

Relationships between Pork Quality Traits and Growth Factor Concentrations in Serum and *Longissimus dorsi* Muscle before and at Slaughter in Female Market Pigs

Min Ho Kim^{1,2}, Moon Sung Kang¹, Duck Min Ha³, Yong Ko¹ and C. Young Lee^{3*}

¹Division of Biotechnology, College of Life Sciences and Biotechnology, Korea University, Seoul 136-701, Korea, ²Eulji Med-Bio Research Institute, Eulji University, Seoul 139-872, Korea, ³Regional Animal Industry Center, Gyeongnam National University of Science and Technology, Jinju 660-758, Korea

ABSTRACT

The present study was conducted to test a hypothesis that pork quality traits would be influenced by the systemic and/or local bioavailability of insulin-like growth factor-I (IGF-I), transforming growth factor- β 1 (TGF- β 1), or epidermal growth factor (EGF) before or at slaughter. To this end, 60 cross-bred female market pigs weighing approximately 110 kg were slaughtered, after which *Longissimus dorsi* muscle (LM) samples taken at slaughter (D 0) and blood samples taken at D -7 and D 0 were analyzed. The 60 carcasses rendered 36 RFN (reddish-pink, firm, and non-exudative), 16 RSE (reddish-pink, soft, and exudative), and 6 PSE (pale, soft, and exudative); 2 DFD (dark, firm, and dry) also were found but were excluded in subsequent experiments. The L* and drip loss were greater in PSE vs. RFN and RSE and in PSE and RSE vs. RFN, respectively, as they should ($P < 0.05$). The pH_{45min} was less in PSE vs. RFN ($P < 0.05$); pH_{24h} tended to be less in the former ($P = 0.09$). The LM IGF-I and TGF- β 1 as well as serum EGF concentrations were less in PSE than in RFN. None of the other LM and serum concentrations of the three growth factors differed across the three pork quality categories. The LM IGF-I and TGF- β 1 concentrations and serum EGF concentration at D 0 were negatively correlated with drip loss [$r = -0.36$ ($P < 0.01$), -0.44 ($P < 0.01$), and -0.32 ($P < 0.05$), respectively]. However, none of the serum and LM growth factor variables was correlated with L* or a* (redness) of LM. Taken together, results suggest that locally expressed IGF-I and TGF- β 1 and blood-borne EGF may have a beneficial effect on *postmortem* water holding capacity of the muscle and that pork quality traits could be predicted to some extent from concentrations of IGF-I and TGF- β 1 in muscle and EGF in serum at slaughter.

(Key words : Pig, Meat Quality, IGF-I, TGF- β , EGF)

INTRODUCTION

Skeletal muscle growth and development is regulated by multiple hormones and growth factors, of which insulin-like growth factor (IGF) appears to be a key regulator (Clemmons, 2009; Duan et al., 2010). IGF-I promotes whole body growth including accretion of muscle mass not only by stimulating myogenesis and protein synthesis but also by inhibiting protein catabolism (Douglas et al., 1991; Koea et al., 1992a,b Fiorotto et al., 2003). IGF-II, however, appears not to have such an effect in postnatal animals although both IGFs are equipotent fetal growth stimulators and also myogenic regulators *in vitro* (Doumit et al., 1993 Jones and Clemmons, 1995). In contrast to IGFs, transforming-growth factor- β (TGF- β) family peptides suppress myogenesis (McCroskery

et al., 2003; Dayton and White, 2008 Kollias and McDermott, 2008). Epidermal growth factor (EGF), which stimulates proliferation and protein synthesis of myogenic cells usually in synergy with IGF *in vitro* (Blachowski et al., 1993 Mau et al., 2008), is known to suppress somatic growth *in vivo* (Chernausek et al., 1991; Chan and Wong, 2000; Xian, 2007). Besides these, several other regulatory peptides including fibroblast growth factor and platelet-derived growth factor are known to be involved in regulation of proliferation and differentiation of myogenic cell lineages (Florini et al., 1991; Doumit et al., 1993).

