Food Sci. Biotechnol. Vol. 14, No. 5, pp. 639 ~ 644 (2005)

Food Science and Biotechnology

Relationships between Myosin Light Chain Isoforms, Muscle Fiber Characteristics, and Meat Quality Traits in Porcine *Longissimus* Muscle

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Abstract The aim of this study was to investigate the effect of the myosin light chain (MLC) isoforms on the muscle fiber characteristics and meat quality traits in porcine *longissimus* muscle. Pale, soft, exudative (PSE) samples had a lower content of essential light chain (ELC) 1S isoforms and a higher proportion of the fiber type IIB than the reddish-pink, firm, non-exudative (RFN) samples. These compositions suggest that the PSE pork has a higher glycolytic and a lower oxidative capacity than the RFN pork. Therefore, these characteristics of PSE pork might affect the metabolic rate and meat quality traits, including protein solubility. In addition, the indicator traits of the postmortem metabolic rate were related to the ELC 1F/3F ratio ($pH_{45\ min}$: $r = -0.43$, $P < 0.001$; *R*-value: $r = 0.53$, $P < 0.001$). These results suggest that the MLC isoform composition can affect the postmortem metabolic rate and meat quality traits.

Keywords: Myosin light chain; Muscle fiber; Metabolic rate; Meat quality; Pig

Introduction

The variety of myosin isoforms reflects the functional diversity of skeletal muscles. Myosins are hexamers composed of two myosin heavy chains (MHC) and four myosin light chains (MLC). Each MHC is associated with one essential MLC (ELC) and one regulatory MLC (RLC). The adult skeletal muscles contain four predominant MHC isoforms (the "slow" 1 or β isoform and the three "fast" 2A, 2X, 2B isoforms), and three predominant MLC isoforms (the "slow" ELC 1S isoform and two "fast" ELC 1F and ELC 3F isoforms). These isoforms are produced by the three multigene families (1). The myosin from slow-twitch fibers consists of two MHC isoforms, two RLC 2 (RLC 2, also called MLC 2) and two ELC 1 (ELC 1, also called MLC 1) isoforms. In contrast, the myosin from fast-twitch fibers consist of two MHC isoforms, two RLC 2 isoforms, and either two of the ELC 1 or two of the ELC 3 isoforms or one of each ELC isoform (2).

The composition of the MHC isoform is strongly correlated with the composition of the muscle fiber type in the adult skeletal muscle (humans: 3; rats: 4; horses: 5). However, there are discrepancies between the composition of the MHC isoforms and that of the fiber types. These differences can be explained by the existence of pure and hybrid fiber types as well as the existence of slow and fast isoforms of other proteins (6). The pure fiber types are the expression of a single MHC isoform, whereas the hybrid fiber types are the expression of two or more MHC isoforms. Moreover, these fibers would be classified as pure fiber type based only on the MHC composition, but such classification is incorrect because it does not provide information on the molecular heterogeneity of the fibers with respect to the composition of the MLC isoform (2).

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Received May 30, 2005; accepted August 10, 2005

The meat quality can be assessed by measuring the biochemical and biophysical properties, such as the water holding capacity (WHC), meat color, muscle pH, texture profile, and protein denaturation (7). The pork quality can be classified into PSE (pale, soft, and exudative), RSE (reddish-pink, soft, and exudative), RFN (reddish-pink, firm, and non-exudative), and DFD (dark, firm, and dry) based on the level of lightness and drip loss (7-9). For example, PSE condition pork has a very light surface, a higher drip loss, and exhibits a higher extent of protein denaturation. The compositions of the fiber type (10, 11) and the MHC isoforms (12-14) make a profound influence on the postmortem changes and subsequent meat quality. However, the relationship between the MLC isoforms on the postmortem metabolic rate and meat quality is unknown. Therefore, this study investigated the effect of the MLC isoforms on the muscle fiber characteristics, postmortem metabolic rate and pork quality traits.

