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ARTICLE

Effects of Morphological Characteristics of Muscle Fibers on Porcine Growth Performance and Pork Quality

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Abstract

The aim of this study was to investigate the effects of morphological characteristics of porcine muscle fibers on growth performance, muscle fiber characteristics, and pork quality taken from the *longissimus dorsi* muscle. A total of 239 crossbred pigs (164 castrated males and 75 females) were used in this study. Experimental pigs were categorized by the total number of muscle fiber (TNF: High and Low) and cross sectional area of muscle fiber (CSAF: Large, Middle, and Small). Their combinations were classified into six groups (High-Large, HL; High-Middle, HM; High-Small, HS; Low-Large, LL; Low-Middle, LM; Low-Small, LS). The TNF and CSAF were significantly ($p<0.05$) correlated with growth rate and carcass productivity, while the only of the type I number had no meaningful relationships excluding the correlation with loin area ($p<0.001$). The proportion of type I area was positively correlated with $pH_{45\,min}$ while the proportion of type IIB area was negatively correlated with $pH_{45\,min}$ and $pH_{24\,h}$ ($p<0.05$). Drip loss and protein denaturation had strong relationships with the proportion of type IIB number or area. The HL group exhibited the greatest growth performance. In addition, the HL group had significantly greater values in protein solubility than the other groups. In conclusion, this study suggest that high TNF combined to large CSAF improve the ultimate lean meat productivity and assure normal meat quality simultaneously with increased both proportion of number and area of type I, type IIA muscle fibers and lowered proportion of number and area of type IIB.

Keywords: muscle fiber morphology, total number of muscle fiber, cross sectional area of muscle fiber, growth performance, pork quality

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Introduction

Producing leaner and favorable quality pork while maintaining efficient and rapid production is the most important task in the present state of meat industries. According to several studies, the rapid production rate and lean meat production ability are closely related to numerical and morphological characteristic of muscle fibers. It is generally reported that lean meat productivity is related to the total number of muscle fibers (TNF) and the size of muscle fiber hypertrophy (Dwyer *et al.*, 1993; Fiedler *et al.*, 1999; Handel and Stickland, 1988; Henckel *et al.*, 1998; Larzul *et al.*, 1997; Rehfeldt *et al.*, 2000). Other studies have reported that rapid lean meat production is significantly associated with poor pork quality in some breeds and that the lean meat production ability is predominantly affected by the size of muscle fiber (Cameron, 1990; Cannon *et al.*, 1995). Moreover, the TNF is positively correlated with muscle mass and pork quality (Kim *et al.*, 2008; Rehfeldt *et al.*, 2000). However, the effect of cross sectional area of muscle fiber (CSAF) on muscle mass and meat quality remains controversial. First, there is a concern about the negative correlation between CSAF and lean meat contents in different birth weight piglets. Rehfeldt and Kuhn (2006) have demonstrated that pigs

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with lower birth weight and larger CSAF have lower muscle mass due to lower TNF with the same level of slaughter weight. Second, there is an inconsistency about the relationship between CSAF and meat quality. It has been reported that pork drip loss and carcass pH are not associated with size parameters of muscle fiber (Larzul *et al.*, 1997; Ryu and Kim, 2005). However, the relationships of muscle fiber number, size, and composition according to morphological characteristics of muscle fiber with growth performance and pork quality traits have not been clearly established yet. Therefore, the aim of this study was to determine the effects of TNF and CSAF on muscle fiber characteristics, growth performance, and pork quality.

Materials and Methods

Animal and muscle samples

A total of 239 crossbred [(Yorkshire × Landrace) × Duroc] pigs (164 castrated male and 75 female pigs) were used in this study. Pigs from the same farm were fed the same commercial diet in accordance with the National Research Council (1998). In this study, halothane gene genotyping was performed for all pigs using the method of Fujii *et al*. (1991). Pigs that were heterozygous for the halothane gene were used. All animals were clinically healthy. In order to evaluate growth performance, the age at 90 kg of body weight and body weights at 100 d were measured after birth. Pigs were slaughtered at 174.5±6.9 d of age during winter. The slaughter procedure was approved by the Ministry of Food, Agriculture, Forestry, and Fisheries of Korea. The slaughter plant employed electrical stunning, after which pigs were exsanguinated. At 45 min postmortem, *longissimus dorsi* (LD) muscles at the 8^{th} to 9^{th} *thoracic vertebrae* were taken. After chilling in a cold room at 4°C for 24 h, pork loins (the 10^{th} to the 13^{th} *thoracic vertebrae*) were taken for meat quality measurements. The mean value of the two measurements was used as the back-fat thickness. The loin-eye area was measured at the 10^{th} *thoracic vertebrae*.

