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Relations between the polymorphism in the coding and 5'-flanking regions of the porcine *MYOD1* and *MYF5* genes and productive traits in pigs*

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ABSTRACT

The *MyoD* family genes were considered as candidate genes for growth rate and carcass meatiness in pigs. Gene mutations (SNPs, single nucleotide polymorphisms) discovered in the coding and 5'-flanking regions of the *MYOD1* and *MYF5* were analysed as possible causal mutations for these traits. Studies of the relation between polymorphisms in both those genes and productive traits were performed on Polish Landrace and Polish Large White gilts. A total of 401 animals (185 Polish Large White and 216 Polish Landrace) was encompassed by the analyses. Homozygotes of the "wild" allele as regards all three mutations of the *MYOD1* taken into consideration in the present study appeared to be more profitable for traits characterizing carcass meatiness than the two remaining genotypes. In turn, heterozygotes for mutations identified in the *MYF5* gene proved to be most favourable in terms of carcass meatiness. The effect of *MyoD* genotypes on performance traits was observed to be similar irrespective of the animals' breed. This may suggest that new mutations, identified in the coding and 5'-flanking regions of *MYOD1* and *MYF5* genes, could be more useful for selection than the earlier known mutations in the non-coding regions of these genes. In our opinion, two mutations identified in exon 1 of the *MYOD1* gene could be most beneficial and useful in selection and breeding of pigs.

KEY WORDS: *MYOD1*, *MYF5*, pig, carcass meatiness

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INTRODUCTION

Given the critical function of myogenic regulatory factors (MRFs) in skeletal muscle cell specification, their genes might be considered as candidate genes affecting the meat content of pig carcasses (te Pas and Visscher, 1994). The MRF family consists of four factors: MyoD1 (Myf-3), Myf-5, myogenin and MRF4 (Myf-6), coded by genes *MYOD1* (*MYF3*), *MYF5*, *MYOG* and *MRF4* (*MYF6*), respectively, known as the *MyoD* family genes. The expression of *MyoD* genes takes place exclusively in skeletal muscles. Thus it has been suggested that the MRF transcription factors play key regulatory roles in the development of the skeletal muscle lineage (Weintraub, 1993). Investigations of the MRF family members during myogenesis have been performed predominantly on rodents. Proteins Myf-3 and Myf-5 are thought to play an important role at the level of myoblast determination and proliferation, whereas myogenin and Myf-6, at the level of myoblast differentiation (Buckingham, 1994). The functional cooperation and redundancy between Myf-3 and Myf-5 factors was investigated by Kablar et al. (1997). Mice lacking a functional *MYOD1* gene were found to have no overt abnormalities in skeletal muscle but expressed about a four-fold higher level of Myf-5. Similarly, newborn Myf-5 deficient mice display apparently normal skeletal muscle but die because of severe rib abnormalities. Newborn animals deficient for both Myf-3 and Myf-5 factors are devoid of skeletal myoblasts and muscle (see review, Megeney et al., 1996).

Postnatal expression of the *MYOD1*, *MYF5* and *MYOG* genes in muscle is much lower than prenatal expression and has been found only in satellite cells (Koishi et al., 1995). Satellite cells proliferate and differentiate, thereby enabling postnatal muscle growth (Beilharz et al., 1992). te Pas and Visscher (1994) also suggested that the *MyoD* genes could have a major effect on muscularity and growth.

A relation between the polymorphism identified in non-coding regions of *MYOD1* and *MYF5* genes (region 3' and intron 1, respectively) and carcass traits has already been reported (te Pas et al., 1999; Cieślak et al., 2000, 2002; Kurył et al., 2002). Moreover, it was shown that the effect of genotype at these loci on carcass quality depended on pig breed. This indicated that mutations in non-coding regions of both genes could not be viewed as causal mutations but as markers of other mutations within *MYOD1* and *MYF5* or other genes linked to them.

The objective of this study was to evaluate the effect of new mutations, which have already been reported (Urbański and Kurył, 2004a,b) and identified in the coding and 5'-flanking regions of the *MYOD1* and *MYF5* genes, on growth rate and traits characterizing meat deposition in pig carcasses.

MATERIAL AND METHODS

The analysis was conducted on 401 gilts of two breeds, Polish Landrace (PL) and Polish Large White (PLW). Between 25 and 100 kg of body weight they were fed a commercial mixed feed *ad libitum*. Right carcass sides were dissected according to the procedure described by Różycki (1996). For the analyses the average daily gain (ADG) was taken into consideration as well as nine carcass traits: weight of right carcass side (WCS), weight of ham (HW), loin (WL) and sirloin (WSL), loin eye width (LW), height (LH) and area (LA), meat content in valuable cuts (MCVC) and in carcass (MCC).