Materials and Methods

Animals A total of 79 crossbred (Yorkshire × Landrace × Duroc) pigs (50 gilts and 29 castrated male pigs) were evaluated. Pigs were slaughtered by electrical stunning during the winter period. The abattoir used a traditional scalding-singeing process. Within 45 min postmortem, muscle samples were taken from the *longissimus* muscle at the 8th *thoracic vertebrate*, and analyzed for the content of the MLC isoforms as well as the muscle fiber characteristics. The samples were attached to a piece of a chop, and then frozen in isopentane, cooled in liquid nitrogen and stored at -80°C until needed. The muscle samples were sectioned with a cryostat (CM 1850, Leica, Germany) at -25°C. The first and last 10 cross-sections were collected to analyze the MLC isoforms. The medial cross-sections were mounted on glass slides, and used for the histochemical analysis. Following 24 hr of chilling, the postmortem metabolic rate, meat quality traits, and protein solubility were evaluated.

SDS-PAGE analysis of myosin light chain isoforms The myofibrils preparation was performed using the method reported by Talmadge and Roy (15). Briefly, 200 μL of an ice-cold homogenization buffer (250 mM sucrose, 100 mM KCl, 5 mM EDTA, 20 mM Tris, pH 6.8) was added to 20 cross-sections. The cross-sections were homogenized using a micropestle and centrifuged at 10,000 × g for 10 min. The supernatant was then discarded and the myofibril pellet was resuspended in 200 μL of an ice-cold washing buffer (175 mM KCl, 5 mM EDTA, 0.5% Triton-X, 20 mM Tris, pH 6.8). Centrifugation was repeated, and the sediment was resuspended in the same volume of an ice-cold, premixed resuspension buffer (150 mM KCl, 20 mM Tris, pH 7.0). The myofibrils at a final protein concentration of 2.00 mg/mL were boiled in the sample buffer (1.0% β-mercaptoethanol, 4.0% SDS, 16.0% 1 M Tris (pH 6.8), 20% glycerol, 0.2% bromophenol blue) for 3 min and stored at -80°C until the gel run. The total protein content was examined using the method reported by Bradford (16).

MLC was analyzed using SDS-PAGE according to the method described by Joo *et al.* (8). This method was modified by increasing the separation gel percentage. MLC was separated into MLC 1S, 1F, 3F, and 2F (Fig. 1). The stacking gel was composed of 10% glycerol, 8% acrylamide-*N,N'*-methylene-bisacrylamide (bis) (200:1), 125 mM Tris (pH 6.8), 4 mM EDTA, 0.1% SDS, 0.01% *N,N,N',N'*-tetramethylenediamine (TEMED), and 0.1% ammonium persulfate. The separating gel was composed of 10% glycerol, 16% acrylamide-N,N'-methylene-bisacrylamide (bis) (200:1), 375 mM Tris (pH 8.8), 100 mM glycine, 0.1% SDS, 0.01% TEMED, and 0.1% ammonium persulfate. The upper running buffer consisted of 100 mM Tris, 150 mM glycine, and 0.15% SDS, and the lower running buffer consisted of 50 mM Tris, 75 mM glycine, and 0.075% SDS. The running condition for the gel was 30 mA at 4°C for 3 hr. The MLC bands were visualized by Coomassie Brilliant Blue staining. Each MLC band was examined with the image analysis system for quantitative analysis (Kodak 1D Image Analysis Software, Eastman Kodak Co., NY, USA).

Muscle fiber characteristics The muscle sections were stained to determine their myosin ATPase reactivity after preincubation at pH 4.7 and pH 10.4 according to the method reported by Brooke and Kaiser (17). All the histochemical samples were examined with the image analysis system. The operational system consisted of a microscope equipped with the CCD color camera (IK-642K, Toshiba, Japan), and a standard workstation computer, which controls the image analysis system (Image-Pro Plus, Media Cybernetics, L. P., USA). About 600 fibers per sample were evaluated. Muscle fibers were identified as type I, IIA, or IIB (Fig. 2). The number percentage of muscle fiber type was obtained from the ratio of the number of each fiber type to the total number of fiber counted, and the area percentage of fiber type was the ratio of the total cross-sectional area of each fiber type to the total measured fiber area.

