Forward	gcatcttaagaccaagccagcag	117
		Reverse	ttgcctttgaagtccaacattcc	

FA composition of intramuscular fat

Total lipids were extracted from approximately 10 g longissimus dorsi muscle samples with a chloroform-methanol (1:1) solvent, and the samples were homogenized and then extracted for 24 h (Yan et al., 2005). Lipid fractions were hydrolyzed in 5 mL 2 M KOH and CH_3OH (1:1) after being dissolved in 2 mL chloroform and petroleum ether-benzene (1:1). After stratification of the petroleum ether methyl ester solution by distilled water, the supernatant was used for gas

chromatography-mass spectrometry. The chromatographic conditions were as follows: 160°C for 2 min, increasing at 5°C/min to 220°C for 1 min, then increasing at 8°C/min to 230°C for 1 min; the injection port was at 250°C, the diversion ratio was 60:1, the carrier gas was He, and the flow rate was 1.2 mL/min. The mass spectrometry conditions were as follows: electron ionization mode was set; the ion source temperature was 250°C, the electron energy was 70 eV, the solvent latency was 1.8 min, and the electron multiplier was 1 x 105 kV; full-scan mode was set; the scanning range was 30-450 aum, and the scanning speed was 563/s (Yang et al., 2008).

Statistical analyses

Data are reported as means and standard deviations. Analyses of variance, independent-sample Student *t*-tests, and correlation analyses were performed in SPSS 18.0. Significance was set at the 0.05 level, and P values lower than 0.01 were considered to be extremely significant.

RESULTS

FA content and composition

FA content and composition in the longissimus dorsi muscles of yaks were significantly different from those of cattle (Table 2). Yaks contained more C15:0, C16:1, C17:0, C20:0, and C24:0 than did cattle, but had significantly lower levels of saturated fatty acid (SFA) ($P < 0.05$). Yaks had significantly higher levels of C18:1, C18:2n6t, C18:3, C20:4, conjugated linoleic acid (CLA), monounsaturated fatty acid (MUFA), and polyunsaturated fatty acid (PUFA) than cattle, whereas C16:0 levels were lower than in cattle ($P < 0.01$). Eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) were not detected.

Table 2. Fatty acid composition in longissimus dorsi of yaks and cattle (means ± SD).

Fatty acid (%)	Yaks	Cattle
SFA	49.30 ± 4.13*	56.11 ± 5.09
C10:0	0.07 ± 0.03	0.05 ± 0.02
C12:0	0.06 ± 0.01	0.06 ± 0.02
C14:0	2.49 ± 0.39	2.32 ± 0.21
C15:0	0.42 ± 0.18*	0.16 ± 0.04
C16:0	21.09 ± 3.10**	30.82 ± 3.21
C17:0	1.12 ± 0.32*	0.55 ± 0.14
C18:0	22.72 ± 2.33	21.16 ± 2.25
C20:0	0.57 ± 0.22*	0.41 ± 0.03
C22:0	0.17 ± 0.04	0.20 ± 0.02
C24:0	0.58 ± 0.15*	0.38 ± 0.02
MUFA	39.91 ± 2.32**	32.03 ± 1.30
C16:1	4.69 ± 1.10*	3.24 ± 0.18
C17:1	0.87 ± 0.24	0.76 ± 0.12
C18:1	33.95 ± 1.48**	27.75 ± 1.18
PUFA	6.81 ± 0.72**	3.28 ± 0.80
C18:2n6c	1.58 ± 0.46	1.30 ± 0.61
C18:2n6t	0.90 ± 0.27**	0.32 ± 0.09
C18:3	0.98 ± 0.14**	0.57 ± 0.24
C20:4	1.56 ± 0.05**	0.38 ± 0.02
CLA C18:2	1.09 ± 0.28*	0.71 ± 0.03
EPA C20:5	0.41 ± 0.05**	ND
DHA C22:6	0.29 ± 0.05**	ND

SFA, saturated fatty acid; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; CLA, conjugated linoleic acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid. *Significantly different ($P < 0.05$); **extremely significantly different ($P < 0.01$).ND = not detected.

PPARα signaling pathway gene expression levels

The expression levels of *FABP4* (P < 0.05), *SCP2* (P < 0.05), and *APOA1* (P < 0.01) in yaks were significantly lower than those in cattle. However, *LPL* expression in yaks was significantly higher than in cattle (P < 0.0; Figure 1).