Histochemical analysis

Within 45 min postmortem, 5 muscle samples were taken from the LD muscle at the 8^{th} *thoracic vertebrae* for histochemical analysis. These samples were cut into 0.5 × 0.5 × 1.0 cm pieces, promptly frozen in isopentane cooled by liquid nitrogen, and stored at -80ºC until analyses. Serial muscle sections (10 μm in thickness) were sliced from each sample with a cryostat microtom (CM 1850, Leica, Germany) at 20ºC. Myosin adenosine triphosphatase (ATP) activities were detected after acid (pH 4.7) pre-incubation (Brooke and Kaiser, 1970). These sections were preincubated at room temperature for 8 min in a the following buffer: 100 mM of potassium chloride in 100 mM sodium acetate, adjusted to pH 4.7 with acetic acid (Lind and Kernell, 1991). After the pre-incubation, the sections were subjected to the following steps: (1) washing with distilled water four times, (2) washing with 20 mM glycine buffer (pH 9.4) containing 20 mM $CaCl_2$ for 30 s, (3) incubation in freshly prepared medium (40 mM glycine buffer containing 20 mM $CaCl_2$ and 2.5 mM ATP disodium salt (pH 9.4)) at room temperature for 20 min, (4) washing with 1% $CaCl_2$ for 30 s three times, (5) washing with 2% cobalt chloride for 3 min, (6) washing with distilled water three times, (7) immersion in 1% yellow ammonium sulfide for 10 s, (8) washing with distilled water several times, and (9) mounting in glycerol jelly (20 g of gelatin, 2.4 g of phenolcrystals, 60 mL of glycerol, and 70 mL of distilled water). All histochemical samples were examined with an image analysis system. The operational system consisted of an optical microscope equipped with a charge-coupled device color camera (IK-642K, Toshiba, Japan) and a standard workstation computer to control the image analysis system (Image-Pro Plus, Media Cybernetics, Silver Springs, USA) for the calculation of fiber size, number, and fiber type composition. All portions of sections analyzed were free from tissue disruption or freeze damage. About 600 fibers per sample were evaluated. Muscle fiber number percentage was obtained based on the ratio of the number of each fiber type to the total number of fiber counted. Muscle fiber area percentage was the ratio of the mean of cross sectional area of each fiber type to the total measured fiber area. The mean of CSAF, diameter, and perimeter of the identified muscle fiber types were also measured.

Meat quality traits

Muscle pH was measured at 45 min ($pH_{45\ min}$) postmortem for the LD muscle using a portable pH meter (HM-17MX, Toadkk, Japan) on carcass. The muscle samples were then removed. After 24 h of chilling, the LD muscle was subjected to pH 24 h ($pH_{24\ h}$) measurement. Drip loss was measured by suspending muscle samples that were standardized for surface area in an inflated plastic bag at 4°C for 48 h (Honikel, 1998). After that, samples were taken from the bags, gently blotted dry, and weighed. Drip loss was expressed as the percentage of the initial sample weight. To measure filter-paper fluid uptake (FFU), filter-paper (Whatman #2, 42.5 mm in diameter) was pre-

weighed, placed on the surface of a sample to absorb fluids (< 2 s), and weighed again (Kauffman *et al.*, 1986). FFU was expressed as milligrams of exudate absorbed into the filter-paper. The color of the meat at the $8^{th}/9^{th}$ *thoracic vertebra* was measured with a chromameter (CR-300, Minolta Camera Co., Japan) at 24 h postmortem. Samples were placed on a table in a 4°C cold room for 30 min to expose their surfaces to air without any packaging (for bloom) prior to color measurement of the meat. CR-300 apparatus contained a pulsed xenon lamp in the measuring head (i.e., light source). It was calibrated against the calibration plate supplied by the manufacturer. Illuminant C and standard observer position of 2° were used. Only light that was reflected perpendicularly to the specimen surface was collected for color analysis using an optical-fiber cable. The average value of triplicate measurements was recorded. Results were expressed as C.I.E. Commission International de l'Eclairage (CIE) lightness (L^*), redness (a^*), and yellowness (b^*) values. To determine protein solubility, two extractions procedures were conducted. First, sarcoplasmic proteins were extracted from 1 g of powdered muscle in 10 ml of ice-cold 0.025 M potassium phosphate buffer (pH 7.2). Total protein was extracted from 1 g of powdered muscle in 20 mL of ice-cold 1.1 M potassium iodide in 0.1 M phosphate buffer (pH 7.2). Samples were homogenized on ice with a Polytron at the lowest setting. Samples were then incubated and then stored at shaker at 4°C overnight. After centrifugation at 1,500 *g* for 20 min, supernatant was taken and protein (sarcoplasmic and total protein) solubility of the supernatant was measured using Biuret method (Gornall *et al.*, 1949). Myofibrillar protein solubility was determined by calculation the difference between total protein solubility and sarcoplasmic protein solubility. Results of all measured traits are shown in supplementary Table 1.