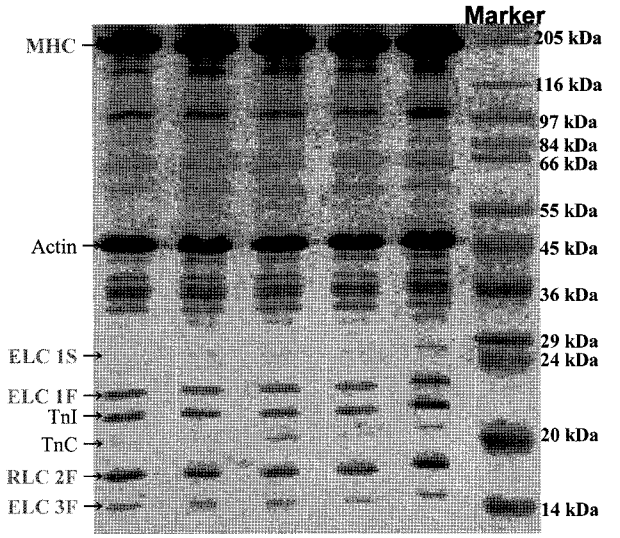

Fig. 1. Electrophoretic separation of the myosin light chain in the porcine *longissimus* muscle. Abbreviations: ELC, essential light chain; RLC, regulatory light chain; MHC, myosin heavy chain; TnI, troponin I; TnC, troponin C.

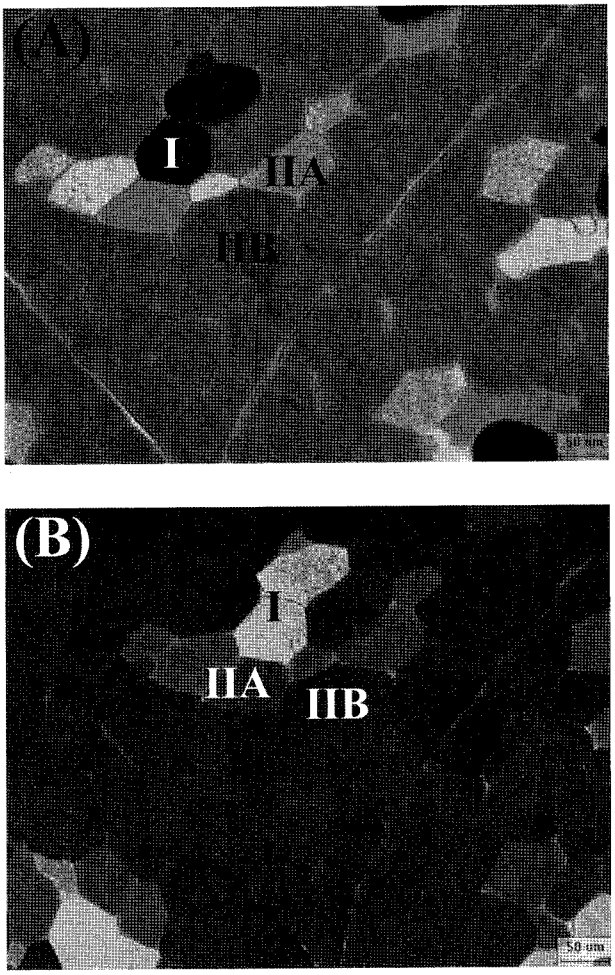

Fig. 2. Myosin ATPase histochemistry after preincubation at pH 4.7 (A) and pH 10.4 (B) in the porcine *longissimus* muscle. Representative staining of the muscle fiber cross-sections. Magnification of 100 × was used (Bar = 50 μm). Abbreviation: I, fiber type I (slow-twitch, oxidative); IIA, fiber type IIA (fast twitch, oxido-glycolytic); IIB, fiber type IIB (fast-twitch, glycolytic).

Postmortem metabolic rate The muscle pH of the 45 min ($pH_{45\ min}$) and 24 hr ($pH_{24\ hr}$) postmortem samples was measured with a spear type pH meter (290A, Orion Research Inc., USA). The *R*-value was measured according to the procedure reported by Calkins *et al.* (18). Briefly, the 45 min postmortem samples, which had been placed in 6% perchloric acid, were homogenized at 5,000 rpm for 90 s and centrifuged at 3,000 × g for 10 min at 4 °C. The absorbances were measured with a calibrated spectrophotometer (Model Du-64, Beckman Co., USA). All the adenine nucleotides showed an absorption maximum at 259-260 nm, whereas the maximum absorption of hypoxanthine was found at 250 nm. The *R*-value (R_{250}) was defined as the ratio of A_{250}/A_{260}.