Genomic DNA was isolated from leukocytes according to Kawasaki (1990). The *RYR1*/*Hin*P1 genotypes were identified using a sequence of primers according to Kamiński et al. (2001), whereas those at the *MYOD1* and *MYF5* loci, according to Urbański and Kurył (2004a, b). The sequences of the *MYOD1* and *MYF5* genes presented by Chang et al. (1995) and te Pas et al. (1999), respectively, were termed the "wild" allele.

Association analyses were carried out for each breed separately using the least squares method of the GLM procedure (SAS 8.2, 2002). The model included a fixed effect of the *RYR1* genotype (Table 1) and the boar effect (sire groups ranged from 1 to 27 animals). Age at slaughter and weight of right carcass side were included as covariates.

Differences between pig groups (with highest and lowest meat content in carcass and greatest and smallest loin eye area) for the frequency of alleles at the *MYOD1* and *MYF5* loci were evaluated according to Weber (1986).

RESULTS

Three point mutations (SNPs, single nucleotide polymorphisms) in each of the *MYOD1* and *MYF5* genes were taken into consideration. They were located in the 5'UTR region (*G*302*A*) and exon 1 (*C*489*T* and *G*566*C*) of the *MYOD1* gene, the 5'-flanking region (*A*65*C* and *C*613*T*) and exon 3 (*C*2931*T*) of the *MYF5* gene (Urbański and Kurył, 2004 a,b).

Table 1 shows the frequency of genotypes at loci *MYOD1* and *MYF5* concerning the mutations identified within these genes as well as *RYR1* genotypes in both breeds. The frequency of genotype *CC* was low at locus *MYOD1* (mutation *G*566*C*) in both PLW and PL breeds (1.4 and 0.7 %, respectively). For this reason it was not taken into consideration in a further analysis on association with traits. Absence of genotype *TT* at the *MYF5* locus (mutation *C*613*T*) was observed in both of the tested breeds, as was a low frequency of heterozygotes in PL gilts.

Table 1. Frequency of genotypes at loci *MYOD1*, *MYF5* and *RYR1* in Polish Large White and Polish Landrace pigs

Gene/ mutation/ localization	Genotype	PLW n=185	PL N=216
MYOD1	GG	37.4	38.4
G302A	GA	42.6	50.3
5'UTR	AA	20.0	11.3
MYOD1	CC	23.3	37.4
C489T	CT	55.5	51.3
Exon 1	TT	21.2	11.3
MYOD1	GG	76.7	79.3
G566C	GC	21.9	20.0
Exon 1	CC	1.4	0.7
MYF5	AA	36.8	37.0
A65C	AC	52.9	51.5
5'-flanking region	CC	10.3	11.5
MYF5	CC	81.3	94.2
C613T	CT	18.7	5.8
5'-flanking region	TT	0.0	0.0
MYF5	CC	57.6	59.6
C2931T	CT	36.1	24.0
Exon 3	TT	6.3	16.4
RYR1	CC	91.2	73.3
C1843T	CT	7.8	25.8
	TT	1.0	0.9

The effect of the *RYR1* genotype on productive traits within PLW and PL gilts analysed in this study appeared to be insignificant.

The results of the association analyses between genotypes at the *MYOD1* and *MYF5* loci and growth rate and carcass traits of PLW gilts are presented in Table 2.

A significant relation was found between the genotype at the *MYOD1* locus and several carcass traits. A comparison of carcass sides from animals with genotypes *GG*, *GA* and *AA* as regards 302nt located in the 5'UTR region of exon 1 showed the highest weight of carcass side (WCS) and ham (WH), as well as a higher value of loin eye height (LH) and area (LA) in *GG* homozygotes. A similar tendency was observed when analysing the relationship between carcass traits and genotype at the two remaining *MYOD1* gene mutations. Homozygotes of the "wild" *C* allele regarding 489nt showed a significantly higher weight of ham (WH) and carcass meat content (MCC) than *TT* homozygotes; this difference amounted to 0.4 kg and 2.15%, respectively. Homozygotes of the "wild" *G* allele as regards 566nt also

Table 2. Relation between SNPs in the porcine genes MYOD1 and MYF5 and carcass traits of Polish Large White pigs - contrasts ± SE