Statistical analysis

Pearson correlation analysis was performed to characterize the relationships between muscle fiber characteristics and other performance traits using partial correlation coefficients. Cluster analysis was performed to classify TNF and CSAF using FASTCLUS procedure of SAS® software. Observations were allocated to groups based on the smallest Euclidean distance from the initial seeds in the cluster. Data were classified into two clusters according to TNF (High, n = 106; Low, n = 133). The two groups were further clustered based on CSAF (Large, n = 48; Middle, n = 94; Small, n = 97). Therefore, a total of 6 groups (High-Large, HL; High-Middle, HM; High-Small, HS; Low-Large, LL; Low-Middle, LM; Low-Small, LS) were obtained by combining TNF (H and L) and CSAF (L, M, and S). They were subjected to further association analysis with other performance traits. Generalized linear model analysis was performed to evaluate the significant

Table 1. Correlation coefficients (*r*) between muscle fiber characteristics and growth rate or carcass productivity traits in porcine *longissimus dorsi* muscle

	Carcass weight	Carcass yield	Loin area	Back-fat thickness	Average daily gain	Days at 90 kg body weight	Body weight in 100 days after birth
Muscle fiber number							
Total fiber number	0.256***	0.055	0.627***	0.143*	0.241***	-0.215**	0.123†
Type I number	0.088	0.120†	0.244***	0.059	0.046	-0.009	0.002
Type IIA number	0.289***	0.067	0.428***	0.221***	0.154*	-0.191**	0.162*
Type IIB number	0.196**	0.023	0.540***	0.094	0.219***	-0.193**	0.100
Proportion of muscle fiber number							
Proportion of type I number	-0.053	0.088	-0.098	-0.016	-0.091	0.123†	-0.054
Proportion of type IIA number	0.171**	0.016	0.112†	0.176**	0.026	-0.077	0.095
Proportion of type IIB number	-0.096	-0.073	-0.016	-0.125†	0.044	-0.023	-0.038
Cross sectional area of muscle fiber							
Mean area	0.434***	0.050	0.921***	0.260***	0.347***	-0.339***	0.259***
Type I area	0.299***	0.002	0.407***	0.190**	0.222**	-0.210**	0.089
Type IIA area	0.351***	0.002	0.548***	0.311***	0.332***	-0.305***	0.283***
Type IIB area	0.384***	0.020	0.884***	0.237***	0.305***	-0.299***	0.236***
Proportion of muscle fiber area							
Proportion of type I area	-0.114	-0.017	-0.060	-0.101	-0.074	0.069	-0.058
Proportion of type IIA area	0.156*	-0.135†	0.134†	0.217**	0.178*	-0.157*	0.168*
Proportion of type IIB area	-0.044	0.115	-0.063	-0.099	-0.088	0.075	-0.090

†$p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

effect ($p<0.05$) of TNF, CSAF, and the interaction between TNF and CSAF. The model included fixed effect of different sexes. Live weight and start weight were included as covariates in the analysis of morphology of muscle fiber carcass weight, back-fat thickness, loin area, daily gain, days at 90 kg body weight, and body weight in 100 d after birth. When significant differences ($p<0.05$) were detected, the mean values were separated by probability difference (PDIFF) option at a predetermined probability rate of 5%. Results were presented as least-square means (LSMs) with standard errors of LSMs for groups.

Results and Discussion

Relationship between muscle fiber characteristics and growth or meat productivity

The correlation coefficients among muscle fiber characteristics and lean meat production ability traits are summarized in Table 1. Almost all muscle fiber characteristics were highly and significantly ($p<0.05$) correlated with growth rate and carcass production ability. Only type I fiber number had no meaningful relationship with growth rate or production ability. However, type I fiber number was significantly ($p<0.001$) correlated with loin area. The lean meat productivity represented by loin area and back-fat thickness were highly and positively correlated with both TNF and CSAF characteristics. Several previous research studies have reported a positive correlation between TNF and lean meat production (Handel and Stickland, 1988; Henckel *et al.*, 1997; Kim *et al.*, 2008). In this study, both TNF and CSAF characteristics were positively correlated with carcass production abilities. In fact, carcass weight, average daily gain, and days at 90 kg body weight were not only significantly correlated with the total number of fibers including IIA and IIB, but also significantly ($p<0.01$) correlated with all cross sectional area of muscle fiber. However, carcass yield had any relationships with muscle fiber characteristics. The major component of muscle is muscle fiber. It is generally accepted that muscle fiber hyperplasia (an increase in fiber number) and hypertrophy (an increase in fiber size) are positively correlated with growth performance and lean meat productivity (Rehfeldt *et al.*, 2008; Ryu *et al.*, 2008). In addition to hypertrophic muscle growth at postnatal stage, ultimate muscle mass can be determined by muscle fiber hyperplasia which is completed at birth (Dwyer *et al.*, 1993). Therefore, CSAF of all muscle types at the same age might have been strongly correlated with growth performance in this study.