Meat quality measurements The drip loss was determined by suspending the muscle samples standardized for the surface area in an inflated plastic bag at 4°C for 48 hr (19). The filter paper fluid uptake (FFU) was measured using the method reported by Kauffman *et al.* (20). The meat color was determined at the 24 hr postmortem with a Minolta chromameter (CR-300, Minolta Camera Co., Japan) after exposing the surface to air for 30 min at 4°C. The average of three measurements was recorded and the results are expressed as the C.I.E. (Commission International de l'Eclairage) lightness (L^*).

The drip loss and lightness were used to classify the samples into one of the following four quality classes (8):

Pale, soft, and exudative (PSE): drip loss > 6.0%, $L^* > 50$

Reddish-pink, soft, and exudative (RSE): drip loss > 6.0%, $L^* \leq 50$

Reddish-pink, firm, and non-exudative (RFN): drip loss ≤ 6.0%, $L^* \leq 50$

Dark, firm, and dry (DFD): drip loss < 2.0%, $L^* < 43$

Protein solubility The protein solubility was used to indicate the level of protein denaturation (8). The sarcoplasmic protein solubility was determined by dissolving 1 g of the muscle powder in 10 mL of an ice-cold, 25 mM potassium phosphate buffer (pH 7.2). The samples and buffer were minced, homogenized on ice with a polytron (SDT-1810, Tekmar Co., Germany) at the lowest setting, and left to stand on a shaker at 4°C overnight. The contents were centrifuged at 1,500 × g for 20 min and the protein concentration in the supernatants was determined using the Biuret method (21). The total protein solubility was determined by homogenizing 1 g of muscle powder in 20 mL of an ice-cold, 1.1 M potassium iodide solution in a 100 mM phosphate buffer (pH 7.2). The procedures used for homogenization, shaking, centrifugation and protein determination are described above. The myofibrillar protein solubility was obtained by determining the difference between the total and sarcoplasmic protein solubility.

Statistical analysis A General Liner Model (22) was to evaluate differences between the different meat quality classes. The results were presented as least square means (LSM) for the four groups together with the standard errors of these LSM. The Pearson correlation coefficients were evaluated using the partial correlation coefficients (22) to determine the relationship between the content of the MLC isoforms and the muscle fiber characteristics, as well as between the content of the MLC isoforms and the meat quality measurements.

Results and Discussion

Myosin light chain isoforms and muscle fiber characteristics The contents of the MLC isoforms and the muscle fiber characteristics in different quality classes are shown in Table 1. The PSE samples had a lower content of the ELC 1S isoform (3.73 vs. 5.10%, $P < 0.05$) than the RFN samples did. However, there were no significant differences in the content of the other MLC isoforms. The number percentage of the fiber type I in the PSE samples was significantly different from that in both the RSE and RFN samples ($P < 0.05$). Moreover, the number ($P < 0.05$) and area ($P < 0.001$) percentage of type IIB in the PSE samples were higher than those of both the RSE and RFN samples. However, the RFN samples had a similar number and area percentage of fiber types to the DFD samples. The fiber type IIB had a higher glycolytic capacity and a lower oxidative capacity, intermuscular fat content and myoglobin level than the fiber type I (23). The composition of the fiber types IIA and IIB, particularly of

Table 1. Comparison of the content of myosin light chain isoforms and muscle fiber characteristics in the different pork quality classes

	Pork quality class				Levels of Significance
	PSE	RSE	RFN	DFD	
Myosin light chain isoform (%)					
ELC 1S	3.73^{a} (0.35)[1]	4.22^{ab} (0.22)	5.10^{c} (0.37)	4.73^{bc} (0.32)	*
ELC 1F	34.73 (2.11)	33.45 (1.38)	32.69 (0.64)	32.25 (1.49)	NS
ELC 3F	9.59 (1.66)	10.39 (1.08)	10.69 (0.50)	10.80 (1.17)	NS
RLC 2F	51.95 (1.66)	51.94 (1.53)	51.51 (0.71)	52.22 (1.53)	NS
1F/3F ratio	3.55 (0.53)	3.99 (0.48)	3.85 (0.22)	4.20 (0.72)	NS
Muscle fiber number percentage (%)					
Type I	3.75^{a} (0.35)	5.35^{b} (0.20)	6.17^{c} (0.36)	6.61^{c} (0.47)	*
Type IIA	6.58 (0.83)	6.24 (0.59)	7.95 (0.36)	8.50 (1.44)	NS
Type IIB	89.67^{b} (1.23)	88.41^{b} (0.87)	85.88^{a} (0.53)	84.89^{a} (2.13)	*
Muscle fiber area percentage (%)					
Type I	6.62 (1.29)	8.16 (0.92)	9.15 (0.53)	10.31 (2.24)	NS
Type IIA	11.02 (1.41)	11.45 (1.00)	13.67 (0.60)	13.65 (2.44)	NS
Type IIB	82.35^{b} (1.73)	80.39^{ab} (0.87)	77.19^{a} (0.74)	76.04^{a} (1.99)	***

