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# Evaluation of Muscle Fiber Characteristics Based on Muscle Fiber Volume in Porcine *Longissimus* Muscle in Relation to Pork Quality

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**Abstract:** In livestock science and meat science, muscle fiber characteristics have been evaluated based on a cross-sectional area (CSA) of muscle fiber. However, muscle fiber is not planar but cylindrical. Thus, muscle fiber volume and volume-based characteristics were evaluated in this study. In addition, their relationships to pork loin quality was assessed and compared with that of CSA-based muscle fiber characteristics. Muscle fiber type IIB was underestimated by CSA-based evaluations with 1.6 times in fiber size and 2.6 times in relative composition. The pennation angle, which ranged from 48.00° to 83.33°, determined the real CSA and total number of fibers (TNF) on the surface of a loin chop. Significant ($P < 0.05$) correlation coefficients were found: fiber volume ($r = –0.37$) and volume % ($r = –0.37$) of type IIX with loin length; volume % of type IIX with CIE L* ($r = 0.40$); volume % of types IIX ($r = 0.39$) and IIB ($r = –0.39$) with Warner-Bratzler shear force. Although those correlations to loin quality differed from those of CSA-based characteristics, the Z-scores did not show any significance between the 2 correlation coefficients, except for TNF. Therefore, the conventional methodology for muscle fiber characteristics can be used for evaluating the relationship to pork quality; however, the new methodology is more useful in estimating the characteristics of muscle fiber, which is elongated and cylindrical and to correct the underestimated fiber size and composition of type IIB.

**Keywords:** loin, meat quality, muscle fiber characteristics, muscle fiber volume; pork
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## Introduction

Studies on muscle fiber characteristics and their relationships to meat quality have been conducted frequently in the field of meat science over the last few decades. Regardless of animal species, muscle fiber characteristics (i.e., fiber type distribution, fiber size and relative composition) were considered important factors or criteria for assessment of the postmortem metabolic properties and meat quality characteristics, such as color, water-holding capacity, tenderness, and sensory property (Ozawa et al., 2000; Chang et al., 2003; Ryu and Kim, 2006; Jeong et al., 2010). In addition, the influences of breed, genotype, sex, age, diet, exercise, and growth promotors on intramuscular fat (IMF) accumulation in the body, growth performance, and development of muscles can be estimated by the muscle fiber characteristics (Lebret et al., 1999; Wegner et al., 2000; Gentry et al., 2002; Bee et al., 2007; Ebarb et al., 2017).

In terms of methodology, most of the previous studies on meat and livestock science were based on

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the transverse sections collected from muscle specimens. In other words, transverse sections of muscle were classified by fiber types, followed by analysis of fiber number, cross-sectional area (CSA), and diameter. Then, the relative area (%) and number (%), mean CSA or fiber diameter, fiber density, and total number of fibers (TNF) could be calculated. However, muscle fibers do not exist only on a planar dimension, but rather exist as 3-dimensional, approximating a cylinder in shape. While livestock and meat science has continued to rely on 2-dimensional estimations of muscle fiber composition, fields such as physiology, morphology and biomechanics areas generally have dealt with skeletal muscle fibers in 3 dimensions. For example, in studies investigating muscle, or muscle fiber, displacement and kinetic change during exercise and movement evaluated morphological traits such as muscle fiber length and the pennation angle, which is the angle between muscle fiber and aponeurosis or tendon (Muhl, 1982; Maganaris et al., 1998; Kawakami and Fukunaga, 2006; Azizi et al., 2008; Roux et al., 2016). Unlike these studies, muscle fiber characteristics, in the context of animal science, has been based on muscle cross-sections and have assumed similar length among the different fiber types. However, fiber lengths are actually different between muscle fiber types and thus inaccurate muscle fiber composition and density have been considered.

Therefore, to understand muscle fiber morphology and to estimate the actual amount of muscle fiber types distributed on muscles, a volume-based method was used to characterize muscle fiber composition. Three-dimensional morphology of muscle fibers was evaluated by muscle fiber volume computed with CSA and length, which were obtained from transverse and vertical sections, respectively, of muscle. In addition, with regard to the pork loin quality, the explanatory power of 3-dimensional morphology (fiber volume)-based muscle fiber characteristics was assessed and compared with those of CSA-based muscle fiber characteristics.

## Materials and Methods

### *Carcass characteristics and sample preparation*

Thirty carcasses (15 barrows and 15 gilts, weight of 132.9 ± 8.9 kg) were randomly selected from among pigs that had been slaughtered under the supervision of the Food Safety and Inspection Service of the United States Department of Agriculture at the University of Illinois Meat Science Laboratory (Urbana, IL). Pigs were slaughtered using a head-to-heart electrical stunning technique, followed immediately by exsanguination. Loin quality was estimated from the left side of each carcass, which was chilled at 4°C for 20 h. Loin length was determined along the whole backbone (first thoracic vertebrae to seventh lumbar vertebrae). Loin-eye area (LEA) was measured according to a previous study (Lowell et al., 2018) . In brief, the loin was separated between the 10th and 11th rib and then the surface of the *longissimus thoracis et lumborum* was traced on double-sided acetate paper. The tracings were measured using a digitizer tablet (Wacom, Vancouver, WA) and Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, CA). Loin volume was estimated by multiplying LEA by loin length.

At 24 h postmortem, the left side of the chilled carcass was fabricated in accordance with the North American Meat Institute's Meat Buyer's Guide (NAMI, 2014) and the loin (NAMI #414) was weighed. The loin posterior to the 10th rib was taken for quality and proximate composition measurements. After the loin was re-faced and exposed to air at 4°C for 20 min for myoglobin oxygenation, instrumental color and ultimate pH were measured. Subsequently, the loin was cut into a thickness of 2.54 cm or 1.27 cm to determine proximate composition, loin quality, and muscle fiber characteristics, as shown in Fig. 1A. The loin chop for proximate composition was packed in Whirl-Pak bags (Nasco, Fort Atkinson, WI) and stored at –20°C until analysis. For measurements of cooking loss and Warner-Bratzler shear force (WBSF), loin chops were vacuum-packed, stored at 4°C until 14 d postmortem, and then frozen at –20°C until analysis. One 1.27 cm thick chop was used to determine drip loss. Another chop was cut vertically into 2 cm thick strips and the two central strips were taken for analysis of muscle fiber pennation angle (Fig. 1B) and immunohistochemistry (IHC). A muscle cube (1 × 1 × 1.5 cm) was cut from each strip, promptly frozen in a 2-methyl ethane cooled with liquid nitrogen, and stored at – 80°C until analysis of IHC.

