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Polymorphism in Coding and Non-coding Regions of the *MyoD* Gene Family and Meat Quality in Pigs*

Wojciech KAPELAŃSKI, Salomea GRAJEWSKA, Jolanta KURYŁ, Maria BOCIAN, Joanna WYSZYŃSKA-KOKO and Paweł URBAŃSKI

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The aim of the study was to evaluate the relations between genotype effects at porcine loci *MYF3*, *MYF4*, *MYF5* and *MYF6* on meat quality traits in pigs of the *CC* genotype at the *RYR1 locus*. Meat traits were analysed in *longissimus lumborum* muscle in 98 pigs (75 of PLW × PL and 25 [PLW × PL] × Pietrain crosses). The determined meat characteristics covered the pH_1 and pH_u records, visual assessment of colour and exudation on fresh meat samples, water holding capacity, drip loss, spectrophotometric measurements of dominant wavelength, colour saturation and lightness, L, a*, b* values according to the CIE system, basic chemical constituents (water, protein, intramuscular fat and ash) and soluble protein fraction in meat. The distribution of animals within particular *MyoD* genotypes only in the *MYF4* and *MYF5* genotypes were spread uniformly. The gene effects at particular *MyoD* loci on studied meat traits were significant. The most pronounced effect on meat quality was exerted by the *myogenin* gene (*MYF4*). Individuals of the *BB* genotype in respect to the *MYF4 locus* showed a better water holding capacity ($P<0.01$), lower drip loss ($P<0.05$), darker colour score ($P<0.01$) and better wateriness score ($P<0.01$), darker and more desirable colour characteristic ($P<0.01$) than pigs with the *AA* genotype, whereas *AB* genotype animals had intermediate values. In respect to meat protein solubility the *AA* genotype pigs had a significantly lower level of soluble protein in meat than *AB* and *BB* ($P<0.01$). On basis of the present study it may be inferred that mutations in coding and the non-coding regions of *MyoD* genes exert significant effects on muscle traits related to oxidative metabolism, as well as related to glycolysis and contractile muscle properties, and thereby on meat quality.

Key words: Pig, meat quality, *MyoD* family genes.

Wojciech KAPELAŃSKI, Salomea GRAJEWSKA, Maria BOCIAN, Department of Pig Breeding, University of Technology and Agriculture, Mazowiecka 28, 85-084 Bydgoszcz, Poland.
E-mail: kapelanski@atr.bydgoszcz.pl
Jolanta KURYŁ, Joanna WYSZYŃSKA-KOKO, Paweł URBAŃSKI, Institute of Genetics and Animal Breeding, Polish Academy of Sciences, Jastrzębiec, 05-552 Wólka Kosowska, Poland.

Variation in meat quality is likely to be caused by differences in various genetic and environmental factors, which interact and determine the course of metabolic processes in muscle tissue and in the postmortem conversion of muscle into meat. An important basis for meat production is the embryonic development and formation of muscle tissue. The myogenesis is under control of the *MyoD* gene family, which regulates the multistep process involved in muscle fibres formation during embryonic development and in their differentiation and maturation (TE PAS *et al*. 1994, 1999; PETTE & STARON 1997). The *MyoD* gene family consists of four structurally and functionally related genes, *MYF3* (*MyoD*1), *MYF4* (*myogenin*), *MYF5* and *MYF6* (*MRF4*) (TE PAS & VISSCHER 1994; HUGHES & SCHIAFFINO 1999).

Expression of the *MyoD* gene family is associated with different stages of muscle fibre formation and is also found in muscles of adult animals (HUGHES *et al*. 1993; TE PAS *et al*. 2000). A significant relation between the *MyoD* gene variants and carcass traits has been shown (TE PAS *et al*. 1999; CIEŚLAK *et al*. 2002; KURYŁ *et al*. 2002) and these genes may be involved in regulating both lean and meat quality (TE PAS *et al*. 1994).