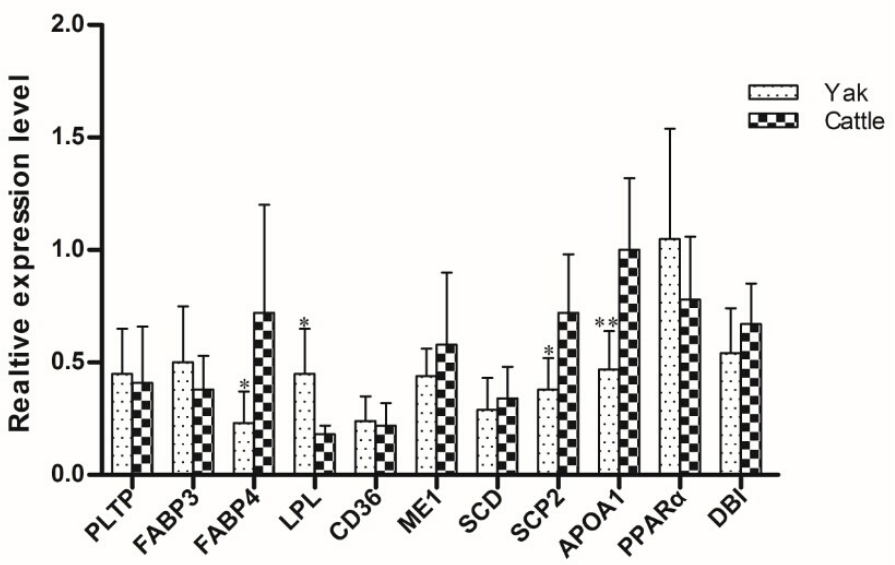

Figure 1. Expression of PPARα signaling pathway genes mRNA in longissimus dorsi of yak and cattle. For abbreviations, see Table 1.

Correlation between gene expression levels and FA content and composition

Gene expression levels were correlated with FA content. Pearson's correlation coefficients between yak FA content and the expression of each gene are shown in Table 3. Overall, MUFA levels were negatively correlated with the expression levels of *FABP3* (P < 0.05) and *LPL* (P < 0.01), and PUFA levels were positively correlated with those of *FABP4* and *SCD* (P < 0.01). *CD36* and *APOA1* were both positively correlated with C12:0 and C15:0 (P < 0.05), and *SCP2* was positively correlated with C10:0, C12:0, and C14:0 (P < 0.05). C22:0 was negatively correlated with *FABP4* and *SCD* (P < 0.05). *PLTP* mRNA expression levels were positively correlated with C18:2n6t (P < 0.05), whereas *DBI* mRNA expression levels were negatively correlated with C20:0 (P < 0.05). No correlations between *PPARα* expression levels and FAs were found.

Pearson's correlation coefficients between cattle FA content and the expression of each gene are shown in Table 4. The mRNA abundance of *PLTP* was positively correlated with SFA and C16:0 (P < 0.05), and *LPL* was positively correlated with MUFA and C20:0 but negatively correlated with C10:0 (P < 0.05). *APOA1* expression levels were negatively correlated with SFA, C16:0, and C18:0 (P < 0.05).

Table 3. Correlation coefficients between gene expression level and fatty acid composition in longissimus dorsi of yaks.