### *Loin quality and proximate composition*

Instrumental color (L*, lightness; a*, redness; b*, yellowness; CIE, 1978) was measured using a Minolta Chroma meter (CR-400, Minolta Camera Co., Ltd., Osaka, Japan) with a D65 light source, 10° observer angle, and an 8-mm aperture after calibration using a white tile. One d pH was measured using a pH meter (MPI pH-Meter, Topeka, KS) equipped with a glass electrode calibrated at 4°C using standard buffers (pH 4 and pH 7). To determine drip loss, the chop was weighed and then suspended from a fish hook attached to a length of string. The suspended

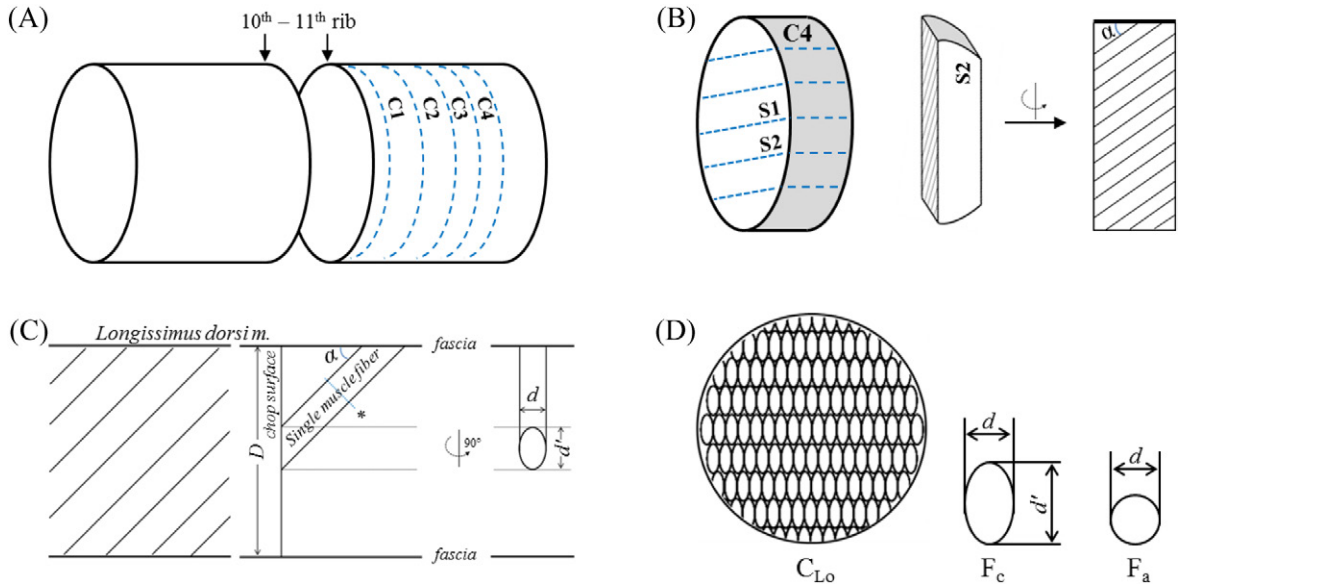


**Figure 1.** Sample preparation for measurements of loin quality, proximate composition and muscle fiber characteristics. A, preparation of chops: C1, for proximate composition; C2, for cooking loss and Warner-Bratzler shear force; C3, drip loss; C4, muscle fiber pennation angle and muscle fiber characteristics. B, measurement of muscle fiber pennation angle and preparation for immunohistochemistry: chop (C4) was cut to parallel to muscle fiber orientation into strips (2 cm thickness) and the pennation angle (α) to the fascia was measured from S1 and S2; the 2 strips were cut into cube (1 × 1 × 1.5 cm) and immediately frozen for immunohistochemistry. C, a model showing a single muscle fiber inside loin muscle: *D*, loin diameter; α, penation angle of muscle fiber; *, cutting orientation for collecting muscle transverse sections; *d*, muscle fiber diameter; *d'*, muscle fiber diameter on the chop surface. D, a model showing cross-sectional area of muscle fiber on loin chop: $C_{Lo}$, muscle fibers on loin chop are ellipse ($F_c$) in shape due to oblique orientation of muscle fiber to fascia of loin muscle; muscle fibers on cross-sections (*) for immunohistochemistry are circle ($F_a$); muscle fiber diameter (major axis, *d'*) of $F_c$ can be calculated by the equation of *d*/cos α.

chop was then placed into an inflated Whirl-Pack bag (Nasco) and allowed to hang for 24 h at 4°C. After 24 h, the chop was removed from the bag and weighed. Drip loss (%) was calculated as a percentage of initial weight. To measure cooking loss, frozen chops were thawed at 1°C for 24 h. The individual chops were weighed and then cooked on a grill (455N, Walter Kidde, Bronx, NY). When the internal temperature reached 35°C, the chops were flipped and then cooked until an internal temperature of 70°C. The temperature was monitored using copper-constantan thermocouples (Type T, Omega Engineering, Stamford, CT) and a digital scanning thermometer (model 92000–00, Barnat Co., Barrington, IL). After cooking, the chops were cooled to approximately 25°C and then weighed to determine percent cooking loss. Five cores (1.25 cm diameter) were obtained from each cooked chop for measurement of WBSF. The cores were removed parallel to the orientation of the muscle fiber. Shear force was measured using a Texture Analyzer TAHD Plus (Stable Micro Systems, Ltd., Godalming, UK) with a blade speed of 3.33 mm/s and a load cell capacity of 100 kg. Warner-Bratzler shear force (N) was presented by the average of the shear force value for the 5 cores.

Frozen loin chops were thawed and then trimmed of subcutaneous fat and fascia tissue. Trimmed chops were homogenized using a Cuisinart food processor (East Windsor, NJ). Moisture and extractable fat content were determined by the choloform:methanol method described by Novakofski et al. (1989). In brief, duplicate 10 g of each sample were dried in a drying oven (Isotemp Oven, Fisher Scientific, Hampton, NH) at 110°C for 24 h and then cooled in a vacuum desiccator for 15 min. The dried sample was weighed and subsequently placed in a soxhlet column. The lipid was extracted using chloroform-methanol solvent for at least 8 h. After drying, cooling, and weighing, moisture and fat content were calculated and presented as a percentage of initial sample weight.

## *Muscle fiber characteristics*

The pennation angle of muscle fiber was determined by measuring the angle degree of obliquely oriented muscle fiber to the fascia of loin muscle, as shown in Fig. 1B and 1C. In brief, the loin chop was cut vertical to the surface of the chop and parallel with the muscle fiber into strips (2 cm thickness). The angle between muscle fiber orientation and the loin fascia was determined using a protractor. The average of the 2 measurements was recorded for the pennation angle (α) of muscle fiber.

Immunohistochemistry was conducted to classify the muscle fiber types using 4 monoclonal antibod-

ies with the following specificities for myosin heavy chain (MHC) isoforms: BA-F8 for MHC I/slow; SC-71 for MHC 2a and 2x; BF-35 for MHC I/slow and 2a; 10F5 for MHC 2b. The primary antibodies were purchased from Developmental Studies Hybridoma Bank (Iowa City, IA). Both the transverse and vertical serial sections (10 μm thickness) were collected from frozen muscle samples using a cryostat microtome (CM1860 UV, Leica Biosystems, Wetzlar, Germany) at –27°C. Sections were blocked with normal goat serum and incubated with primary antibodies for 1 h at room temperature. Secondary antibodies (biotinylated goat anti-mouse IgG and IgM) were applied for 1 h at room temperature. The immunocomplex was formed with the avidin-biotin complex (32020, Thermo Fisher Scientific, Waltham, MA) and visualized with 3,3′-diaminobenzidine tetrahydrochloride and $H_2O_2$ (D3939, Sigma-Aldrich Inc., Saint Louis, MO). Representative stained sections are shown in Fig. 2. Muscle fibers were classified into 4 types (I, IIA, IIX, and IIB) according to the reactivity to anti-MHCs. Approximately 400 fibers of duplicate sections per sample were analyzed and the average was recorded.