The linkage between muscle regulatory factors and meat quantity and quality traits is focused on muscle fibre type composition, their diameter or fibre number per unit area (KLONT *et al*. 1998;

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Table 1

Frequency of genotypes at the *MyoD* loci

Locus	Genotype	Number (n)	Frequency (%)
MYF3	*TT/GG*	5	5.3
	TC/CG	28	29.5
	TC/GG	17	17.9
	TT/CG	4	4.2
	CC/GG	41	43.1
	Total	95	
MYF4	*AA*	30	31.9
	AB	49	52.1
	BB	15	16.0
	Total	94	
MYF5	*AA*	22	23.7
	AC	36	38.7
	CC	35	37.6
	Total	93	
MYF6E	*CACA*	54	55.7
	CAGC	39	40.2
	GCGC	4	4.1
	Total	97	
MYF6P	*TT*	55	56.7
	TC	38	39.2
	CC	4	4.1
	Total	97	

MYF6E – polymorphism in exon 1
MYF6P – polymorphism in promoter region

KŁOSOWSKA *et al*. 2001; 2004). A characteristic of skeletal muscle is its diversity consisting of different kinds of fibres which are responsible for oxidative or glycolytic biochemical processes and thereby affecting some meat properties (KLONT *et al*. 1998; MALTIN *et al*. 1997).

In an earlier study an evaluation was put forth for the associations between meat quality traits and polymorphism of *RYR1, MYF3* and *MYF4* genes in crossbred pigs, however the results were confounded by the effect of the $RYR1^T$ gene (KAPELAŃSKI *et al*. 2001; KAPELAŃSKI *et al*. 2004). Therefore, the objective of this study was to investigate the genotype effects at the *loci MYF3*, *MYF4*, *MYF5* and *MYF6* on meat quality traits in pigs not carrying the stress susceptibility gene.

Material and Methods

The experiment was carried out on 98 pigs in half gilts and barrows reared in a breeding centre at Broniewo and Agro-Wronie farms. Both maintenance and feeding were similar for all animals and in accordance with obligatory standards. The pigs were crossbred progeny from PLW x PL (73 animals) and from PLW × PL sows mated to Pietrain sires (25 animals). At a live body weight of about 105 kg the pigs were slaughtered in accordance with current regulations.

Blood samples were taken from the vena cava or at the slaughter into test-tubes containing K_3EDTA and stored at –25° C until analysed. Genomic DNA was isolated (KAWASAKI 1990). PCR/RFLP polymorphism of genes was determined according to the following procedures: *MYF3*/*Bss*SI – in exon 1 (URBAŃSKI & KURYŁ 2004a), *MYF6*/*Msp*I – in the promoter region (WYSZYŃSKA-KOKO & KURYŁ 2004b), *MYF6/Aci*I and *MYF6/Eae*I – in exon 1 (WYSZYŃSKA-KOKO & KURYŁ 2004a), *MYF4/Msp*I – in the 3' region (SOUMILLION *et al*. 1997), *MYF5* – in the promotor region (URBAŃSKI & KURYŁ 2004b). *RYR1*/*HinP*I genotypes were identified according to FUJI *et al*. (1991). All analysed animals were of the *CC* genotype at *RYR1 locus*.

Meat quality traits were measured in the *longissimus lumborum* muscle (*LL*). The pH_1 value was recorded using a pistol pH-meter (R. Matthaus, Germany) and ultimate pH (pH_u) was measured in minced meat-water slury 48h after slaughter. Visual assessment of colour and wateriness on fresh meat samples was performed by a trained panel according to a five point scale, where score 3 was judged as an optimal value. Water holding capacity (WHC) was determined according to the filter press method (GRAU & HAMM 1952) with modification by POHJA and NIINIVAARA (1957) and was expressed as the percentage of free water in meat. Drip loss was recorded on about 150 g slice of meat (HONIKEL 1987). Meat colour was determined twofold, first on the Specol 11 spectrophotometer with a reflectance attachment and the use of regression equations (RÓŻYCZKA *et al*. 1968) to calculate the colour parameters such as dominant wavelength, saturation and lightness, and repeatedly on a second apparatus Chromameter Minolta CR 310 giving values L, a*, b* according to the CIE system (1976).

The basic chemical meat components: water, crude protein, intramuscular fat and ash content were determined (AOAC 1990) and also the soluble protein fraction (KOTIK 1970).

Statistical calculations of the arithmetic average (x), standard deviation (s), analysis of variance and significance of differences (Student's *t*-test) between particular genotypes were made using STATISTICA 5.5 PL software (2000).

The study was conducted with approval of the Regional Ethical Committee (No.13/2004).