Pork quality is commonly classified into normal RFN (reddish-pink, firm, and non-exudative) and three abnormal categories, i.e. RSE (reddish-pink, soft, and exudative), PSE (pale, soft, and exudative) and DFD (dark, firm, and dry),

* Corresponding author : C. Young Lee, Regional Animal Industry Center, Gyeongnam National University of Science and Technology, Jinju 660-758, Korea. Tel: +82 55-751-3285, Fax: +82 55-753-4422, E-mail: cylee@gntech.ac.kr

according to the color, drip loss, and pH of the muscle (Warner et al., 1997). Ryu and Kim (2006) have reported that PSE and RSE had lower percentages of type IIa ('intermediate') muscle fibers than RFN and DFD. Furthermore, Lynch et al. (2001) have reported that IGF-I infusion in mice resulted in an increase in proportion of the type IIa or IIa and IIb (fast-glycolytic) fibers depending on the muscle and a decrease in the type I (slow-oxidative) fibers. In the transgenic mouse model, however, only type IIb fiber expression was up-regulated by transgenic IGF-I (Fiorotto et al., 2003). These results suggest that aforementioned growth factors could influence the pork quality trait through their effects on muscle cells. On the contrary to this scenario, Ryu et al. (2007) found minimal correlations between pork quality traits and serum concentrations of IGF, EGF, or TGF- β at day -7 from slaughter. These workers, however, did not investigate the relationship of the growth factor concentration to the pork quality category and also did not measure the growth factor contents in muscle or serum at slaughter. The present study therefore began with a hypothesis that concentrations of these growth factors in serum and/or muscle at slaughter should be reflected into the pork quality trait and accordingly the pork quality category as well.

MATERIALS AND METHODS

1. Animals and slaughtering

Sixty 150-day-old cross-bred finishing gilts which had been raised in a commercial farm were selected on day -7 from slaughter and at the same time blood samples from these animals were collected via jugular venipuncture. The animals were slaughtered by electrical stunning at a local abattoir following a standard procedure under the supervision of Korea Institute for Animal Products Quality Evaluation. Blood samples were taken again at bloodletting; carcass weight and backfat thickness were measured after evisceration. Serum was collected following centrifugation of the blood sample and aliquots were stored at -70°C until used. All the animal handling protocols followed the guideline released by the Ministry of Food, Agriculture, Forestry, and Fisheries of Korea.

2. Measurements of meat quality traits

For the measurement of growth factor concentrations in the *Longissimus dorsi* muscle (LM), approximately 100-g LM (loin) sample was taken at the loin-Boston Butt cut upon arrival of the carcass at the 4°C -chilling room. The LM sample was immediately frozen in liquid nitrogen and subsequently stored frozen at -70°C until used. The 45-min and 24-h *postmortem* pH, muscle color, and 48-h drip loss of LM were measured in the chilling room using a spear-type electrode (Model 290A, Orion Research Inc., Atlanta, GA, USA), by the Commission International de l'Eclairage (CIE, 1978) standard, and by the suspension method (Honikel et al., 1986), respectively, as described previously (Lee et al., 2002; Ryu et al., 2007).

The four pork quality categories (Warner et al., 1997) were defined as below according to the lightness [CIE (1978) L^*] at 24 h *postmortem* and the 48-h drip loss.

RFN (reddish-pink, firm, and non-exudative): drip loss $\leq 5.0\%$ and $L^* \leq 49$

RSE (reddish-pink, soft, and exudative): drip loss $> 5.0\%$ and $L^* \leq 49$

PSE (pale, soft, and exudative): drip loss $> 5.0\%$ and $L^* > 49$

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

3. Measurements of growth factor concentrations

After thawing the frozen LM sample, 1-g tissue was homogenized in 5-ml pre-chilled RIPA lysis buffer (Burr et al., 1980) supplemented with protease inhibitors (100 mM PMSF and 1.0 mg aprotinin/ml in 50 mM Tris, pH 8.0, containing 150 mM NaCl, 1% Triton X-100, 0.5% sodium deoxycholate, and 0.1% SDS). The homogenate was incubated at 4°C for 30 min, centrifuged at $10,000 \times g$ for 15 min at 4°C , and the supernatant was saved. The pellet was re-extracted with 5-ml lysis buffer and the supernatant after centrifugation was combined with the first supernatant, after which aliquots were lyophilized and stored at -70°C . At the time of each growth factor assay, the lyophilized aliquot was reconstituted with the corresponding assay buffer.