[1]Standard error of least-square means.
Levels of significance: NS = not significance, * $P < 0.05$, *** $P < 0.001$.
[a-c]Least-square means with different superscripts in the same row significantly differ ($P < 0.05$).
Abbreviations: ELC, essential light chain; RLC, regulatory light chain.

the latter, of the porcine muscles is related to the occurrence of the PSE condition pork (24, 25). In this study, compared to the RFN pork, the PSE pork had a lower percentage of the ELC 1S isoforms and the fiber type I, and a higher percentage of the fiber type IIB. These compositions suggest that the PSE pork has a higher glycolytic capacity and a lower oxidative capacity than the RFN pork.

Table 2 shows the correlations between the content of the MLC isoforms and the muscle fiber characteristics in the porcine *longissimus* muscle. The content of the ELC 1S isoform showed a positive correlation with the number and area percentage of the fiber type I (r = .36 and .33, respectively). Schiaffino and Reggiani (26) reported that the ELC 1F isoform is more abundant in the fiber type IIA than IIB. On the other hand, the ELC 3F isoform is more abundant in the fiber type IIB. These results examine the relationship between the MLC isoform composition and the pure fiber type in the single fibers. Whereas, the current study was to investigate the relationship between the MLC isoform composition and the muscle fiber characteristics including all the fiber types in a cross section. Therefore, the correlation with the MLC isoform composition and the muscle fiber composition in a cross section was limited. In this study, the content of the ELC 1F isoform showed a positive correlation with the number and area percentage of the fiber type IIA (r = .40 and .36, respectively), whereas there was a negative correlation with the number and area percentage of the fiber type IIB (r = -.36 and -.32, respectively). A negative correlation was observed between the ELC 1F/3F ratio and the number percentage of the fiber type IIB (r = -.35, P < 0.001), but a positive correlation between the 1F/3F ratio and the area percentage of the fiber type IIA (r = .25, P < 0.001). Similar results were reported by Mabuchi *et al.* (27) who found that the 1F/3F ratio in the fiber type IIA is higher than in the fiber type IIB, and that the 3F/1F ratio in the fiber type IIB is higher than in the fiber type IIA (28). These results suggest that the MLC isoform composition affects the muscle fiber characteristics.

Table 2. Correlations between the content of myosin light chain isoforms and muscle fiber characteristics in the porcine *longissimus* muscle

	Myosin light chain isoform (%)				
	ELC 1S	ELC 1F	ELC 3F	RLC 2F	1F/3F ratio
Muscle fiber number percentage (%)					
Type I	.36**	-.11	-.11	-.16	.05
Type IIA	.17	.40**	-.05	-.21	.11
Type IIB	-.04	-.36**	.12	.23	-.35**
Muscle fiber area percentage (%)					
Type I	.33*	.07	-.08	-.04	-.04
Type IIA	.08	.38**	-.04	.11	.25*
Type IIB	-.05	-.32*	.08	-.04	-.04

Levels of significance: * P < 0.05, ** P < 0.01.
Abbreviations: ELC, essential light chain; RLC, regulatory light chain.