Table 2

Significance of genotype effects at the loci *MYF3, MYF4, MYF5, MYF6E AND MYF6P* on meat quality traits

Trait	*MYF3*	*MYF4*	*MYF5*	MYF6E	*MYF6P*
pH_1	ns	ns	*	ns	ns
pH_u	*	ns	ns	ns	ns
WHC, % loose water	ns	**	ns	ns	ns
Drip loss, %	ns	*	*	**	**
Visual appraisal					
Colour, score	*	**	ns	ns	ns
Wateriness, score	ns	**	ns	ns	ns
Objective colour measurement					
Dominant wavelength, nm	ns	**	ns	ns	ns
Saturation, %	ns	**	ns	ns	ns
Lightness, %	ns	**	ns	ns	ns
Minolta CIE values					
L*	ns	**	ns	ns	ns
a*	ns	**	ns	ns	ns
b*	ns	ns	ns	ns	ns
Chemical composition					
Water, %	ns	ns	ns	ns	ns
Crude protein, %	ns	ns	ns	ns	ns
Intramuscular fat, %	ns	ns	ns	ns	ns
Ash content, %	**	ns	ns	ns	ns
Meat soluble protein, g	ns	**	ns	ns	ns
Soluble protein, % of total N	ns	**	ns	ns	ns

Ns – nonsignificant
* P = 0.05
**P = 0.01
MYF6E – polymorphism in exon 1; *MYF6P* – polymorphism in promoter region.

Results

The number of animals and frequency of genotypes at the *MYF3*, *MYF4*, *MYF5* and *MYF6 loci* are shown in Table 1. As regards the distribution of individuals within a particular genotype, only in the *MYF4* and *MYF5* genes were the genotypes spread uniformly.

The significance of gene variant effects at particular *MyoD* loci on studied meat traits is presented in Table 2. The most pronounced effect of genotype at the *myogenin* locus on meat quality was evidenced and will be discussed in detail below. As can be seen, some meat characteristics are under the control of several genes of the *MyoD* gene family. The data showed a significant effect of the *MYF3* genotype on ultimate meat pH (P<0.05), on meat color score (P<0.05), and on total mineral constituents determined as ash content in muscle tissue (P<0.01). The *MYF5* genotype affected the pH_1 value (P<0.01) and drip loss during meat storage (P<0.05). Also, *MYF6* gene variants as regards point mutations in both the promoter region and in exon 1 exert a significant influence on drip loss from meat (P<0.01).

The *myogenin* (*MYF4*) genotype showed a significant effect on most of the studied meat characteristic. Individuals of the *BB* genotype had better water holding capacity of meat (P<0.01), lower drip loss (P<0.05), darker colour scores (P<0.01) and better wateriness score (P<0.01), darker and more desirable colour characteristics (P<0.01) than pigs with *AA* genotype, whereas *AB* genotype animals had intermediate values. However, in respect to meat protein solubility (the lowest value was found in PSE meat) the *AA* genotype pigs had a significantly lower level than *AB* and *BB* ones (P<0.01).

Discussion

Myogenesis and postnatal tissue growth are regulated by the muscle regulatory factors gene family (*MyoD*) consisting of four genes (*MYF3*, *MYF4*, *MYF5* and *MYF6*). Their polymorphism has been reported in several pig breeds and pig lines to affect the meat deposition in carcass (CIEŚLAK *et al*. 2002; KURYŁ *et al*. 2002) and the microstructural characteristics of muscle tissue (KŁOSOWSKA & FIEDLER 2003; KŁOSOWSKA *et al*. 2001, 2004). There were also some attempts to find a relation between meat quality traits and effects of *myogenin* and *MYF3* polymorphism (KAPELAŃSKI *et al*. 2001, 2004). However, the results were not clear enough because of screening effects of different *RYR1* gene status of pigs on both meat quality and quantity. The significant influence of *RYR1* genotype on mutual variation for pork quality and muscle fibre type characteristics is well known (BOGUCKA & KAPELAŃSKI 2004; DEPREUX *et al*. 2002; EGGERT *et al*. 2002; KŁOSOWSKA & FIEDLER 2003).

A clearer association between meat quality traits and the polymorphism of *MyoD* genes was obtained in this study, since the pigs used were not carriers of the $RYR1^T$ gene. Thus, meat quality variation could be ascribed to the effects of *MyoD* gene family.

It seems reasonably to assume that meat colour, with all its parameters, is associated in part with the oxidative metabolic process. This concerns a higher muscle myoglobin concentration, higher proportion of red slow twitch fibres, which in turn give a darker meat colour, higher dominant wavelength, higher colour saturation and greater a* value (redness). Meat with such properties was shown mainly in pigs of the *BB* genotype at *MYF4* locus (Table 3), suggesting that this genotype is