Fatty acid (%)	*PLTP*	*FABP3*	*FABP4*	*LPL*	*CD36*	*ME1*	*SCD*	*SCP2*	*APOA1*	*PPARα*	*DBI*
SFA	0.400	-0.387	-0.119	-0.212	-0.398	0.072	0.044	0.150	-0.253	-0.448	0.063
C10:0	0.482	0.362	0.320	0.264	0.556	0.489	0.463	0.820*	0.497	0.391	0.740
C12:0	0.073	0.557	0.280	0.363	0.897**	0.328	0.273	0.842*	0.858*	0.383	0.368
C14:0	0.533	0.564	0.183	0.709	0.463	0.268	0.368	0.794*	0.495	0.614	0.721
C15:0	-0.062	0.635	0.146	0.651	0.806*	0.255	0.432	0.599	0.768*	0.346	0.214
C16:0	0.581	-0.190	-0.544	-0.010	-0.542	0.441	-0.422	-0.296	-0.501	-0.205	-0.035
C17:0	-0.239	0.358	0.528	0.277	0.838*	0.159	0.065	0.630	0.716	0.238	0.342
C18:0	-0.259	-0.572	0.520	-0.556	-0.143	-0.620	0.542	0.362	0.025	-0.637	0.002
C20:0	-0.122	-0.094	-0.729	0.063	-0.305	-0.173	-0.793*	-0.315	-0.060	-0.559	-0.882*
C22:0	0.092	0.026	-0.779*	0.228	-0.177	0.398	-0.813*	-0.420	-0.126	-0.328	-0.648
C24:0	0.705	0.261	-0.342	0.177	-0.039	0.801*	-0.345	-0.033	-0.174	0.444	0.404
MUFA	-0.268	-0.797*	0.618	-0.985**	-0.486	-0.709	0.351	-0.070	-0.436	-0.438	0.109
C16:1	-0.316	-0.772	0.401	-0.841*	-0.578	-0.491	0.025	-0.540	-0.667	-0.235	-0.022
C17:1	-0.516	-0.057	0.438	-0.251	0.568	-0.407	0.215	0.608	0.679	-0.340	-0.213
C18:1	-0.096	-0.672	0.588	-0.884*	-0.399	-0.666	0.514	0.215	-0.269	-0.449	0.224
PUFA	-0.498	-0.439	0.988**	-0.539	0.092	-0.546	0.907**	0.154	-0.036	-0.072	0.403
CLA 18:2	-0.186	-0.577	0.673	-0.572	-0.169	-0.544	0.733	0.319	-0.091	-0.458	0.256
C18:2n6c	0.076	-0.437	0.665	-0.571	-0.316	-0.094	0.530	-0.171	-0.530	0.222	0.664
C18:2n6t	0.845*	-0.182	0.527	-0.298	0.411	-0.666	0.293	0.221	0.459	-0.351	0.368
C18:3	-0.122	0.463	0.447	0.401	0.688	-0.052	0.591	0.332	0.558	0.450	0.260
C20:4	-0.468	0.349	0.104	0.487	0.565	-0.028	0.286	0.130	0.512	0.054	-0.207
EPA 20:5	-0.044	-0.061	0.332	0.036	-0.050	0.240	0.497	-0.352	-0.339	0.312	0.420
DHA 22:6	-0.662	-0.014	0.086	0.124	0.165	-0.542	0.164	-0.065	0.260	-0.313	-0.514

SFA, saturated fatty acid; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; CLA, conjugated linoleic acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid. *Significantly different ($P < 0.05$); **extremely significantly different ($P < 0.01$).

Table 4. Correlation coefficients between gene expression level and fatty acid composition in longissimus dorsi of cattle.

Fatty acid (%)	*PLTP*	*FABP3*	*FABP4*	*LPL*	*CD36*	*ME1*	*SCD*	*SCP2*	*APOA1*	*PPARα*	*DBI*
SFA	0.918*	0.056	0.446	0.414	0.432	0.067	-0.034	0.356	-0.881*	-0.410	0.273
C10:0	-0.673	-0.501	-0.101	-0.858*	-0.166	-0.107	-0.132	-0.401	0.740	0.148	-0.784
C12:0	-0.837	-0.386	-0.249	-0.787	-0.291	-0.104	-0.083	-0.425	0.870	0.269	-0.678
C14:0	0.201	0.564	-0.177	0.754	-0.089	0.083	0.182	0.255	-0.311	0.096	0.759
C15:0	-0.360	0.443	-0.390	0.409	-0.309	0.034	0.171	0.011	0.245	0.303	0.490
C16:0	0.920*	0.224	0.372	0.623	0.385	0.089	0.022	0.407	-0.917*	-0.362	0.491
C17:0	0.483	-0.391	0.424	-0.301	0.349	-0.020	-0.160	0.052	-0.374	-0.340	-0.397
C18:0	0.739	-0.224	0.475	-0.003	0.421	0.018	-0.118	0.202	-0.653	-0.405	-0.129
C20:0	0.432	0.561	-0.058	0.835*	0.023	0.098	0.167	0.335	-0.526	-0.011	0.805
C22:0	-0.265	-0.567	0.147	-0.780	0.060	-0.088	-0.179	-0.278	0.371	-0.069	-0.776
C24:0	0.689	-0.266	0.468	-0.074	0.408	0.009	-0.129	0.169	-0.596	-0.394	-0.194
MUFA	0.798	0.425	0.208	0.817	0.258	0.106	0.098	0.422	-0.841	-0.236	0.717
C16:1	-0.775	0.190	-0.478	-0.053	-0.428	-0.025	0.109	-0.226	0.694	0.411	0.077
C17:1	-0.036	-0.547	0.249	-0.673	0.161	-0.071	-0.185	-0.190	0.152	-0.164	-0.702
C18:1	0.857	0.362	0.272	0.765	0.309	0.102	0.073	0.425	-0.884*	-0.287	0.651
PUFA	0.226	-0.488	0.347	-0.511	0.262	-0.048	-0.179	-0.076	-0.108	-0.259	-0.574
C18:2 CLA	-0.155	-0.561	0.198	-0.733	0.110	-0.080	-0.183	-0.238	0.267	-0.116	-0.745
C18:2n6c	0.178	-0.502	0.330	-0.544	0.244	-0.052	-0.181	-0.098	-0.059	-0.242	-0.601
C18:2n6t	-0.251	0.481	-0.355	0.493	-0.271	0.045	0.178	0.064	0.133	0.267	0.560
C18:3	0.352	-0.446	0.387	-0.416	0.306	-0.035	-0.172	-0.015	-0.237	-0.300	-0.495
C20:4	0.689	-0.266	0.468	-0.074	0.408	0.009	-0.129	0.169	-0.596	-0.394	-0.194