Myosin light chain isoforms and meat quality The early postmortem pH ($pH_{45\ min}$) (P < 0.05), and ultimate pH ($pH_{24\ hr}$) (P < 0.001) of the PSE samples were significantly different from those of both the RFN and DFD samples (Table 3). The drip loss (P < 0.001), FFU (P < 0.001), and

Table 3. Comparison of the meat quality traits in the different pork quality classes

	Pork quality class				Levels of Significance
	PSE	RSE	RFN	DFD	
Postmortem metabolic rate					
Muscle $pH_{45\ min}$	5.94[a] (0.08)[1]	6.03[ab] (0.06)	6.09[b] (0.04)	6.35[c] (0.08)	*
Muscle $pH_{24\ hr}$	5.45[a] (0.03)	5.56[b] (0.06)	5.61[c] (0.01)	6.00[d] (0.05)	***
R-value	1.05[b] (0.04)	1.03[ab] (0.03)	0.98[a] (0.02)	1.16[b] (0.06)	*
Meat quality measurements					
Drip loss (%)	7.46[c] (0.40)	6.65[c] (0.28)	3.48[b] (0.17)	0.67[a] (0.37)	***
FFU (mg)	83.92[c] (4.86)	64.87[c] (4.85)	44.72[b] (2.94)	20.58[a] (3.78)	***
Lightness (L^*)	52.87[c] (0.71)	46.52[b] (0.50)	46.01[b] (0.30)	38.07[a] (0.62)	***
Protein solubility					
SPS (mg/g)	63.34[a] (2.41)	70.26[b] (2.60)	73.42[b] (1.11)	99.14[c] (2.51)	**
TPS (mg/g)	172.92[a] (5.66)	185.09[b] (6.12)	194.16[b] (2.61)	223.24[c] (6.49)	**
MPS (mg/g)	109.58[a] (3.41)	114.83[ab] (3.76)	120.74[b] (2.03)	124.10[c] (5.24)	*

[1]Standard error of least-square means.
Levels of significance: * P < 0.05, ** P < 0.01, *** P < 0.001.
[a-d]Least-square means with different superscripts in the same row significantly differ (P < 0.05).
Abbreviations: FFU, filter-paper fluid uptake; SPS, sarcoplasmic protein solubility; TPS, total protein solubility; MPS, myofibrillar protein solubility.

lightness ($P < 0.001$) of the PSE samples were significantly different from those of both the RFN and DFD samples. However, the drip loss and FFU in the RSE and PSE samples were similar, and the lightness was similar in the RSE and RFN samples. The muscle $pH_{45\ min}$, $pH_{24\ hr}$, and *R*-value are used as indicators of postmortem metabolic rate (29). Generally, the PSE condition pork usually develops as a result of the rapid muscle metabolism during the early postmortem period (< 1hr). Since the RFN muscle at 1 hr postmortem has a high content in adenine nucleotide, the A_{250}/A_{260} ratio (*R*-value) is expected to be low ($R < 1.05$). On the other hand, the PSE and DFD muscle has a high IMP, inosine and hypoxanthine content; therefore the *R*-value is expected to be high ($R > 1.05$) (29). In this study, the PSE samples also had a lower $pH_{45\ min}$ (5.94 vs. 6.09, $P < 0.05$) and $pH_{24\ hr}$ (5.45 vs. 5.61, $P < 0.001$), and a higher *R*-value (1.05 vs. 0.98, $P < 0.05$) than the RFN samples. According to Gil *et al.* (30), the porcine *longissimus* muscles with a higher content of the MHC 1 isoform had a higher muscle $pH_{45\ min}$ and $pH_{24\ hr}$, and a higher level of oxidative enzyme activity. In contrast, they had a lower level of glycolytic enzyme activity, a lower drip loss and a lighter surface than the muscles with a lower content of the MHC 1 isoform. According to Kalsson *et al.* (31), muscles with a higher percentage of the fiber type IIB showed more accelerated pH decline than muscles with a higher percentage of type I did. In this study, the PSE pork with a high glycolytic capacity and low oxidative capacity had a higher drip loss, lighter surface, lower muscle pH, and higher *R*-value. These results suggest that the biochemical characteristics, such as oxidative or glycolytic capacity, of muscles may affect the meat quality traits.

The RFN samples were significantly different from the PSE and DFD samples in terms of the sarcoplasmic ($P < 0.01$), total ($P < 0.01$), and myofibrillar ($P < 0.05$) protein solubility. Myosin denaturation has been suggested to be the cause of the high rate of drip loss in the PSE pork (8). The PSE samples exhibited a more pronounced level of protein denaturation, whereas the RSE samples had a similar sarcoplasmic, total, and myofibrillar protein solubility as those of the RFN samples. Joo *et al.* (8) similarly reported that the RSE samples had a similar sarcoplasmic, total, and myofibrillar protein solubility as those of the RFN samples, but that they had significantly higher solubilities than those of the PSE samples. However, the high glycolytic capacity of the RSE samples also might affect the metabolic rate and meat quality traits.