Prior to IGF-I RIA, IGF-binding proteins of the sample, which interfere with the immunoreaction between IGF and its antibodies in RIA, were removed by the acid-ethanol extraction method (Daughaday et al., 1980). IGF-I concentration of the acid-ethanol extract was determined by the double-antibody RIA using a rabbit IGF-I antiserum (GroPep Pty Ltd., Adelaide, Australia) and [^{125}I]IGF-I which had been iodinated by the chloramine T method as described

previously (Lee et al., 2002, Yun et al., 2003).

Concentrations of TGF-1 and EGF in serum and muscle homogenate were measured using corresponding ELISA kits (R&D Systems Inc., Minneapolis, MN, USA) following the manufacturer's instruction as described by Ryu et al. (2007). In the former assay, samples were diluted, acidified, incubated briefly, and neutralized to release the active form of the peptide during the pretreatment.

4. Statistical analysis

Variance of the pork quality and growth factor measurements and the correlation between these two classes of variables were analyzed by using the PROC ANOVA and PROC CORR options of SAS (SAS Inst. Inc., Cary, NC, USA), respectively. In comparison of means between the pork quality categories, t-test was used.

RESULTS

1. Pork quality traits

The 60 gilt carcasses which were examined in the present study yielded 36 RFN (reddish-pink, firm, and non-exudative), 16 RSE (reddish-pink, soft, and exudative), and 6 PSE (pale, soft, and exudative) carcasses (Table 1). Two DFD (dark, firm, and dry) carcasses were also found, but this category was excluded from Table 1 as well as in subsequent experiments because of the insufficient number of replicates.

Carcass weight did not differ across the pork quality

categories. Backfat thickness was lesser in RSE and PSE than in RFN, but differences between means were not significant ($P=0.12$ for RSE vs. RFN). The lightness (CIE L*) of the *Longissimus dorsi* muscle (LM) was greater in PSE than in RFN and RSE ($P<0.01$), whereas the redness (CIE a*) of LM did not differ across the pork quality categories. The 48-h drip loss was greater in PSE and RSE than in RFN ($P<0.01$). The pH_{45min} was less in PSE vs. RFN ($P<0.05$); pH_{24h} tended to be less in the former ($P=0.09$).

2. Concentrations of growth factors in serum and muscle

Serum IGF-I concentration did not differ among RFN, RSE, and PSE seven days before (D -7) or at (D 0) slaughter (Table 2). The LM IGF-I content at D 0, however, was less in PSE than in RFN ($P<0.05$). The LM TGF- β 1 content also was less in PSE vs. RFN ($P<0.05$), although the effect of the pork quality category was not significant in ANOVA. Furthermore, serum EGF concentration at D 0 was also less in PSE vs. RFN ($P<0.05$), whereas the EGF content in LM did not differ across the pork quality categories.

3. Correlations between growth factor concentrations and pork quality traits

The LM IGF-I and TGF- β 1 concentrations were negatively correlated ($p<0.01$) with drip loss ($r = -0.36$ and -0.44 , respectively). Moreover, serum EGF concentration at D 0 was also negatively correlated with drip loss ($r = -0.32$,

Table 1. Physicochemical characteristics of the carcass and *Longissimus dorsi* muscle from female market pigs by the pork quality category

Item	Meat quality			Significance
	RFN ¹⁾ (n = 36)	RSE ²⁾ (n = 16)	PSE ³⁾ (n = 6)	
Carcass wt, kg	88.0 \pm 1.4	86.1 \pm 2.0	86.8 \pm 3.3	
Backfat thickness, mm	17.3 \pm 0.6	15.6 \pm 0.9	15.2 \pm 1.5	
Muscle color				
Lightness, CIE L*	46.6 \pm 0.3	46.8 \pm 0.4	50.2 \pm 0.7	**
Redness, CIE a*	7.41 \pm 0.15	7.61 \pm 0.22	8.02 \pm 0.36	
48 h drip loss, %	3.52 \pm 0.16	6.08 \pm 0.24	7.22 \pm 0.39	**
45 min pH	6.02 \pm 0.03	5.93 \pm 0.05	5.81 \pm 0.08	*
24 h pH	5.53 \pm 0.02	5.52 \pm 0.03	5.44 \pm 0.04	

^{1),2),3)} Stand for [reddish-pink, firm, and non-exudative], [reddish-pink, soft, and exudative], and [pale, soft, and exudative], respectively.