SFA, saturated fatty acid; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; CLA, conjugated linoleic acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid. *Significantly different ($P < 0.05$); **extremely significantly different ($P < 0.01$).

DISCUSSION

FA composition and content in yaks and cattle differed significantly, with higher levels of MUFA and PUFA and lower levels of SFA in yaks. These results agree with those of previous studies, which reported that yaks had more unsaturated fatty acids in their longissimus dorsi muscle than did cattle (Li et al., 2008; Wan et al., 2012). MUFA has a positive effect on the absorption of other fatty acids, so that it can increase the mobility and metabolism of fat globules (Schmid et al., 1998). Yak meat contained a certain amount of EPA and DHA, which were not detected in beef. The main physiological functions of EPA are lowering blood fat and cholesterol, anticarcinogenic activity, and improving brain function; DHA promoting intelligence and healthy growth and development (Dai et al., 1998). CLA is present in ruminant meat and milk, and enhances immunity, is anticarcinogenic, lowers cholesterol, and improves meat quality (Wei and Wang, 2002); the CLA content in yaks was higher than in cattle. PUFA plays a variety of physiological roles, and is extremely important in biological systems (Yu, 1998); yak meat is more nutritious and healthier than beef because of its high PUFA levels.

The mRNA expression levels of the *PLTP* gene were positively correlated with C18:2n6t levels in yaks, and with SFA levels and C16:0 levels in cattle. *PLTP* mediates the exchange of phospholipids between lipoproteins, and plays an important role in regulating the metabolism of high-density lipoproteins and very-low-density lipoproteins (Albers and Cheung, 2004). A recent study reported that *PLTP* affects the n-6/n-3 ratio (Dunner et al., 2013). *APOA1* (another lipid transport gene) mRNA expression was positively correlated with C12:0 and C15:0 in yaks, but was negatively correlated with SFA, C16:0, and C18:1 in cattle. *APOA1* is an important component of high-density lipoprotein, which is a key factor in reverse cholesterol transport, and dissociative *APOA1* is a cholesterol and phospholipid receptor (Wang et al., 2008). Our findings suggest that *PLTP* and *APOA1* may play pivotal roles in lipid transport in the longissimus dorsi muscle of yaks and cattle. We also found that *APOA1* expression levels in yaks were significantly lower than those in cattle, suggesting that *APOA1* may be a genetic marker that is predictive of FA deposition; further research is required to identify *APOA1* gene markers, such as SNPs, that are associated with FA content.