Relationship between muscle fiber characteristics and meat quality

The correlation coefficients of muscle fiber characteristics and meat quality traits are summarized in Table 2. When the results of correlations with growth and carcass productivity traits were compared, the relationships between muscle fiber characteristics and meat quality traits were not frequently significant. However, the proportions of muscle fiber number and area were significantly correlated with meat quality traits. Especially, the proportion of type I area was positively correlated with $pH_{45\ min}$ and the proportion of type IIB area was negatively correlated with $pH_{45\ min}$ and $pH_{24\ h}$ (all $p<0.05$). Both muscle fiber number and the proportion of type IIA area were significantly ($p<0.001$) correlated with $pH_{24\ h}$. Drip loss had a strong and significant ($p<0.001$) relationship with the proportion of type IIB number and area. These significant correlation coefficients between fiber type compositions and meat quality characteristics are consistent with results of many previous studies (Choe *et al.*, 2008; Choi *et al.*, 2007; Kauffman *et al.*, 1998; Larzul *et al.*, 1997; Rosenvold *et al.*, 2001; Ryu and Kim, 2005). The conventional selection for improving meat productivity was strongly correlated with muscle fiber hypertrophy. Consequently, meat animals, especially porcine, have been selected for growth rate and lean tissue has caused changes in muscle fiber type compositions toward higher proportions of type IIB muscle fibers (Karlsson *et al.*, 1999). In skeletal muscle of domestic pigs, type IIB muscle fibers are usually glycolytic. Therefore, they contain more glycogen and need less oxygen than type I muscle fibers for energy metabolism (Ruusunen *et al.*, 1996). Our results of this study were also in agreement with these observations.

Protein solubility has been used as a marker for protein denaturation. The condition of pH and temperature that muscle proteins are exposed to during early postmortem play key roles in determining meat quality (Bowker *et al.*, 2005). It has been reported that paler muscle and/or meat due to fast glycolyzation in early postmortem periods has a higher degree of protein (both sarcoplasmic and myofibrillar) denaturation as defined by protein solubility than muscle with a normal rate of postmortem pH decline (Joo *et al.*, 1999; Sayre and Briskey, 1963; Warner *et al.*, 1997). In this study, the number and proportion of type IIB fibers showed significantly ($p<0.05$) negative correlation with protein solubility while the proportion of type IIB fiber number exhibited a positive correlation with L^* ($p<0.01$). Muscle fibers can be classified by metabolic characteristics as type I (slow twitch, oxidative), type IIA (fast twitch,

Table 2. Correlation coefficients (*r*) between muscle fiber characteristics and meat quality traits in porcine *longissimus dorsi* muscle

	$pH_{45\ min}$	$pH_{24\ h}$	Drip loss	FFU	*L**	*a**	*b**	Sarcoplasmic protein solubility	Myofibrillar protein solubility	Total protein solubility
Muscle fiber number										
Total fiber number	0.117	-0.025	0.114	0.144*	0.135†	-0.256***	0.001	-0.202**	-0.063	-0.060
Type I number	0.311***	0.001	-0.160*	0.018	0.048	0.021	-0.050	-0.129*	0.145*	0.105
Type IIA number	0.115	0.211**	-0.296***	-0.008	-0.068	0.189*	-0.089	0.183**	0.213***	0.224***
Type IIB number	0.044	-0.079	0.226**	0.153*	0.157†	-0.328***	0.035	-0.239***	-0.144*	-0.136*
Proportion of muscle fiber number										
Proportion of type I number	0.221***	0.017	-0.116†	-0.056	-0.072	0.127†	-0.019	-0.017	0.174**	0.137*
Proportion of type IIA number	-0.081	0.134†	-0.346***	-0.083	-0.189**	0.431***	-0.022	0.291***	0.243***	0.257***
Proportion of type IIB number	-0.077	-0.116†	0.350***	0.104	0.205**	-0.421***	0.036	-0.216***	-0.307***	-0.292***
Cross sectional area of muscle fiber										
Mean area	-0.195*	0.045	-0.069	0.013	0.090	0.146†	-0.105	0.275***	0.284***	0.236***
Type I area	-0.193*	0.043	-0.018	-0.008	-0.045	0.079	-0.007	0.199**	-0.016	-0.004
Type IIA area	-0.159*	0.030	-0.075	0.005	0.075	0.063	-0.072	0.217***	0.235***	0.204**
Type IIB area	-0.146†	0.079	-0.133†	-0.009	0.061	0.199*	-0.116	0.281***	0.325***	0.276***
Proportion of muscle fiber area										
Proportion of type I area	0.224**	-0.036	-0.192*	-0.056	-0.077	0.128	0.022	-0.048	0.039	0.020
Proportion of type IIA area	0.041	0.254***	-0.332***	-0.082	-0.140†	0.322***	-0.090	0.266***	0.236***	0.250***
Proportion of type IIB area	-0.172*	-0.166*	0.368***	0.097	0.153*	-0.320***	0.053	-0.169**	-0.204**	-0.201**

FFU, Filter-paper fluid uptake; *L**, Lightness; *a**, Redness; *b**, Yellowness.
†$p<0.1$, *$p<0.05$, **$p<0.01$, ***$p<0.001$.