Data are means \pm SEM.

* $P<0.05$; ** $P<0.01$.

Table 2. Growth factor concentrations in serum and *Longissimus dorsi* muscle from female market pigs by the pork quality category

Item	Meat quality ¹⁾			Significance
	RFN	RSE	PSE	
IGF-I (ng/ml serum or g tissue)				
D-7 Serum	122 ± 7	150 ± 10	134 ± 17	
D 0 Serum	131 ± 6	145 ± 9	121 ± 14	
D 0 Muscle	4.0 ± 0.3	3.3 ± 0.4	2.4 ± 0.6	*
TGF-β1 (ng/ml serum or g tissue)				
D-7 Serum	222 ± 8	236 ± 17	228 ± 19	
D 0 Serum	311 ± 11	315 ± 16	355 ± 26	
D 0 Muscle	24.0 ± 2.3	18.8 ± 3.4	10.1 ± 5.0	
EGF (pg/ml serum or g tissue)				
D-7 Serum	93 ± 9	85 ± 3.3	93 ± 15	
D 0 Serum	78 ± 7	58 ± 11	33 ± 17	*
D 0 Muscle	64 ± 6	43 ± 9	56 ± 14	

¹⁾ See the Table 1 legend for details for each pork quality category.

* P<0.05.

p<0.05). However, CIE L* and a* were not correlated with any growth factor concentration.

DISCUSSION

It is well known that IGF-I plays a central role in genesis, growth, and maintenance of muscle mass (Clemmons, 2009; Duan et al., 2010). IGF-I stimulates muscle growth in a fiber type-specific manner (Lynch et al., 2001; Fiorotto et al., 2003), which can potentially influence the muscle quality traits (Rehfeldt et al., 2000; Ryu and Kim, 2006). TGF-β and

Table 3. Correlation coefficients between pork quality traits and growth factor concentrations in serum and *Longissimus dorsi* muscle from female market pigs before and at slaughter

Variable	CIE L*	CIE a*	Drip loss
IGF-I			
D-7 Serum	-0.05	-0.17	0.16
D 0 Serum	0.20	-0.09	0.02
D 0 Muscle	-0.19	0.18	-0.36**
TGF-β1			
D-7 Serum	-0.04	0.25	0.16
D 0 Serum	0.00	0.05	0.07
D 0 Muscle	-0.16	-0.06	-0.44**
EGF			
D-7 Serum	-0.10	0.27	-0.16
D 0 Serum	-0.21	-0.10	-0.32*
D 0 Muscle	0.19	-0.13	-0.23

* P<0.05; ** P<0.01.

EGF, however, inhibit somatic growth including myogenesis *in vivo* (Chernausek et al., 1991; Dayton and White, 2008). Interestingly, the well known anti-mitogenic action of TGF-β in myogenic and other types of cells *in vitro* is believed to be mediated in part by TGF-β-induced IGF-binding protein (IGFBP)-3, which inhibits IGF action (Oh, et al., 1995; Kamanga-Sollo et al., 2003). Similarly, EGF seems to suppress growth *in vivo* by regulating the expression of IGFBPs (Murray et al., 1993; Vinter-Jensen et al., 1996; Chan and Wong, 2000). Taken together, these reports suggest that systemic and/or local availabilities of IGF-I, TGF-β, and EGF may influence the *postmortem* muscle quality, which was the basis of the hypothesis of the present study.

Results on the muscle quality traits measured in the present study were consistent with known characteristics of RFN, RSE, and PSE (Warner et al., 1997). The LM lightness (CIE L*) and drip loss were greater in PSE vs. RFN and RSE and also RSE and PSE vs. RFN, respectively, as they should because the muscle quality was categorized according to the results of these variables. Similarly, the lower pH_{45min} in PSE vs. RFN is a typical characteristic of the former resulting from fast glycolysis (Ryu and Kim, 2006). In addition, the unreduced redness (CIE a*) of RSE vs. RFN is also a known characteristic of the former.