Muscle fiber number and CSA were measured on the transverse section, whereas muscle fiber length was measured on the vertical section using image analysis software (Image-Pro plus 5.1, Media Cybernetic Inc., Rockville, MD). Muscle fiber volume was calculated by multiplying CSA by fiber length. The relative fiber number, relative fiber area, and relative fiber volume were presented as a proportion (%) of each fiber type to total number, area, and volume, respectively. Three TNF were considered in this study. The general TNF (TNFa), which has been regarded previously (Larzul et al., 1997; Ryu et al., 2008; Wegner et al., 2000) was the fiber number counted on the transverse section in direct ratio to LEA. Cross-section-based TNF (TNFc) was the fiber number based on the cross-section adjusted by pennation angle. The adjusted cross-section (Fig. 1C and 1D) was modeled to be an ellipse ($F_c$) and its area was calculated by the following mathematical formula:

$$\text{Area}\,(F_c) = \frac{1}{4} dd'\pi,$$

where $d$ was the minor axis; $d'$ was the major axis, calculated as $d/\cos\alpha$. Thus, TNFc was determined by directly proportioning the area of $F_c$ to LEA. For the determination of volume-based TNF (TNFv), the sum of fiber volume corresponding to 100 fibers was calculated using the percent fiber number and volume of each fiber type, and then that was directly proportioned to loin volume.

### Statistical analysis

Statistical analyses were performed using SAS (v. 9.4, SAS Inst. Inc., Cary, NC). Population summary statistics, including mean, standard deviation, minimum, and maximum were calculated using the MEANS procedure. The GLM procedure was used to compare muscle fiber size (CSA, length, and volume) and proportion (relative number, area, and volume) among the 4 fiber types. Slopes, intercepts and coefficients of determination for linear regression was calculated using the REG procedure of SAS. Cross-sectional area and volume-based fiber characteristics within same fiber types were coded as the dependent variables and CSA-based fiber characteristics were coded as the independent variables. To compare TNFa and TNFc, a paired $t$ test was conducted. Pearson correlation coefficients were determined for the relationships between loin quality traits and muscle fiber characteristics using the CORR procedure. To test the difference between 2 dependent (correlated) correlations (CSA-based and fiber volume-based muscle fiber characteristics), Williams-Hotelling test (Kenny, 1987) was conducted using the following formula:

$$t(n-3) = \frac{(r_{13} - r_{23})\sqrt{(n-1)(1+r_{12})}}{\sqrt{2K\frac{(n-1)}{(n-3)} + \frac{(r_{23}+r_{13})^2}{4}(1-r_{12})^3}},$$

where n, sample size; $r_{12}$, correlation between meat quality and CSA-based muscle fiber characteristics; $r_{13}$, correlation between meat quality and volume-based muscle fiber characteristics; $r_{23}$, correlation between CSA- and volume-based muscle fiber characteristics, $K = 1 - r_{12}^2 - r_{13}^2 - r_{23}^2 + 2r_{12}r_{13}r_{23}$. For all statistical tests, significance was declared at $P < 0.05$.

## Results

### Characterization of loin quality and muscle fiber traits

All quality traits, except for CIE b*, presented low variation among the samples (Table 1). Loin-eye area (50.89 to 69.29 $cm^2$), loin length (49.53 to 59.69 cm), and loin weight (4.81 to 6.40 kg) showed a coefficient of variation (CV) of below 10.0. Loin volume, which was derived from LEA and loin length, ranged from 2,598.99 to 4,047.59 cm3. Moisture content ranged from 71.84 to 76.36% and its CV was 1.28, whereas extractable lipid content was 1.57–3.93% with a CV of 27.94.

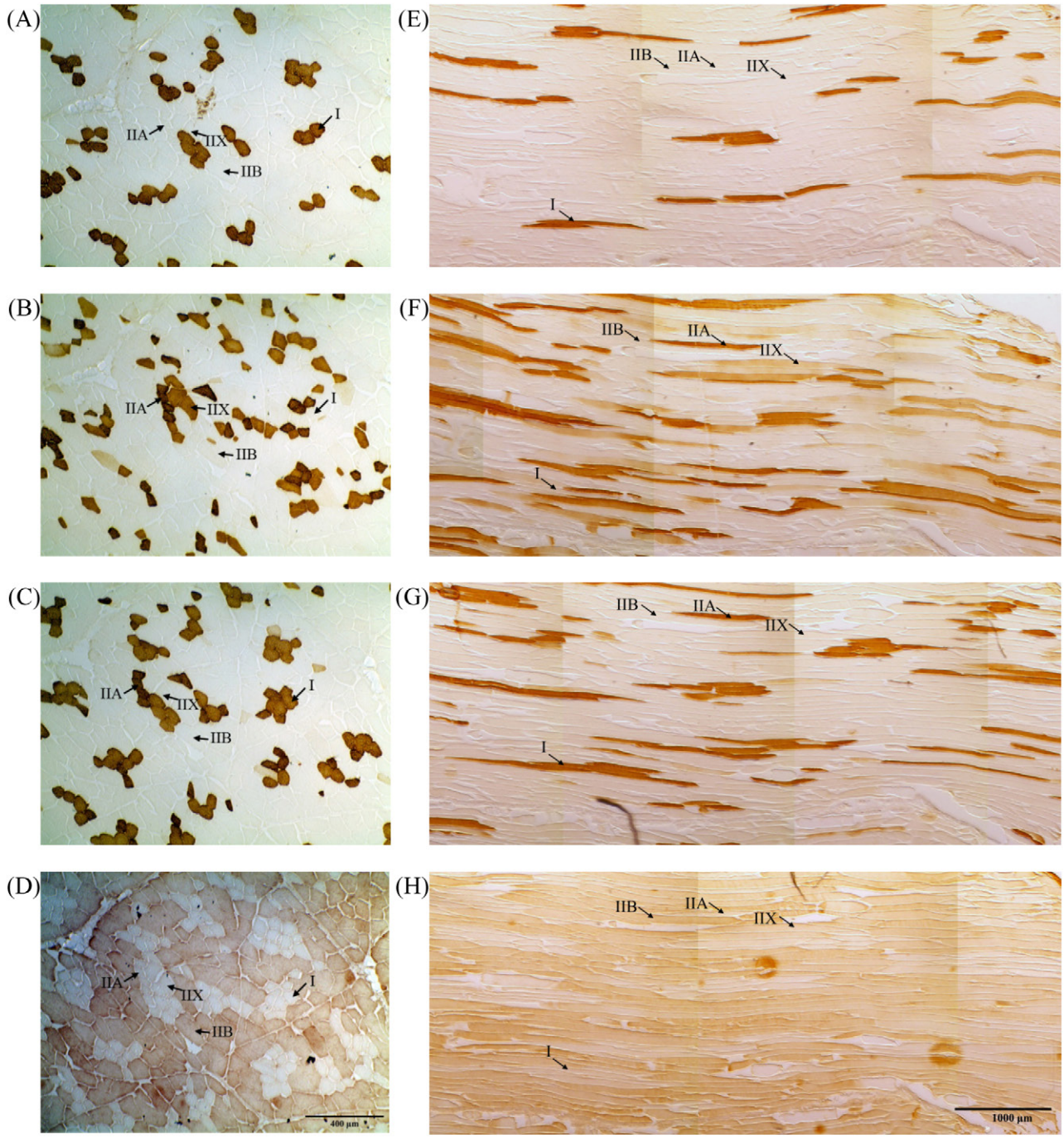


**Figure 2.** Serial sections stained with antibodies specific to myosin heavy chain (MHC) isoforms. A-D, transverse; E-H, vertical; A and E, stained with BA-F8 (anti-MHC I/slow); B and F, stained with SC-71 (anti-MHC 2a and 2x); C and G, stained with BF-35 (anti-MHC I/slow and 2a); D and H, stained with 10F5 (anti-MHC 2b). Muscle fiber types: I, stained with BA-F8 and BF-35; IIA, stained with SC-71 and BF-35; IIX, stained with SC-71; IIB, stained with 10F5.