The ME1 protein is a part of the tricarboxylic acid shuttle; the nicotinamide adenine dinucleotide phosphate and Coenzyme A (CoA) produced by the process of releasing CoA by ME1 from mitochondria into the cytoplasm are used in the biosynthesis of FAs, and in many other metabolic processes (Vidal et al., 2006). *ME1* gene expression level is significantly positively related to FA synthesis in rat adipose tissue (Stelmanska et al., 2004). In the present study, *ME1* expression was positively associated with C24:0 in yaks. SCD is a rate-limiting enzyme that is responsible for the conversion of SFA into MUFA by inserting a double bond between carbons 9 and 10 of the fatty acyl chain to affect the FA composition of membrane phospholipids, triglycerides, and cholesterol esters (Ntambi and Miyazaki, 2004). Previous studies have found significant differences between different genotypes of the *SCD* gene and FA content and composition in cattle milk and meat (Orrù et al., 2011; Li et al., 2012). In the present study, *SCD* expression was found to be significantly negatively associated with C20:0 and C22:0 in the yak; however, it was even more significantly positively associated with PUFA in the yak. Neither *ME1* nor *SCD* were correlated with FA composition in cattle, so *ME1* and *SCD* may have much more influence on FA content and composition in yaks than in cattle.

FABPs are widely distributed in a variety of animal tissues, and have high affinity with long-chain FAs and play an important role in the oxidation, esterification, and metabolism of FAs (Ockner et al., 1972; Zimmerman and Veerkamp, 1998). Fifteen types of FABP have been found,

including FABP3 and FABP4, which are heart-type FA binding proteins (H-FABPs) and fat-type FA binding proteins (A-FABPs), respectively (Chmurzyńska, 2006). There is a significant association between *FABP4* polymorphisms and milk FA composition in bovine milk (Nafikov et al., 2013). In yaks, we found that *FABP3* mRNA expression levels were significantly negatively correlated with MUFA levels, while *FABP4* mRNA expression levels were significantly negatively correlated with C22:0 and significantly positively associated with PUFA. We did not find a correlation between *FABP3* or *FABP4* and FA composition in cattle. Overall, *FABP3* and *FABP4*, particularly *FABP4*, may have a very important effect on FA composition in yaks, because the mRNA expression level of *FABP4* in yaks was lower than in cattle.

LPL is a triglyceride-acyl hydrolase protein of the hydrolase family (Emmerich et al., 1992) that is a rate-limiting enzyme that decomposes chylomicrons in circulating lipoproteins and triglycerides of very-low-density lipoproteins, and releases FAs and glycerol. *LPL* was significantly negatively correlated with MUFA, C16:1, and C18:1 in yaks, while it was significantly negatively correlated with C10:0 and significantly positively correlated with C20:0 in cattle. In accordance with our data, Zhu et al. (2013) found that LPL activity is correlated with FA composition in meat. Correlation analyses revealed positive correlations between *CD36* gene expression levels and C12:0, C15:0, and C17:0 in yaks, while the *DBI* gene was negatively correlated with C20:0. However, there were no significant correlations between *CD36* or *DBI* expression levels and FA content in cattle. These results provide a theoretical basis for the further study of the molecular mechanisms that underlie FA metabolism in meat (Guidotti et al., 1983; Rosendal et al., 1993; Silverstein and Febbraio, 2009).

SCP2, known as the nonspecific lipid transfer protein, enhances transport between plasma membranes and plays an important role in lipid metabolism (Starodub et al., 2000; Stolowich et al., 2002). McLean et al. (1995) suggested that SCP2 expression levels are altered in a number of diseases in which lipid metabolism is abnormal. In this study, a significant association was observed between *SCP2* gene expression level and C10:0, C12:0, and C14:0 in yaks; there was no significant association between *SCP2* expression level and FA content in cattle. After comparing *SCP2* mRNA expression levels in yaks and cattle, we found that the *SCP2* expression level in yaks was significantly lower than in cattle. These results suggest that *SCP2* is important for lipid metabolism in the yak.

In conclusion, we found differences in FA composition of the longissimus dorsi muscle of yaks and cattle. PUFA is beneficial to human health, and we found higher levels of PUFA in yak meat than in beef. Of the 11 PPARα genes that we examined, the mRNA expression levels of the lipid transport gene *APOA1* may have the most important influence on the FA composition of yak and cattle meat. The mRNA expression levels of *FABP4*, *LPL,* and *SCP2* were also important predictors of FA composition. Our results indicate that these genes may participate in the regulation and control of intramuscular FA metabolism in yaks, and they can be used as candidate genes for FA selection in yaks.

Conflicts of interest

The authors declare no conflict of interest.

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