oxidative-glycolytic), and type IIB (fast twitch, glycolytic). Type IIA fibers tend to be intermediate fibers (i.e., fast oxidative-glycolytic fibers) (Brooke and Kaiser, 1970; Klont *et al.*, 1998). In general, glycolysis and onset of rigor mortis are faster in white muscles than in red muscles. Type IIA and IIB fibers mainly carry out the glycolytic pathway. Their metabolism contributes to a fast pH decline and extended pH fall. These fiber type compositions of porcine muscles are related to the occurrence of abnormal condition such as PSE (Candek-Potokar *et al.*, 1999). On the other hand, Lefaucheur (2010) has revealed that pigs as carriers of Rendement Napole (RN) gene only have increased cross sectional area of fast-twitch oxidative-glycolytic fibers. Moreover, RN carrier pigs have higher levels of glycogen and the expression of AMPK signaling genes in *longissimus muscle* compared to wild type pigs (Park *et al.*, 2009). These results suggest that glycolytic muscles of mutated RN pigs might rely more on fatty acid metabolism than those in wild pigs. Lebret *et al.* (1999) have also reported that the *longissimus muscles* of RN carrier pigs have higher oxidative metabolism, muscle fiber size, and relative area of type IIA such as oxidative-glycolytic fibers but lower glycolytic metabolism than those of wild pigs. In this study, the number, area, and proportions of type IIA fibers were positively correlated with protein solubility ($p<0.01$). Type IIA fiber number and the proportion of type IIB area were positively correlated with $pH_{24\ h}$ but negatively correlated with drip loss. These results were in agreement with the results of a previous study showing that postmortem metabolic rate is correlated with numerical abundance of a given fiber type (Ryu *et al.*, 2004). Although this study determined the RN genotypes of experimental pigs, further study is needed to determine inconstancy.

Effects of TNF and CSAF groups on muscle fiber characteristics

The effects of TNF and CSAF groups on muscle fiber characteristics of pigs are summarized in Table 3. Regarding the total number of fibers, the HS group exhibited the highest number among all groups, whereas the LL group showed the lowest number. The effects of TNA and

Table 3. Effects of groups categorized by total number and cross sectional area of muscle fiber on muscle fiber characteristics

TNF	High			Low			Levels of significance		
CSAF	Large	Middle	Small	Large	Middle	Small			
Group	HL (n=9)	HM (n=33)	HS (n=64)	LL (n=39)	LM (n=61)	LS (n=33)	TNF	CSAF	TNF× CSAF
Muscle fiber number (×1000)									
Total fiber number	1203^{b} (46.1)^{A}	1303^{b} (24.3)	1381^{a} (17.3)	900.3^{d} (23.2)	984.9^{c} (18.4)	1041^{c} (24.5)	***	***	NS
Type I number	129^{a} (13.1)	117^{a} (6.9)	108^{ab} (4.9)	91^{c} (6.6)	96^{bc} (5.2)	94^{bc} (7.0)	***	NS	NS
Type IIA number	173^{a} (16.6)	143^{ab} (8.8)	128^{bc} (6.2)	104^{d} (8.4)	114^{cd} (6.6)	98^{d} (8.8)	***	*	NS
Type IIB number	905^{c} (45.3)	1043^{b} (23.9)	1146^{a} (17.0)	705^{c} (22.8)	775^{d} (18.1)	849^{c} (24.0)	***	***	NS
Muscle fiber number percentage (%)									
Type I fiber	10.58^{a} (1.29)	9.03^{ab} (0.68)	7.90^{b} (0.48)	10.62^{a} (0.65)	9.84^{ab} (0.52)	9.24^{ab} (0.68)	NS	*	NS
Type IIA fiber	14.45^{a} (1.45)	10.78^{bc} (0.77)	9.06^{c} (0.55)	11.51^{ab} (0.73)	11.58^{ab} (0.58)	9.28^{c} (0.77)	NS	***	NS
Type IIB fiber	75.30^{d} (1.81)	80.23^{bc} (0.95)	83.05^{a} (0.68)	77.90^{cd} (0.91)	78.62^{cd} (0.72)	81.47^{ab} (0.96)	NS	***	NS
Cross sectional area of muscle fiber (um^{2})									
Mean area	5083^{b} (113.8)	4314^{c} (60.2)	3520^{e} (42.8)	5390^{a} (57.4)	4371^{c} (45.5)	3701^{d} (60.4)	**	***	NS
Type I fiber area	3594^{a} (191.4)	3176^{ab} (101.2)	2678^{c} (71.9)	3587^{a} (96.5)	3143^{b} (76.5)	2838^{c} (101.6)	NS	***	NS
Type IIA fiber area	3102^{a} (169.5)	2718^{b} (89.6)	2111^{c} (63.7)	3237^{a} (85.4)	2625^{b} (67.7)	2222^{c} (89.9)	NS	***	NS
Type IIB fiber area	5709^{a} (155.6)	4658^{b} (82.2)	3758^{d} (58.4)	6000^{a} (78.4)	4798^{b} (62.1)	3975^{c} (82.6)	**	***	NS
Muscle fiber area percentage (%)									
Type I fiber	7.45 (0.86)	6.58 (0.45)	5.95 (0.32)	6.90 (0.43)	6.96 (0.34)	6.90 (0.46)	NS	NS	NS
Type IIA fiber	8.62^{a} (0.99)	6.84^{ab} (0.52)	5.46^{c} (0.37)	6.88^{ab} (0.50)	6.90^{ab} (0.40)	5.69^{b} (0.53)	NS	***	NS
Type IIB fiber	83.92^{c} (1.30)	86.58^{bc} (0.69)	88.59^{a} (0.49)	86.22^{bc} (0.66)	86.14^{bc} (0.52)	87.41^{ab} (0.69)	NS	***	NS

TNF, total number of muscle fiber; CSAF, cross sectional area of muscle fiber; HL, high TNF and large CSAF; HM, high TNF and middle CSAF; HS, high TNF and small CSAF; LL, low TNF and large CSAF; LM, low TNF and middle; LS, low TNF and small CSAF.
NS, not significant; *p<0.05, **p<0.01, ***p<0.001.
[a-e]Least-square means with different superscripts in the same row are significantly different (p<0.05).
[A]Standard error of least-square means.