The min pH (5.35) and the max CIE L* (64.11) and drip loss (7.08%) indicate that some loins presented marginal pale and exudative characteristics. The CIE b* value had the greatest CV (42.61) among loin quality traits.

The pennation angle of muscle fiber, which is the angle between muscle fiber and the force-generating axis, was 48.00° to 80.33°. Type IIB fibers were the largest among all fiber types based on CSA, fiber length, and volume. The TNFa value was almost twice as great as TNFc. These 2 TNF values were considerably less than TNFv, because TNFa and TNFc were evaluated on a chop, whereas TNFv was estimated in the whole loin (loin volume). Relative number, relative area, and relative volume of muscle fibers exhibited a similar trend as muscle fiber size. Fiber type IIB presented a greater proportion than the other types, and again its variations among samples were low.

### *Comparison of characteristics between CSA- and volume-based muscle fibers*

Cross-section area was the greatest ($P < 0.0001$) for type IIB, followed by type IIX, whereas type I and IIA were not significantly ($P > 0.05$) different each other (Fig. 3A). There was a similar trend observed for fiber length and volume, although magnitudes of difference among fiber types varied. Cross-section area and length of type IIB fibers were 1.87× and 1.61× greater, respectively, than those of type I, whereas fiber volume was 2.98× greater in type IIB than in type I. The difference of proportions between type IIB and the other types were much larger than that of fiber size (Fig. 3B). Although type I and IIA were not significantly ($P > 0.05$) different in fiber proportions regardless of proportion types (relative number, area, and volume), both fiber types had lower ($P < 0.0001$) proportions than type IIX and IIB, as was seen in the result for fiber size. Type IIB had much higher ($P < 0.0001$) proportions (12.91, 7.85, and 20.51-fold changes for relative number, area, and volume, respectively) compared with type I. TNF showed significant ($P < 0.0001$) difference between TNFa and TNFc (Fig. 3C).

To evaluate the relationships between CSA- and volume-based fiber characteristics within same fiber types, linear regression was investigated using volume-based fiber characteristics as the dependent and CSA-based fiber characteristics as the independent variables (Table 2; Fig. 4). Regression models for fiber size fitted significantly ($P < 0.0001$) in all fiber types with accounting for 46.20 to 67.71% of variability. Regression coefficients for type I, IIA, IIX, and IIB were 1.80, 1.57, 2.42, and 3.57, respectively, which means muscle fiber volume changes were larger than CSA within fiber types, even more in type IIB (Fig. 4A). Proportion of muscle fiber was also fitted significantly ($P < 0.0001$) by regression models with explanation of 44.36 to 86.44% in all fiber types. Among the fiber types, type I scattered widely and resulted in higher CV (29.70) and lower explanation (44.36%) than the other fiber types. The regression coefficients were below 1.0 regardless of fiber types, which means relative volume changes were smaller than the relative area (Fig. 4B). A remarkable finding was the relatively large intercept for type IIB (24.70, $P < 0.01$), which means relative volume was at least 24.70% greater than relative area. In addition, the scattering of type IIB was highly concentrated to the estimated regression model with a low CV of 3.67. The regression model for TNFa and TNFv showed extremely high regression coefficient. The relatively large values were estimated in TNFv rather than in TNFa, because of a different analytical methodology (based on LEA vs. loin volume). However, TNFc was estimated in an approximately half value (regression coefficient of 0.52, $P < 0.0001$) of TNFa, similar to the result of the *t* test (Fig. 3C).

### *Comparison of correlation coefficients between CSA- and volume-based muscle fiber characteristics with pork loin quality*

Correlation coefficients between muscle fiber size (CSA and volume) and pork loin quality are shown in Table 3. The CSA of type I was negatively correlated with CIE a* ($r = –0.46$, $P < 0.05$) and b* ($r = –0.47$, $P < 0.01$). CSA of type IIA was negatively correlated with LEA ($r = –0.37$, $P < 0.05$), but positively correlated with loin length ($r = 0.38$, $P < 0.05$). Type IIX presented positive correlation between its CSA and pH ($r = 0.40$, $P < 0.05$). However, CSA of type IIB did not have significant correlations with any traits of loin quality ($P > 0.05$). For muscle fiber volume, type IIX had negative correlation with loin length ($r = –0.37$, $P < 0.05$), whereas the other fiber types did not have significant correlations with loin quality traits ($P > 0.05$). *Z*-scores, which are correlation coefficients between the 2 (CSA and fiber volume) correlations with loin quality traits, showed significantly ($P < 0.05$) positive values in pH of type I, drip loss of type IIA, loin length of type IIs, and loin volume of type IIB. However, CIE L*, a*, and b* of type I and LEA of type IIX were negatively ($P < 0.05$) correlated between the 2 correlations.

Correlation coefficients between muscle fiber proportion and pork loin quality showed a similar trend between relative area and relative volume of muscle fiber types (Table 4). In particular, loin length, CIE L*, and WBSF were correlated ($P < 0.05$) with the proportions of fiber type IIX and IIB, regardless of whether calculated as relative area or relative volume. In other words, both the relative area and volume of type IIX were negatively correlated ($P < 0.05$) with loin length and positively correlated ($P < 0.05$) with CIE L* and WBSF. Type IIB was negatively correlated ($P < 0.05$) with WBSF in its relative area and volume. Except for those correlations, relative areas of type I and IIB were correlated with loin volume, however, they were the opposite ($r = –0.38$ for type I and $r = 0.38$ for type IIB, $P < 0.05$) correlations. Although a similar trend was found between those two proportions, significant *Z*-scores presented mostly negative ($P < 0.05$) values (loin length and volume, CIE a* and b*, drip loss of type I; CIE a* and cooking loss of type IIA; LEA and loin volume of type IIX). However, LEA and loin volume of type IIB showed positive ($P < 0.05$) *Z*-scores between the 2 proportions.

The TNF was positively correlated ($P < 0.05$) with LEA, loin length, and loin volume, whereas TNF was

**Table 1.** Mean, SD, minimum, maximum and CV of quality characteristics and muscle fiber characteristics in porcine *longissimus dorsi muscles* ($N = 30$)