Table 4 shows the correlations between the contents of the MLC isoforms and the postmortem metabolic rate, meat quality traits, and protein solubility. The content of the ELC 3F isoform showed a negative correlation with lightness ($r = -.30$, $P < 0.05$). The 1F/3F ratio showed a positive correlation with lightness ($r = .40$, $P < 0.01$) and a negative correlation with muscle $pH_{45\ min}$ ($r = -.30$, $P < 0.05$). The content of the ELC 1S ($r = -.36$, $P < 0.01$) and 3F ($r = -.41$, $P < 0.01$) isoforms showed a negative correlation with the *R*-value, whereas that of the ELC 1F ($r = .55$, $P < 0.001$) isoform and the 1F/3F ratio ($r = .53$, $P < 0.001$) showed a positive correlation with the *R*-value. Moreover, the 1F/3F ratio showed a negative correlation with the sarcoplasmic protein solubility ($r = -.26$, $P < 0.05$). The content of the RLC 2F isoform showed a positive correlation with the *R*-value ($r = .28$, $P < 0.05$), and a negative correlation with the total protein solubility ($r = -.29$, $P < 0.05$) and myofibrillar protein solubility ($r = -.38$, $P < 0.05$). The MHC and ELC isoforms are responsible for determining the maximum velocity of the shortening and energy release rate in the muscle fiber (26). The ELC 3F isoform has a higher maximum velocity than the ELC 1F isoform, and a higher ELC 3F/1F ratio is positively correlated with the maximum velocity in the fast type of single fibers (32). Therefore, the myosin isoforms can influence the biochemical characteristics of the skeletal muscle. These biochemical characteristics play a key role in determining the postmortem metabolic rate and ultimate the pork quality. According to Karlsson *et al.* (31), the percentage of the fiber type IIB in the porcine *longissimus* muscle showed a positive correlation with the early postmortem pH and ultimate pH, and a negative correlation with the drip loss and lightness. In large white pigs, the percentage of the fiber type I showed a positive correlation to $pH_{30\ min}$, and a negative correlation to lightness (33). The content of MHC 1 isoform in the porcine *longissimus* muscle showed a negative correlation to $pH_{24\ hr}$ and lightness, whereas the content of MHC 2B isoform showed a positive correlation to $pH_{24\ hr}$ (12). In this study, the indicator trait of the metabolic rate, such as the *R*-value, was related to the relative proportion of the ELC isoforms. Moreover, the correlation between the early postmortem $pH_{45\ min}$ and ELC 1F/3f ratio demonstrated that the muscle pH decreases with increasing 1F/3F ratio. These results suggest that the MLC isoform composition, particularly the content of the ELC isoforms, may affect the postmortem metabolic rate and the meat quality traits.

Table 4. Correlations between the content of myosin light chain isoforms and meat quality traits in the porcine *longissimus* muscle

	Myosin light chain isoform				
	ELC 1S	ELC 1F	ELC 3F	RLC 2F	1F/3F ratio
Postmortem metabolic rate					
Muscle $pH_{45\ min}$	-.03	-.16	.22	-.20	-.43***
Muscle $pH_{24\ hr}$	-.08	.04	.01	.06	.03
R-value	-.36**	.55***	-.41***	.28*	.53***
Meat quality measurements					
Drip loss (%)	.09	-.04	-.02	-.05	-.02
FFU (mg)	.07	.01	-.07	.04	-.01
Lightness (L^*)	.06	.25	-.30*	.05	.40**
Protein solubility					
SPS (mg/g)	.01	-.15	.19	.01	-.26*
TPS (mg/g)	.14	-.22	.23	-.29*	-.22
MPS (mg/g)	.18	-.01	.21	-.38**	-.17

Levels of significance: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.
Abbreviations: FFU, filter-paper fluid uptake; SPS, sarcoplasmic protein solubility; TPS, total protein solubility; MPS, myofibrillar protein solubility; ELC, essential light chain; RLC, regulatory light chain.

Acknowledgments

This work was supported by a Korea University grant.

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