CSAF on muscle fiber characteristics of pigs were highly significant (p<0.001). Moreover, the effects of TNF on the number each fiber type including type I, IIA, and IIB were highly significant (p<0.001). The levels of significances for the effects of CSAF on the number of type IIA and IIB (p<0.05 and p<0.001, respectively) effects were moderate or high, although the effect of CSAF on the number of type I fiber was insignificant. There was no meaningful effect in the interactions between TNF and CASF. The HL group had a relatively high number of type I fiber but a relatively low number of type IIB fiber compared to other groups. The effects of CSAF on all area characteristics represented by cross sectional area were highly significant (p<0.001). There was no meaningful effect for interactions between TNF and CSAF. However, the effects of TNF on type I and IIA fiber area were not statistically significant, although the effects of TNF on the mean of CSAF and type IIB fiber area were significant. Bigger CSAF in type I, type IIA, and type IIB area were found in HL and LL groups (categorized into large CSAF) compared to those in middle or small CSAF groups. Muscle fiber type compositions in area characteristics were not significantly associated with TNF groups or interactions between TNF and CSAF. However, the

effects of CSAF on type IIA and IIB compositions were significant ($p<0.001$).

In skeletal muscle of domestic pig, the growth rate of type IIB fibers is about two times faster than that of type I or IIA fibers during the growth period. Therefore, type IIB fibers are exclusively larger than type I or IIA fibers at the same age (Ruusunen and Puolanne, 2004). As expected, our results showed type IIB fibers had greater size than type I and type IIA fibers. In correlations among the mean of cross sectional area and muscle fiber types, the greatest correlation coefficient was found between the mean of cross sectional area and type IIB area (Supplementary Table 2). Especially, the HL group exhibited the greatest proportion of fiber I number and the proportion of type IIA area among all groups.

Effects of TNF and CSAF groups on growth performance

Results of growth performance and carcass traits of LSMs categorized according to TNF and CSAF are shown in Table 4. For carcass weight, there were significant differences in both TNF and CSAF groups ($p<0.001$). High TNF large CSAF group (HL), and high TNF middle CSAF group (HM) showed high values of carcass weight ($p<0.001$). In carcass yield, there were significant differences among CSAF groups. However, there was no significant difference among TNF groups. On the other hand, no interaction between TNF and CSAF was observed through carcass weight and yield. For loin eye area, significant interaction between TNF and CSAF was found. The HL group had the greatest loin eye area, while the LS group had the smallest value ($p<0.05$). In the case of back-fat thickness, the LS group had the thinnest ($p<0.05$) value among all groups. At a constant body weight, a negative phenotypic correlation between TNF and CSAF has been reported (Rehfeldt *et al.*, 2000), while a positive correlation between TNF and lean tissue growth has been commonly reported (Dwyer *et al.*, 1993; Handel and Stickland, 1988; Henckel *et al.*, 1997). On the other hand, Lefaucheur (2010) has suggested that a strong positive correlation between CSAF and muscle development is expected at a constant TNF. Lefaucheur (2010) has also suggested that one should first take TNF into account before studying any relationships between muscle development and CSAF. A positive relationship between CSAF and lean meat productivity within each TNF group has also been reported by Lefaucheur (2010). The results of our current study were in agreement with these results. Results of partial correlation coefficients are shown in Table 3. Daily gain, days at 90 kg of body weight, and body weight in

Table 4. Effects of groups categorized by total number and cross sectional area of muscle fiber on carcass and lean meat productivity traits