| Variable | | Mean | SD | Min | Max | CV |
|---|---|---|---|---|---|---|
| Loin quality | | | | | | |
| Loin-eye area, $cm^2$ | | 57.94 | 5.52 | 50.89 | 69.29 | 9.53 |
| Loin length, cm | | 54.86 | 2.80 | 49.53 | 59.69 | 5.10 |
| Loin volume, $cm^3$ | | 3,178.18 | 342.04 | 2,598.99 | 4,047.59 | 10.76 |
| Loin weight, kg | | 5.56 | 0.44 | 4.81 | 6.40 | 7.96 |
| Moisture content, % | | 74.37 | 0.95 | 71.84 | 76.36 | 1.28 |
| Fat content, % | | 2.29 | 0.64 | 1.57 | 3.93 | 27.94 |
| pH | | 5.43 | 0.05 | 5.35 | 5.57 | 0.93 |
| Meat color | CIE $L^*$ | 55.25 | 3.52 | 49.32 | 64.11 | 6.37 |
| | CIE $a^*$ | 10.46 | 1.67 | 6.91 | 13.63 | 15.99 |
| | CIE $b^*$ | 4.38 | 1.87 | 1.72 | 8.42 | 42.61 |
| Drip loss, % | | 5.23 | 1.26 | 2.84 | 7.08 | 24.04 |
| Cooking loss, % | | 22.13 | 2.91 | 16.34 | 27.94 | 13.14 |
| Warner-Bratzler shear force, N | | 33.08 | 5.41 | 24.94 | 47.34 | 16.35 |
| Muscle fiber characteristics | | | | | | |
| Fiber pennation angle, ° | | 61.03 | 7.38 | 48.00 | 80.33 | 12.09 |
| Cross-sectional area, $\mu m^2$ | I | 3,128.88 | 797.64 | 1,979.33 | 5,723.95 | 25.49 |
| | IIA | 2,853.30 | 808.44 | 1,761.23 | 5,569.75 | 28.33 |
| | IIX | 4,595.47 | 940.34 | 3,298.82 | 6,759.57 | 20.46 |
| | IIB | 5,682.09 | 872.82 | 4,132.16 | 7,371.06 | 15.36 |
| Muscle fiber length, μm | I | 1,848.61 | 438.77 | 1,118.35 | 3,099.68 | 23.74 |
| | IIA | 2,081.03 | 380.17 | 1,534.31 | 3,030.08 | 18.27 |
| | IIX | 2,481.23 | 429.12 | 1,820.40 | 3,442.90 | 17.29 |
| | IIB | 2,835.37 | 598.81 | 1,786.62 | 4,079.79 | 21.12 |
| Muscle fiber volume, $\times 10^3$ $\mu m^3$ | I | 5,796.69 | 1,964.00 | 2,636.38 | 9,877.57 | 33.88 |
| | IIA | 5,833.29 | 1,539.24 | 3,904.71 | 10,376.51 | 26.39 |
| | IIX | 11,412.71 | 2,981.24 | 6,138.94 | 18,105.25 | 26.12 |
| | IIB | 16,198.35 | 4,589.54 | 9,248.88 | 25,582.14 | 28.33 |
| Total number of fiber[1] | TNFa ($\times 10^6$) | 1.19 | 0.22 | 0.81 | 1.53 | 18.14 |
| | TNFc ($\times 10^6$) | 0.57 | 0.17 | 0.15 | 0.88 | 29.67 |
| | TNFv ($\times 10^{12}$) | 253.63 | 74.85 | 136.81 | 440.63 | 29.51 |
| Relative number, % | I | 10.30 | 3.11 | 4.87 | 18.51 | 30.17 |
| | IIA | 9.38 | 3.68 | 3.90 | 17.21 | 39.17 |
| | IIX | 13.93 | 3.78 | 8.77 | 23.38 | 27.14 |
| | IIB | 66.39 | 6.66 | 52.92 | 78.90 | 10.04 |
| Relative area, % | I | 6.34 | 1.74 | 3.08 | 9.74 | 27.44 |
| | IIA | 5.33 | 2.21 | 2.10 | 9.89 | 41.49 |
| | IIX | 13.01 | 4.29 | 7.05 | 24.37 | 32.95 |
| | IIB | 75.32 | 5.76 | 61.53 | 85.78 | 7.65 |
| Relative volume, % | I | 4.45 | 1.74 | 2.33 | 8.44 | 39.13 |
| | IIA | 4.11 | 1.57 | 1.53 | 7.18 | 38.31 |
| | IIX | 12.09 | 4.19 | 5.78 | 20.55 | 34.64 |
| | IIB | 79.35 | 5.06 | 71.11 | 90.01 | 6.38 |

[1]TNFa, based on transverse section and loin-eye area; TNFc, based on cross-sectional area adjusted by pennation angle; TNFv, based on muscle fiber volume in whole loin.

not correlated ($P > 0.05$) with any meat quality traits (Table 5). The TNFa was positively correlated with LEA ($r = 0.41$, $P < 0.05$), while TNFv was positively correlated with loin length ($r = 0.39$, $P < 0.05$) and loin volume ($r = 0.43$, $P < 0.05$). However, TNFc, TNF adjusted by TNFa and the pennation angle of muscle fiber, did not show any correlation with pork loin quality ($P > 0.05$). The 2 correlations of TNFa and TNFv were negatively ($P < 0.05$) correlated with loin length and with drip loss, however loin weight was positively

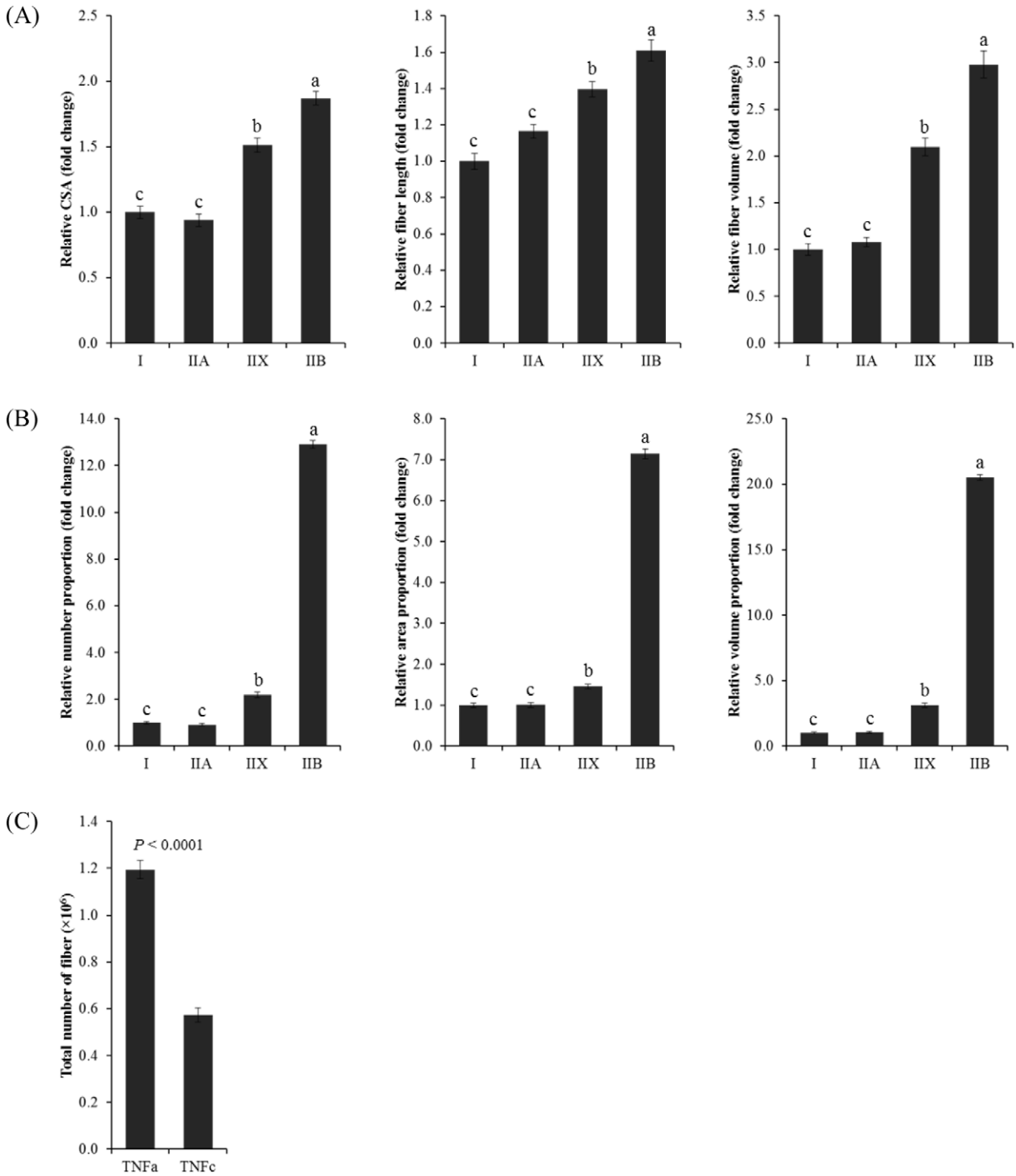


**Figure 3.** Muscle fiber characteristics of porcine *longissimus dorsi* muscle. Relative muscle fiber size (A) and proportion (B) were compared among fiber types. Total number of fiber based on loin-eye area (TNFa) and that adjusted by pennation angle of muscle fiber (TNFc) were compared (C). Different superscripts (a-c) on the bar indicate significant ($P < 0.0001$) differences among fiber types.