The LM IGF-I and TGF-β1 and serum EGF concentrations at slaughter were less in PSE vs. RFN but were not different between PSE and RSE. This was opposite to the relative drip loss in these three pork quality categories, which resulted in negative correlations between drip loss and

these growth factor variables. In contrast, the L* and a* were not correlated with any growth factor variable. Taken together, these results suggest that locally expressed IGF-I and TGF- β 1 as well as blood-borne EGF may play a role directly or indirectly in unknown *postmortem* histochemical reactions associated with water retention rather than color development and thereby contribute to sustaining the textural integrity and quality of normal pork. In this connection, it was also noteworthy that PSE and RSE carcasses exhibited lesser backfat thickness than RFN carcasses, which was consistent with previous reports (Dilley et al., 1970; Ryu and Kim, 2006) implicating that leaner pigs are more prone to the 'exudative' pork quality (Rehfeldt et al., 2000).

IGF-I, TGF- β 1, and EGF are known to act on the target cell in both autocrine/paracrine and endocrine manners, but relative significance of the local vs. systemic availability of these peptides is as yet controversial (Xian, 2007; Dayton and White, 2008; Ohlsson et al., 2009). For instance, Sjogren et al. (1999) found that liver-specific IGF-I knockout mice, which had only 25% serum IGF-I concentration of normal mice, grew normally and asserted from this result that locally expressed IGF-I is enough for normal postnatal growth. However, there are also several lines of evidence indicating that liver-derived endocrine IGF-I has a growth-promoting effect comparable to that expressed in non-hepatic tissues in IGF-I-transgenic mice on an IGF-I null background (Stratikopoulou et al., 2008; Ohlsson et al., 2009; Wu et al., 2009). In line with the latter, it has been known for a long time that circulating IGF-I concentration and growth rate are correlated in the pig (Owens et al., 1999; Lee et al., 2002) and other species (Blair et al., 1989; Blum et al., 1993). As such, not only how IGF-I, EGF, and TGF- β 1 act on the muscle around the time of slaughter to influence the pork quality but also how much each of endocrine and local availabilities of these growth factors contributes to this effect remains to be further studied.

Collectively, results are interpreted to suggest that concentrations of IGF-I and TGF- β 1 in muscle and EGF in serum of the market pig at slaughter are reflective of the *postmortem* water holding capacity of the muscle to some extent.

ACKNOWLEDGMENT

This work was supported by grants from Gyeongnam National University of Science and Technology (GNTech) and

Regional Animal Industry Center at GNTEch.

REFERENCES

- Blachowski, S., Motyl, T., Orzechowski, A., Grzelkowska, K. and Interewicz, B. 1993. Comparison of metabolic effects of EGF, TGF- α , TGF- β 1 in primary culture of fetal bovine myoblasts and rat L6 myoblasts. *Int. J. Biochem.* 25:1571-1577.
- Blair, H. T., McCutcheon, S. N., Mackenzie, D. D., Gluckman, P. D., Ormsby, J. E. and Breier, B. H. 1989. Responses to divergent selection for plasma concentrations of insulin-like growth factor-I in mice. *Genet. Res.* 53:187-191.
- Blum, W. F., Albertsson-Wikland, K., Rosberg, S. and Ranke, M. B. 1993. Serum levels of insulin-like growth factor I (IGF-I) and IGF binding protein 3 reflect spontaneous growth hormone secretion. *J. Clin. Endocrinol. Metab.* 76:1610-1616.
- Burr, J. G., Dreyfuss, G., Penman, S. and Buchanan, J. M. 1980. Association of the src gene product of Rous sarcoma virus with cytoskeletal structure of chicken embryo fibroblasts. *Proc. Natl. Acad. Sci. USA* 77:3484-3488.
- Chan, S. Y. and Wong, R. W. 2000. Expression of epidermal growth factor in transgenic mice causes growth retardation. *J. Biol. Chem.* 275:38693-38698.
- Chernausek, S. D., Dickson, B. A., Smith, E. P. and Hoat, S. B. 1991. Suppression of insulin-like growth factor I during epidermal growth factor-induced growth retardation. *Am. J. Physiol.* 260:E416-E421.
- CIE. 1978. Recommendations on uniform color spaces-color difference equations, psychometric color terms. Supplement no. 2 to CIE Publication No. 15 (E-1.3.1) 1971/(TC-1-3). Commission Internationale de l'Eclairage, Paris.
- Clemmons, D. R. 2009. Role of IGF-I in skeletal muscle mass maintenance. *Trends Endocrinol. Metab.* 20:349-356.
- Daughaday, W. H., Mariz, I. K. and Blethen, S. L. 1980. Inhibition of access of bound somatomedin to membrane receptor and immunoblotting sites: a comparison of radioreceptor and radioimmunoassay of somatomedin in native and acid-ethanol-extracted serum. *J. Clin. Endocrinol. Metab.* 51:781-788.
- Dayton, W. R. and White, M. E. 2008. Cellular and molecular regulation of muscle growth and development in meat animals. *J. Anim. Sci.* 86 (E. Suppl.):E217-E225.
- Dilley, D. D., Aberle, E. D., Forrest, J. C. and Judge, D. 1970. Porcine muscularity and properties associated with pale, soft, exudative muscle. *J. Anim. Sci.* 31:681-685.
- Douglas, R. G., Gluckman, P. D., Breier, B. H., McCall, J. L., Parry, B. and Shaw, J. H. 1991. Effects of recombinant IGF-I