TNF	High			Low			Levels of significance		
CSAF	Large	Middle	Small	Large	Middle	Small			
Group	HL (n=9)	HM (n=33)	HS (n=64)	LL (n=39)	LM (n=61)	LS (n=33)	TNF	CSAF	TNF× CSAF
Carcass weight (kg)	88.41^{a} (3.23)^{A}	86.54^{a} (1.70)	79.88^{bc} (1.21)	82.75^{ab} (1.63)	77.86^{c} (1.29)	71.66^{d} (1.71)	***	***	NS
Carcass yield (%)	76.97^{a} (1.09)	74.83^{ab} (0.58)	73.89^{b} (0.41)	74.63^{ab} (0.55)	74.12^{b} (0.44)	74.06^{b} (0.58)	†	*	NS
Loin area (cm^2)	61.69^{a} (1.84)	56.03^{b} (0.97)	48.09^{c} (0.69)	47.86^{c} (0.93)	43.03^{d} (0.74)	38.97^{e} (0.98)	***	***	*
Back-fat thickness (mm)	17.24^{ab} (1.87)	18.13^{a} (0.99)	16.21^{ab} (0.70)	16.13^{ab} (0.94)	14.87^{b} (0.75)	11.82^{c} (0.99)	**	**	NS
Daily gain (g/day)	611.5^{b} (22.94)	650.4^{a} (12.12)	616.4^{b} (8.62)	622.5^{ab} (11.56)	599.39^{b} (9.16)	552.4^{c} (12.17)	**	***	*
Days at 90 kg body weight (kg)	154.5^{bc} (4.41)	145.9^{c} (2.58)	151.2^{bc} (1.72)	148.1^{c} (2.57)	154.8^{b} (1.92)	164.7^{a} (2.35)	*	**	**
Body weight in 100 days after birth (kg)	45.16^{bc} (1.87)	47.22^{ab} (1.11)	47.63^{ab} (0.75)	49.86^{a} (1.11)	46.88^{b} (0.83)	43.63^{c} (1.02)	NS	NS	**
Plant age (d)	174.59 (2.55)	174.6 (1.39)	172.7 (0.92)	173.1 (1.39)	175.6 (1.03)	173.7 (1.27)	NS	NS	NS

TNF, total number of muscle fiber; CSAF, cross sectional area of muscle fiber; HL, high TNF and large CSAF; HM, high TNF and middle CSAF; HS, high TNF and small CSAF; LL, low TNF and large CSAF; LM, low TNF and middle; LS, low TNF and small CSAF.
NS, not significant; †$p<0.1$, *$p<0.05$, **$p<0.01$, ***$p<0.001$.
[a-e]Least-square means with different superscripts in the same row are significantly different ($p<0.05$).
[A]Standard error of least-square means.

100 d after birth directly were used to represent growth rate. In daily gain, there were significant differences in the interaction between TNF and CSAF ($p<0.05$). The HM group showed the highest value among all groups. Pigs with low TNF and small CSAF (LS) grew more slowly than pigs in other groups. However, there was no significant difference in growth among HL, HS, and LM groups. In the case of days to 90 kg of body weight, similar tendency to daily gain was observed ($p<0.05$). HM and LL pigs exhibited the fastest growth rate until 90 kg body weight, while LS pigs needed more days to reach 90 kg of body weight compared to other groups. From gestation to 100 d, HM, HS, and LL pigs showed the heaviest weight among all groups with significant effect from the TNF×CSAF interaction. The body weight at 100 d after birth in LL was obviously higher compared to that in HL or LS. According to a previous study (Rehfeldt and Kuhn, 2006), when the number of muscle fibers is high, fibers generally grow more slowly in pigs during postnatal development. In the present work, results for HL were in agreement with results of the previous study (Rehfeldt and Kuhn, 2006). LS also showed slow growth rate during postnatal development. This result indicates that low TNF and small CSAF might not only decrease lean meat productivity, but also delay early postnatal development. In summary, from the viewpoint of ultimate lean meat production, HL group exhibited the greatest growth performance, including carcass weight, carcass yield, and loin area at constant plant age, even though LL groups showed shorter days for 90 kg body weight and heavier weight at 100 d after birth than other groups.

Effects of TNF and CSAF on meat quality traits

The effects of TNF and CSAF on meat quality traits are shown in Table 5. Significant effects of the interactions between TNF and CSAF on $pH_{45\ min}$ and redness ($p<0.01$ and $p<0.05$, respectively) were found. The $pH_{45\ min}$ values of HL and LS pigs were higher than those of HM and LL pigs. For redness, the LS group had the lowest *a** value. Some studies have reported that pH decline during post-

Table 5. Effects of groups categorized by total number and cross sectional area of muscle fiber on meat quality traits

TNF	High			Low			Levels of significance		
CSAF	Large	Middle	Small	Large	Middle	Small			
Group	HL (n=9)	HM (n=33)	HS (n=64)	LL (n=39)	LM (n=61)	LS (n=33)	TNF	CSAF	TNF×CSAF
Postmortem metabolic traits									
$pH_{45\ min}$	6.16^{a} (0.08)^{A}	6.01^{b} (0.05)	6.09^{ab} (0.03)	5.91^{c} (0.04)	6.10^{ab} (0.03)	6.16^{a} (0.04)	NS	NS	**
$pH_{24\ h}$	5.56 (0.04)	5.53 (0.02)	5.53 (0.02)	5.58 (0.02)	5.55 (0.02)	5.55 (0.03)	NS	NS	NS
Drip loss (%)	4.96 (0.73)	5.40 (0.40)	5.47 (0.30)	5.24 (0.39)	4.60 (0.32)	5.95 (0.41)	NS	NS	NS
FFU (mg)	68.99 (13.05)	59.79 (6.90)	55.12 (4.90)	60.63 (6.58)	47.49 (5.21)	60.78 (6.93)	NS	NS	NS
*L**	49.41 (0.76)	48.16 (0.41)	48.06 (0.30)	47.79 (0.39)	47.64 (0.31)	48.60 (0.41)	NS	NS	NS
*a**	6.46^{abc} (0.42)	6.33^{bc} (0.22)	6.24^{bc} (0.16)	6.71^{ab} (0.21)	6.91^{a} (0.17)	5.77^{c} (0.22)	NS	**	*
*b**	2.77 (0.36)	3.42 (0.19)	3.52 (0.13)	3.28 (0.18)	3.41 (0.14)	3.15 (0.19)	NS	NS	NS?
Protein Solubility (mg/g)									
Sarcoplasmic protein	66.17^{ab} (2.22)	67.89^{ab} (1.19)	65.72^{b} (0.84)	70.43^{a} (1.12)	68.45^{a} (0.91)	64.87^{b} (1.18)	NS	*	NS
Myofibrillar protein	164.29^{a} (7.41)	132.56^{b} (3.97)	121.15^{c} (2.78)	133.50^{b} (3.74)	128.63^{bc} (3.02)	123.93^{bc} (3.93)	*	***	**
Total protein	237.04^{a} (10.32)	201.28^{b} (4.89)	187.70^{c} (3.43)	200.92^{b} (4.61)	197.82^{b} (3.72)	189.21^{bc} (4.84)	**	***	**