($P < 0.05$) correlated between TNFa and TNFv. The *Z*-scores between TNFc and TNFv presented positive ($P < 0.05$) correlations in loin length and drip loss dislike the correlations between TNFa and TNFv. However, all *Z*-scores between TNFa and TNFc did not show significant ($P > 0.05$) correlations.

# Discussion

## *Muscle fiber characteristics*

Muscle fibers, the cellular units of striated muscle, are elongated multinucleated cylinders (Huddart, 1975; Gans and Gorniak, 1979). In this study, muscle fiber

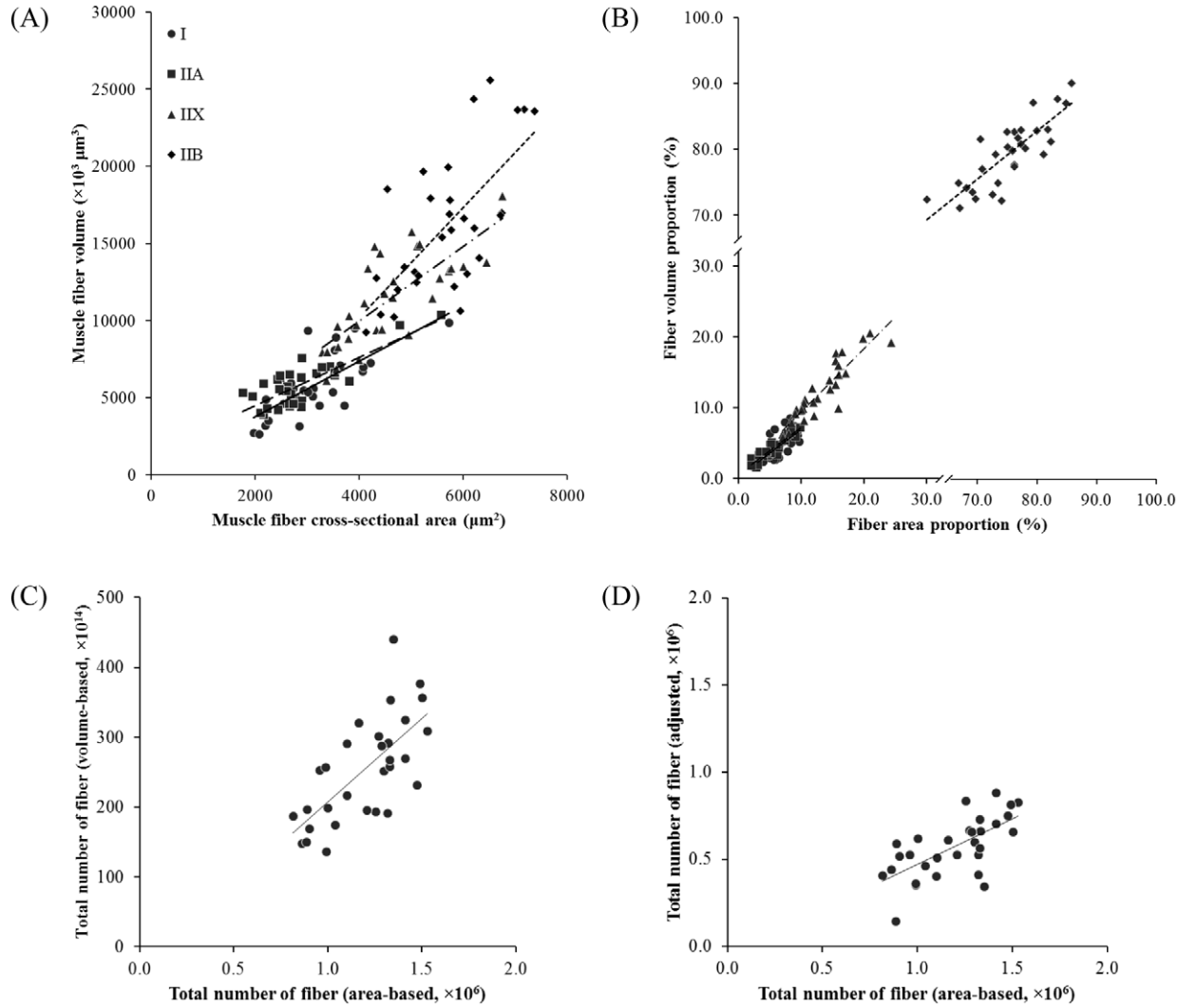


**Figure 4.** Scatterplots showing relationship between cross-sectional area-based and volume-based muscle fiber characteristics in porcine *longissimus dorsi* muscle. A, muscle fiber size; B, muscle fiber proportion; C, total number of fiber. Trend lines on A and B: solid line, type I; dashed, type IIA; dot-dashed, type IIX; dotted, type IIB.

**Table 2.** Linear regression results of cross-sectional area (CSA)-based and volume-based muscle fiber characteristics in porcine *longissimus dorsi muscle*[1]

| | Dependent variable | Independent variable | $B_0$ | $B_1$ | *P*-value | $R^2$ | CV |
|---|---|---|---|---|---|---|---|
| Type I | Muscle fiber volume | CSA of muscle fiber | 160.04 | 1.80*** | 0.0001 | 0.5353 | 23.51 |
| | Relative volume | Relative area | 0.22 | 0.67*** | 0.0001 | 0.4436 | 29.70 |
| Type IIA | Muscle fiber volume | CSA of muscle fiber | 1,363.06* | 1.57*** | 0.0001 | 0.6771 | 15.26 |
| | Relative volume | Relative area | 0.58 | 0.66*** | 0.0001 | 0.8644 | 14.36 |
| Type IIX | Muscle fiber volume | CSA of muscle fiber | 304.15 | 2.42*** | 0.0001 | 0.5813 | 17.20 |
| | Relative volume | Relative area | 0.46 | 0.89*** | 0.0001 | 0.8371 | 14.23 |
| Type IIB | Muscle fiber volume | CSA of muscle fiber | –4,109.10 | 3.57*** | 0.0001 | 0.4620 | 21.15 |
| | Relative volume | Relative area | 24.70** | 0.72*** | 0.0001 | 0.6810 | 3.67 |
| Total number of fiber | TNFv | TNFa | –30.42 | 238.16*** | 0.0001 | 0.4739 | 21.79 |
| | TNFc | TNFa | –0.05 | 0.52*** | 0.0001 | 0.4397 | 22.60 |

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.0001$.

[1]TNFa, based on transverse section and loin-eye area; TNFv, total number of fiber assessed by muscle fiber volume to whole loin; TNFc, total number of fiber based on cross-sectional area adjusted by pennation angle of muscle fiber.