- on protein and glucose metabolism in rTNF-infused lambs. *Am. J. Physiol.* 261:E606-612.
- Doumit, M. E., Cook, D. R. and Merkel, R. A. 1993. Fibroblast growth factor, epidermal growth factor, insulin-like growth factors, and platelet-derived growth factor-BB stimulate proliferation of clonally derived porcine myogenic satellite cells. *J. Cell Physiol.* 157:325-332.
- Duan, C., Ren, H. and Gao, S. 2010. Insulin-like growth factors (IGFs), IGF receptors, and IGF-binding proteins: roles in skeletal muscle growth and differentiation. *Gen. Comp. Endocrinol.* 167:344-351.
- Fiorotto, M. L., Schwartz, R. and Delaughter, M. C. 2003. Persistent IGF-I overexpression in skeletal muscle transiently enhances DNA accretion and growth. *FASEB J.* 17:59-60.
- Florini, J. R., Ewton, D. Z. and Magri, K. A. 1991. Hormones, growth factors, and myogenic differentiation. *Ann. Rev. Physiol.* 53:210-216.
- Honikel, K. O., Kim, C. J. and Hamm, R. 1986. Sarcomere shortening of prerigor muscles and its influence on drip loss. *Meat Sci.* 16:267-282.
- Jones J. I. and Clemmons, D. R. 1995. Insulin-like growth factors and their binding proteins: biological actions. *Endocr. Rev.* 16:3-34.
- Kamanga-Sollo, E., Pampusch, M. S., White, M. E. and Dayton, S. R. 2003. Role of insulin-like growth factor binding protein (IGFBP)-3 in TGF- β - and GDF-8 (myostatin)-induced suppression of proliferation in porcine embryonic myogenic cell cultures. *J. Cell. Physiol.* 197:225-231.
- Koea J. B., Breier, B. H., Shaw, J. H. and Gluckman, P. D. 1992a. A possible role for IGF-II: evidence in sheep for *in vivo* regulation of IGF-I mediated protein anabolism. *Endocrinology* 130:2423-2425.
- Koea, J. B., Douglas, R. G., Breier, B. H., Shaw, J. H. and Gluckman, P. D. 1992b. Synergistic effect of insulin-like growth factor-I administration on the protein-sparing effects of total parenteral nutrition in fasted lambs. *Endocrinology* 131: 643-648.
- Kollias, H. D. and McDermott, J. C. 2008. Transforming growth factor- β and myostatin signaling in skeletal muscle. *J. Appl. Physiol.* 104:579-587.
- Lee, C. Y., Lee, H. P., Jeong, J. H., Baik, K. H., Jin, S. K., Lee, J. H. and Sohn, S. H. 2002. Effects of restricted feeding, low-energy diet, and implantation of trenbolone acetate plus estradiol on growth, carcass traits, and circulating concentrations of insulin-like growth factor (IGF)-I and IGF-binding protein-3 in finishing barrows. *J. Anim. Sci.* 80:84-93.
- Lynch, G. S., Cuffe, S. A., Plant, D. R., Gregorevic, P. 2001. IGF-I treatment improves the functional properties of fast- and slow-twitch skeletal muscles from dystrophic mice. *Neuromuscular Disorders* 11:260-268.
- Mau, M., Kalbe, C., Wollenhaupt, K., Nurnberg, G. and Rehfeldt, C. 2008. IGF-I- and EGF-dependent DNA synthesis of porcine myoblasts is influenced by the dietary isoflavones genistein and daidzein. *Domest. Anim. Endocrinol.* 35:281-289.
- McCroskery, S., Thomas, M., Maxwell, L., Sharma, M. and Kambadur, R. 2003. Myostatin negatively regulates satellite cell activation and self-renewal. *J. Cell Biol.* 162:1135-1147.
- Murray, M. A., Dickson, B. A., Smith, E. P., Hoath, S. B. and Chernausek, S. D. 1993. Epidermal growth factor stimulates insulin-like growth factor-binding protein-1 expression in the neonatal rat. *Endocrinology* 133:159-165.
- Oh, Y., Muller, H. L., Ng, L. and Rosenfeld, R. G. 1995. Transforming growth factor- β -induced cell growth inhibition in human breast cancer cells is mediated through insulin-like growth factor-binding protein-3 action. *J. Biol. Chem.* 270: 13589-13592.
- Ohlsson, C., Mohan, S., Sjogren, K., Tivesten, A., Isgaard, J., Isaksson, O., Jansson, J.-O. and Svensson, J. 2009. The role of liver-derived insulin-like growth factor-1. *Endocr. Rev.* 30:494-535.
- Owens, P. C., Gatford, K. L., Walton, P. E., Morley, W. and Campbell, R. G. 1999. The relationship between endogenous insulin-like growth factors and growth in pigs. *J. Anim. Sci.* 77:2098-2103.
- Rehfeldt, C., Fiedler, I., Dietl, G. and Ender, K. 2000. Myogenesis and postnatal skeletal muscle growth as influenced by selection. *Livest. Prod. Sci.* 66:177-188.
- Ryu, Y. C. and Kim, B. C. 2006. Comparison of histochemical characteristics in various pork groups categorized by postmortem metabolic rate and pork quality. *J. Anim. Sci.* 84:894-901.
- Ryu, Y.-C., Choi, Y.-M., Ko, Y. and Kim, B.-C. 2007. Relationship between serum endocrine factors, histochemical characteristics of *longissimus dorsi* muscle and meat quality in pigs. *J. Muscle Foods* 18:95-108.
- Sjogren, K., Liu, J.-L., Blad, K., Skrtic, S., Vidal, O., Wallenius, V., LeRoith, D., Tornell, J., Isaksson, O. G. P., Jansson, J.-O. and Ohlsson, C. 1999. Liver-derived insulin-like growth factor I (IGF-I) is the principal source of IGF-I in blood but is not required for postnatal body growth in mice. *Proc. Natl. Acad. Sci. USA* 96:7088-7092.
- Stratikopoulos, E., Szabolcs, M., Dragatsis, I., Klinakis, A. and