TNF, total number of muscle fiber; CSAF, cross sectional area of muscle fiber; HL, high TNF and large CSAF; HM, high TNF and middle CSAF; HS, high TNF and small CSAF; LL, low TNF and large CSAF; LM, low TNF and middle; LS, low TNF and small CSAF; *L**, Lightness; *a**, Redness; *b**, Yellowness.

NS, not significant; *$p<0.05$, **$p<0.01$, ***$p<0.001$.

[a-c]Least-square means with different superscripts in the same row are significantly different ($p<0.05$).

[A]Standard error of least-square means.

mortem periods can results in increased lightness of the meat (Joo *et al.*, 1999). In this study, there was no significant difference in lightness, although the difference was observed in $pH_{45\ min}$. In addition, drip loss and lightness were not associated with CSAF in this study, in agreement with the report of Candek-Potokar *et al.* (1999). Increased CSAF is generally considered as detrimental to pork quality such as water holding capacity and tenderness (Rehfeldt *et al.*, 2000). No clear relationship between CSAF and muscle $pH_{45\ min}$ was observed in this study, in agreement with the study of Larzul *et al.* (1997). In pigs, it has been generally reported that TNF has a positive correlation with meat quality (Rehfeldt *et al.*, 2000; Ryu and Kim, 2005). TNF is positively correlated with muscle $pH_{45\ min}$ and negatively correlated with drip loss (Fiedler *et al.*, 1994). In this study, type I fiber number, proportion of type I fiber, and proportion of fiber I area were positively correlated with $pH_{45\ min}$ (Table 2). In addition, drip loss was positively correlated with type IIB number, proportion of type IIB number, and proportion of type IIB area. In the case of CSAF, some studies have suggested that increasing muscle fiber size can negatively influence meat quality, particularly drip loss (Rehfeldt *et al.*, 2000; Seideman *et al.*, 1986). However, the association between CSAF and drip loss or muscle pH is still controversial (Larzul *et al.*, 1997; Ryu and Kim, 2005). In present study, although the $pH_{45\ min}$ of the HL group was not significantly different from that of LS, the $pH_{45\ min}$ of the LL group was the lowest among all groups. These results suggest that lager CSAF with higher TNF might guarantee normal pH decline while larger CSAF with lower TNF might induce rapid pH decline during early postmortem.

Color and water holding capacity of meat are related to the extent of protein denaturation, lateral shrinkage of myofibrils, and subsequent increase in light scattering (Huff-Lonergan and Lonergan, 2005; Offer, 1991). It has been reported that sarcoplasmic protein denaturation is highly correlated to the paleness of meat surface (Ryu and Kim, 2005). In this study, the HL group had significantly greater values in myofibrillar and total protein solubility than other groups, whereas the HS group exhibited the lowest value in sarcoplasmic, myofibrillar, and total protein solubility ($p<0.05$).

Taken together, our results showed that TNF and CSAF were positively correlated with lean meat productivity and growth performance. On the other hand, larger fiber size with low total number of muscle fiber induced the decrement of meat acidity during early postmortem. As mentioned above, the relationships of CSAF with meat quality and quantity are still controversial. Despite disputes, the present results revealed that higher TNF with larger CSAF did not significantly deteriorate meat quality. In fact, the HL group showed excellent protein solubility. Lefaucheur (2010) has suggested that one of the ways to improve lean meat productivity without negative changes of meat quality might be the combination of high TNF with moderate CSAF. It has been reported that a high TNF combined with a low percentage of type IIB fibers which are positively correlated with CSAF would guarantee both lean meat productivity and meat quality in pigs (Candek-Potokar, *et al.*, 1999; Kim, *et al.*, 2008; Larzul, *et al.*, 1997; Ryu, *et al.*, 2006).

In conclusion, our study suggest that high TNF combined with large CSAF can improve the ultimate lean meat productivity and assure normal meat quality simultaneously with increased proportion of number and area of type I, type IIA muscle fibers, and lower proportions of the number and area of type IIB.

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