**Table 3.** Comparison of correlation coefficients between cross-sectional area and muscle fiber volume with pork loin quality

| | Cross-sectional area | | | | Muscle fiber volume | | | | *Z*-score[1] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Loin quality traits | I | IIA | IIX | IIB | I | IIA | IIX | IIB | I | IIA | IIX | IIB |
| Loin-eye area | 0.03 | -0.37* | -0.11 | 0.16 | 0.02 | -0.27 | 0.12 | 0.05 | 0.05 | -1.26 | -2.45$^{x}$ | 0.91 |
| Loin length | -0.02 | 0.38* | -0.10 | 0.08 | 0.11 | 0.12 | -0.37* | -0.25 | -1.20 | 3.58$^{y}$ | 3.04$^{y}$ | 3.03$^{y}$ |
| Loin volume | 0.00 | -0.16 | -0.17 | 0.17 | 0.06 | -0.20 | -0.09 | -0.08 | -0.49 | 0.39 | -0.81 | 2.18$^{x}$ |
| Loin weight | 0.04 | -0.11 | 0.20 | 0.11 | -0.03 | -0.09 | 0.28 | 0.20 | 0.63 | -0.31 | -0.87 | -0.83 |
| Moisture content | 0.06 | 0.09 | 0.12 | 0.15 | 0.12 | 0.03 | 0.09 | -0.07 | -0.61 | 0.67 | 0.31 | 1.92 |
| Extractable lipid content | 0.17 | -0.01 | 0.12 | 0.07 | 0.14 | -0.02 | 0.10 | 0.20 | 0.27 | 0.15 | 0.18 | -1.12 |
| pH | 0.30 | 0.12 | 0.40* | 0.13 | 0.02 | 0.12 | 0.27 | 0.19 | 2.90$^{y}$ | -0.05 | 1.41 | -0.50 |
| CIE L* | -0.33 | -0.06 | -0.05 | -0.15 | -0.04 | -0.02 | 0.03 | -0.08 | -2.95$^{y}$ | -0.49 | -0.86 | -0.58 |
| CIE a* | -0.46* | -0.10 | -0.11 | -0.34 | -0.11 | 0.00 | -0.18 | -0.32 | -3.92$^{z}$ | -1.10 | 0.68 | -0.13 |
| CIE b* | -0.47** | -0.04 | -0.18 | -0.34 | -0.10 | -0.03 | -0.20 | -0.28 | -4.29$^{z}$ | -0.05 | 0.26 | -0.47 |
| Drip loss | -0.29 | -0.13 | 0.10 | -0.14 | -0.14 | -0.29 | -0.08 | -0.31 | -1.43 | 2.08$^{x}$ | 1.79 | 1.51 |
| Cooking loss | -0.22 | -0.20 | -0.30 | -0.19 | -0.10 | -0.06 | -0.19 | -0.25 | -1.14 | -1.67 | -1.20 | 0.50 |
| Warner-Bratzler shear force | -0.19 | -0.08 | 0.21 | -0.21 | -0.13 | 0.05 | 0.17 | -0.03 | -0.54 | -1.62 | 0.35 | -1.54 |

*$P < 0.05$.

**$P < 0.01$.

[1]*P*-value for test comparing dependent correlation coefficients based on the test statistic *t* (from *t*-distribution) with degrees of freedom = *n* - 3 (Kenny, 1987); $^{x}$, $P < 0.05$; $^{y}$, $P < 0.01$; $^{z}$, $P < 0.001$.

types differ in length and CSA, with the exception between type I and IIA, as shown in Fig. 2 and 3A. Muscle fiber volume-based estimates of type IIX and IIB fibers, calculated by multiplying CSA by fiber length, were routinely greater than CSA-based estimates. This amplified differences that existed among relative volumes of these fiber types. This is perhaps most clearly demonstrated by the fact that the type IIB: type I volume proportion was 2.6× than the same ratio calculated from CSA based measures. The results of linear regression analysis support those unexpected results. However, a somewhat different trend was seen between fiber size and fiber proportions. Fiber volume could be greatly influenced by an increase of CSA, whereas relative volume changed less than relative area, regardless of fiber type. As shown in Table 2, the greater regression coefficients were predicted between muscle fiber volume and CSA than between relative volume and relative area. In previous studies conducted on CSA-based porcine muscle fiber characteristics, the proportion of type IIB did not exceed 10× that of type I: 1.9 to 7.7× (Van den Maagdenberg et al., 2008; Lefaucheur et al., 2002; Abreu et al., 2006).

Muscle fiber architecture depends on muscle function (Gans and Bock, 1965; Herring et al., 1979). Muscles architecture can be used to categorize muscles as parallel fibered, fusiform, and pennate (Maclntosh et al., 2005). Loin (*longissimus dorsi* m.) is a unipennate muscle, and muscle fibers are oriented to the force-generating axis. As illustrated in Fig. 1, loin muscle fibers leaned and the angle is related with contraction force. Therefore, the pennation angles differ among the muscles within an animal (Otten, 1988; Gans and Gaunt, 1991). In the present study, the fiber pennation angle varied among loins with 12.09 of CV, however the angle degree did not affect loin quality and muscle fiber characteristics, except for TNFc ($r$ = –0.76, $P < 0.0001$), which was based on CSA adjusted by the pennation angle (Data not shown). The pennation angle also determines the shape of muscle fiber on a loin chop. As outlined in Fig. 1C and 1D, an ellipse ($F_c$) can be derived from CSA of muscle fiber ($F_a$) and pennation angle, α. In addition, TNFc, the real number of total fibers exposed on the face of a loin chop, which was cut vertically to loin length, is also determined by the pennation angle. In other words, the pennation angle observed in the *longissimus dorsi* muscle causes the cross-sectional area of the muscle fibers to be presented as an ellipse, with increasing pennation angle resulting in increasingly elongated ellipses. However, none of the loin quality and muscle fiber characteristics were correlated with either pennation angle or pennation angle-dependent TNFc.

## *Relationships between volume-based muscle fiber characteristics and pork loin quality*

In general, slow-twitch or oxidative fiber types (type I or IIA) are positively correlated with pH, redness, and yellowness, but negatively correlated with water-holding capacity, lightness, and WBSF (Larzul et

**Table 4.** Comparison of correlation coefficients between relative area and relative volume of muscle fiber with pork loin quality