Table 3

Meat quality traits as related to genotype at locus *MYF4*

Trait	*MYF4*			Overall
	AA	*AB*	*BB*	
Number, n	30	49	15	94
pH_1	6.40 ± 0.37	6.56 ± 0.36	6.64 ± 0.21	6.52 ± 0.35
pH_u	5.43 ± 0.07	5.46 ± 0.15	5.45 ± 0.09	5.45 ± 0.12
WHC, % loose water	23.10^{A} ± 2.78	22.03 ± 2.14	21.14^{B} ± 2.70	22.22 ± 2.51
Drip loss, %	5.32^{a} ± 2.23	4.49 ± 1.83	4.05^{b} ± 1.82	4.68 ± 1.99
Visual appraisal				
Colour, score	2.6^{A} ± 0.3	2.8 ± 0.3	2.9^{B} ± 0.3	2.7 ± 0.3
Wateriness, score	2.7^{Aa} ± 0.2	2.8^{b} ± 0.2	2.9^{B} ± 0.2	2.8 ± 0.2
Objective colour measurement				
Dominant wavelength, nm	584.0^{A} ± 1.39	585.2 ± 2.45	586.3^{B} ± 2.46	585.0 ± 2.29
Saturation, %	20.98^{A} ± 2.37	21.75^{a} ± 3.30	23.49^{Bb} ± 2.92	21.78 ± 3.06
Lightness, %	24.52^{Aa} ± 2.86	22.72^{b} ± 2.41	22.21^{B} ± 2.89	23.20 ± 2.76
Minolta CIE values				
L*	53.43^{Aa} ± 1.90	52.26^{b} ± 1.79	51.71^{B} ± 1.64	52.54 ± 1.89
a*	13.21^{A} ± 0.66	13.57 ± 0.81	13.80^{B} ± 0.69	13.49 ± 0.77
b*	2.15 ± 0.63	2.00 ± 0.77	1.99 ± 0.64	2.04 ± 0.70
Chemical composition				
Water, %	74.26 ± 0.65	73.95 ± 0.72	74.11 ± 0.64	74.08 ± 0.70
Crude protein, %	22.69 ± 0.66	22.94 ± 0.62	22.78 ± 0.61	22.84 ± 0.63
Intramuscular fat, %	1.80 ± 0.57	1.89 ± 0.61	1.89 ± 0.56	1.86 ± 0.58
Ash content, %	9.20^{A} ± 0.67	9.73^{B} ± 0.64	9.98^{B} ± 0.72	9.58 ± 0.73
Meat soluble protein, g	40.19^{A} ± 2.85	42.41^{B} ± 2.30	43.82^{B} ± 3.00	41.94 ± 2.87

a, b – P≤0.05
A, B – P≤0.01.

more advantageous for a breeding programme and selection due to its better value in respect to meat quality traits related to oxidative metabolism. TE PAS *et al*. (2000) suggested that *MYF3* and *MYF4* mRNA expression level may be related to muscle fibre type and that the expression of the *MYF3* gene was specifically found in white muscles, and *myogenin* expression was localized mainly in red muscles in animals at slaughter. However, the present results were obtained on *longissimus lumborum* muscle rating as white-coloured muscle. Furthermore, this study was intended to disclose the effects of polymorphic variants of gene on meat quality determination.

The alternative to oxidation dependent meat traits are e.g., pH_1, water holding capacity, drip loss and muscle protein extractability, which are closely connected to glycolysis or contractile properties of muscle fibres, their diameter or cross-sectional area (KARLSSON *et al*. 2000). Lately, much attention is paid to the relationship between myosin heavy chain (MyHC) isoforms and pork quality (BEE *et al*. 1999; EGGERT *et al*. 2002; GIL *et al.* 2003). Histochemically determined fibre distribution is highly correlated with the MyHC isoforms of muscle fibre types (BEE *et al*. 1999). MyHC isoforms are the major structural proteins of myofibrillar filaments responsible for contractile properties of fast and slow muscle fibres and determine the functional properties of a muscle, thereby meat quality.

A significantly lower water holding capacity, higher drip loss, larger exudation score and lower soluble protein content was found in meat of *AA* pigs than of the *BB* genotype at the *MYF4* locus. These results may suggest that mutation in the non-coding (3' flanking) region of the *myogenin* gene may be linked to another mutation(s) in another region of this gene, being a causal mutation for different functional and morphological muscle properties in pigs, resulting in differentiation of meat quality trait values.

The significant effect of genotypes at *MYF3*, *MYF5* and *MYF6 loc*i on meat traits were directed on the meat traits which are connected with glycolysis and contractile properties of cytoskeletal proteins, i.e., pH_1, pH_u , drip loss, and pale colour.

On the basis of the present study and obtained results it may be inferred that mutations in coding and non-coding regions of *MyoD* genes exert significant effects on many muscle characteristics, and thereby on meat quality.

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