- Efstratiadis, A. 2008. The hormonal action of IGF1 in postnatal mouse growth. *Proc. Natl. Acad. Sci. USA* 105: 19378-19383.
- Vinter-Jensen, L., Juhl, C. O., Frstyk, J., Dajani, E. Z., Oksbjerg, N. and Flyvbjerg, A. 1996. The effect of epidermal growth factor on circulating levels of IGF and IGF-binding proteins in adult Goettingen minipigs. *J. Endocrinol.* 151:401-407.
- Warner, R. D., Kauffman, R. G. and Greaser, M. L. 1997. Muscle protein changes post mortem in relation to pork quality traits. *Meat Sci.* 45:339-352.
- Wu, Y, Sun, H., Yakar, S. and LeRoith, D. 2009. Elevated levels of insulin-like growth factor (IGF)-I in serum rescue the severe growth retardation of IGF-I null mice. *Endocrinology* 150:4395-4403.
- Xian, C. J. 2007. Roles of epidermal growth factor family in the regulation of postnatal somatic growth. *Endocr. Rev.* 28:284-296.
- Yun, J. S., Seo, D. S., Rhee, M. S., Oh, S., Kim, B. C. and Ko, Y. 2003. Relationships of concentrations of endocrine factors at antemortem and postmortem periods to carcass weight and backfat thickness in pigs. *Asian-Aust. J. Anim. Sci.* 16:335-341.

(Received Oct. 25, 2012; Revised Dec. 13, 2012; Accepted Dec. 17, 2012)