| | Relative area | | | | Relative volume | | | | *Z*-score[1] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Loin quality traits | I | IIA | IIX | IIB | I | IIA | IIX | IIB | I | IIA | IIX | IIB |
| Loin-eye area | –0.34 | –0.04 | –0.19 | 0.26 | –0.19 | 0.04 | –0.03 | 0.08 | –1.32 | –1.53 | –3.12$^{y}$ | 2.34$^{x}$ |
| Loin length | –0.17 | 0.12 | –0.37$^{*}$ | 0.28 | 0.20 | 0.11 | –0.37$^{*}$ | 0.20 | –3.33$^{y}$ | 0.19 | 0.05 | 0.91 |
| Loin volume | –0.38$^{*}$ | 0.01 | –0.35 | 0.37$^{*}$ | –0.07 | 0.07 | –0.20 | 0.17 | –2.75$^{y}$ | –1.30 | –2.75$^{y}$ | 2.58$^{y}$ |
| Loin weight | –0.24 | 0.19 | –0.04 | 0.03 | –0.27 | 0.15 | –0.02 | 0.07 | 0.30 | 0.79 | –0.35 | –0.43 |
| Moisture content | –0.08 | 0.14 | –0.17 | 0.10 | 0.03 | 0.19 | –0.10 | 0.01 | –0.89 | –1.00 | –1.20 | 0.97 |
| Extractable lipid content | 0.14 | –0.25 | –0.03 | 0.08 | 0.07 | –0.34 | –0.09 | 0.15 | 0.53 | 1.74 | 1.02 | –0.89 |
| pH | –0.18 | –0.03 | 0.26 | –0.13 | –0.34 | –0.04 | 0.17 | –0.01 | 1.41 | 0.30 | 1.68 | –1.46 |
| CIE L$^{*}$ | –0.16 | –0.02 | 0.38$^{*}$ | –0.23 | 0.04 | –0.03 | 0.40$^{*}$ | –0.33 | –1.68 | 0.27 | –0.39 | 1.35 |
| CIE a$^{*}$ | 0.00 | 0.12 | 0.11 | –0.13 | 0.29 | 0.25 | 0.09 | –0.26 | –2.62$^{y}$ | –2.68$^{y}$ | 0.34 | 1.56 |
| CIE b$^{*}$ | –0.03 | 0.14 | 0.16 | –0.16 | 0.23 | 0.16 | 0.15 | –0.26 | –2.33$^{x}$ | –0.47 | 0.20 | 1.13 |
| Drip loss | –0.09 | 0.01 | 0.20 | –0.13 | 0.16 | 0.05 | 0.22 | –0.25 | –2.14$^{x}$ | –0.79 | –0.34 | 1.56 |
| Cooking loss | 0.07 | 0.20 | 0.18 | –0.23 | 0.10 | 0.33 | 0.25 | –0.35 | –0.25 | –2.88$^{y}$ | –1.25 | 1.43 |
| Warner-Bratzler shear force | –0.04 | 0.24 | 0.49$^{**}$ | –0.44$^{*}$ | –0.08 | 0.31 | 0.39$^{*}$ | –0.39$^{*}$ | 0.33 | –1.38 | 1.93 | –0.69 |

$^{*}P < 0.05$.

$^{**}P < 0.01$.

$^{x}P < 0.05$.

$^{y}P < 0.01$.

[1]*P*-value for test comparing dependent correlation coefficients based on the test statistic *t* (from *t*-distribution) with degrees of freedom = *n* - 3 (Kenny, 1987).

al., 1997; Kim et al., 2013; Ryu et al., 2008). In contrast, fast-twitch or glycolytic fiber types, such as type IIX and IIB, have an opposite relationship with meat quality traits to slow-twitch oxidative types (Huff-Lonergan et al., 2002; Karlsson et al., 1993; Kim et al., 2013; Ryu et al., 2008). Regardless of significance, in this study, CSA of all fiber types were positively correlated with pH and negatively correlated with CIE L*, a*, and b*. Moreover, the relative area of type IIB was negatively correlated with WBSF and CIE L*. These results are contrary to trends observed with the previous study (Larzul et al., 1997; Ryu et al., 2008; Kim et al., 2013). It seems that North American pigs are slaughtered at a much heavier weight than is typical in other countries and that this may have caused differences. For recent two decades in the USA pork production, live weight at slaughter was increased from 116.2 (1997) to 128.2 kg (2017) and its difference is 12 kg (USDA, 2018). In the present study, the average weight of the pigs is 132.9 kg, which is much greater than those in other countries.

Muscle fiber volume-based characteristics showed relatively few significant correlations with pork loin quality traits compared with CSA-based characteristics. In particular, fiber size traits, such as CSA and fiber volume, did not show the same trend of correlations with pork loin quality. However, a similar trend in correlations with loin quality traits, such as loin length, CIE L*, and WBSF, was found between relative area and relative volume. The result for TNF may be influenced by the computed traits: TNFa derived from LEA, TNFv derived from loin length, and loin volume. Regardless of the similarity of the trend in correlation with loin quality, *Z*-scores, which mean the significant differences correlation coefficients between the two traits (CSA-based and volume-based muscle fiber characteristics), indicated that the relationships between muscle fiber characteristics of type I and pork quality traits such as CIE L*, a*, and b*, drip loss, loin length, and loin volume should be distinguished between CSA-based and volume-based characteristics, because of the opposite trends in *Z*-scores. However, despite of dramatic differences between CSA-based and volume-based fiber size and proportion of type IIB, there were no negative *Z*-scores with significance. In other words, the explanation of the correlations between muscle fiber type IIB characteristics and pork loin quality is not different between those two traits. The relationships of TNF with loin length or drip loss could be explained by the opposite correlations between TNFa and TNFv, however, TNFc, adjusted by the pennation angle of muscle fiber is not different from TNFa.

## Conclusion

Accounting for the 3-dimensional shape of muscle fibers could be used to estimate muscle fiber characteristics and composition. This volume based method

**Table 5.** Comparison of correlation coefficients among 3 different total number of fiber values with pork loin quality

| | Total number of fiber[1] | | | *Z*-score[2] | | |
|---|---|---|---|---|---|---|
| Loin quality traits | TNFa | TNFc | TNFv | TNFa vs.TNFv | TNFa vs. TNFc | TNFc vs. TNFv |
| Loin-eye area | 0.41* | 0.27 | 0.25 | 1.51 | 1.29 | –0.09 |
| Loin length | –0.13 | –0.04 | 0.39* | –6.04z | –0.69 | 2.69y |
| Loin volume | 0.32 | 0.22 | 0.43* | –0.99 | 0.90 | 1.27 |
| Loin weight | 0.27 | 0.27 | 0.03 | 2.13x | 0.00 | –1.34 |
| Moisture content | –0.20 | –0.24 | –0.05 | –1.41 | 0.29 | 1.10 |
| Extractable lipid content | –0.04 | –0.05 | –0.16 | 1.05 | 0.02 | –0.66 |
| pH | –0.21 | –0.22 | –0.28 | 0.55 | 0.01 | –0.35 |
| CIE L* | 0.17 | 0.06 | 0.14 | 0.22 | 0.86 | 0.44 |
| CIE a* | 0.24 | 0.05 | 0.32 | –0.69 | 1.58 | 1.52 |
| CIE b* | 0.23 | 0.14 | 0.31 | –0.70 | 0.76 | 0.98 |
| Drip loss | –0.03 | –0.20 | 0.24 | –2.40x | 1.43 | 2.60y |
| Cooking loss | 0.27 | 0.18 | 0.25 | 0.12 | 0.75 | 0.43 |
| Warner–Bratzler shear force | 0.18 | 0.08 | –0.01 | 1.68 | 0.77 | –0.54 |

*$P < 0.05$.

x$P < 0.05$.

y$P < 0.01$.

z$P < 0.001$.

[1]TNFa, based on transverse section and loin-eye area; TNFc, total number of fiber based on cross-sectional area adjusted by pennation angle of muscle fiber; TNFv, total number of fiber assessed by muscle fiber volume to whole loin.

[2]*P*-value for test comparing dependent correlation coefficients based on the test statistic *t* (from *t*-distribution) with degrees of freedom = *n* - 3 (Kenny, 1987).

corrected the dramatic underestimation of type IIB fiber size and proportion by the CSA-based method, providing a more accurate profile of muscle fiber composition. Moreover, the pennation angle of loin muscle fiber helps to estimate the real CSA and TNF on the face of a loin chop. There were few differences in the correlations between the muscle fiber characteristics derived from the two methods and pork loin quality traits. Especially, fiber type I clearly presented the opposite explanations on relationships between muscle fiber characteristics and pork loin quality such as meat color and drip loss between the two methods. In addition, TNF may have the different explanation to drip loss and loin length by the different estimating methods. This indicates that both the volume-based and the conventional CSA-based methodologies should be distinguished for evaluating relationships between muscle fiber characteristics and pork loin quality, although both methods have a clear advantage in predicting pork loin quality.

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