Gene/ mutation/ localization	Contrasts between genotypes	WCS kg	WH kg	WSL kg	WL kg	LW cm	LH cm	LA cm^2	MCVC %
MYOD1	GG-GA	0.66 ± 0.51*	0.18 ± 0.15*	Ns	ns	ns	0.27 ± 0.11**	2.21 ± 1.35	ns
G302A	GA-AA	-0.06 ± 0.47	0.00 ± 0.15				-0.05 ± 0.12	0.56 ± 1.24	
5'UTR	GG-AA	0.60 ± 0.47	0.18 ± 0.15*				0.22 ± 0.13	2.77 ± 1.45*	
MYOD1	CC-CT	ns	0.18 ± 0.09	0.015 ± 0.01*	ns	ns	ns	ns	ns
C489T	CT-TT		0.22 ± 0.11	-0.007 ± 0.01					
Exon 1	CC-TT		0.40 ± 0.12**	0.008 ± 0.01					
MYOD1 G566C Exon 1	GG-GC	ns	ns	Ns	0.21 ± 0.08*	0.26 ± 0.12*	0.27 ± 0.11*	3.23 ± 1.17**	1.77 ± 0.47**
MYF5	AA-AC	ns	ns	Ns	0.16 ± 0.03*	0.19 ± 0.13	ns	2.25 ± 1.23*	ns
A65C	AC-CC				-0.11 ± 0.11	-0.81 ± 0.15**		-5.33 ± 1.54*	
5'region	AA-CC				0.05 ± 0.13	-0.62 ± 0.17**		-3.08 ± 1.72	
MYF5 C613T 5'region	CC-CT	ns	ns	Ns	ns	ns	ns	4.01 ± 1.26*	ns
MYF5	CC-CT	ns	ns	Ns	ns	ns	ns	2.40 ± 1.48*	ns
C2931T	CT-TT							-4.54 ± 1.94*	
Exon3	CC-TT							-2.14 ± 1.89	

* P<0.05; **P<0.01; ns - P>0.05

WCS - weight of right carcass side; WH - weight of ham; WSL - weight of sirloin; WL - weight of loin; LW - width of loin eye; LH - height of loin eye; LA - loin eye area; MCVC meat content in valuable carcass cuts; MCC - meat content in carcass

proved more profitable than heterozygotes for weight of loin (WL) and size of loin eye (width - LW, height - LH and area LA), meat content in valuable cuts (MCVC) and in carcass (MCC). *CC* homozygotes were not included in the analysis because this genotype was found in only two gilts of the PLW breed.

Mutations identified in the 5' flanking region and in exon 3 of the *MYF*5 gene also affected some carcass traits characterizing carcass meat deposition. All of these mutations affected loin eye area (LA). Moreover, loin weight (WL) and carcass meat content (MCC) were significantly affected by genotype at the 65nt (5'-flanking region). In all cases, the value of traits was lowest in heterozygotes (compared with both homozygous genotypes). Of interest is the relation between the genotype at the *MYF5* locus as regards mutation *A*65*C* and loin eye area – as it was observed that in *CC* gilts it was 5.33 cm^2 greater than that observed in heterozygotes.

The associations between genotype at the *MYOD1* and *MYF5* loci and productive traits in PL gilts were similar to those described in PLW pigs (Table 3). As a rule, homozygotes of the "wild" allele regarding individual mutations of the *MYOD1* gene showed the highest value of carcass traits (excluding width of loin eye in animals with the *GG* genotype as regards 302nt) of all the animals analysed. On the other hand, heterozygotes as regards mutations of the *MYF*5 gene, proved to have the lowest weight and size of loin (WL, LW, LA) as well as carcass meat content (MCC). Of particular interest was the effect of an individual mutation in the *MYF5* gene on the loin eye area because it led to a difference between individual genotypes that ranged from 2.26 to 5.92 cm^2, depending on the mutation (*A*65*C* and *C*613*T*, respectively).

Groups of animals with the highest (>63%) and lowest (56%) carcass meat content were selected from gilts of each breed separately, basing on the mean value of the trait (x±SD). The frequency of genotypes regarding individual mutations within the *MYOD1* and *MYF5* genes was compared between these groups of pigs. They did not differ in frequency of *MYF5* genotypes. The frequency of individual *MYOD1* genotypes did, however, differ between groups of PL and PLW pigs (Table 4). The share of homozygotes of the "wild" allele of all mutations identified within the *MYOD1* gene was significantly higher among pigs showing a carcass meat content exceeding 63% when compared with those with the lowest value of this trait (<56 %). A similar relation was observed for mutation *G*566*C* within the PLW breed.

An analogous analysis was performed to evaluate the share of individual *MYOD1* and *MYF5* genotypes within two groups of pigs with the greatest (> 62 cm^2) or smallest (<49 cm^2) loin eye area (Table 4). Each of the two breeds examined in the present study was analysed separately. No significant differences in the frequency of individual *MYF5* genotypes were identified between groups of pigs differing in loin eye area. Homozygotes of "wild" alleles for all mutations within the *MYOD1* gene showed a significantly higher frequency in the group of

Table 3. A relations between SNPs in the porcine genes MYOD1 and MYF5 and carcass traits of Polish Landrace pigs - contrasts ± SE

Gene/ mutation/ localization	Contrasts between genotypes	WH kg	WL kg	LW Cm	LH cm	LA cm^2	MCVC %	MCC %
MYOD1 G302A 5'UTR	GG-GA	ns	ns	-0.04 ± 0.09	ns	ns	ns	ns
	GA-AA			0.30 ± 0.14*				
	GG-AA			0.26 ± 0.15				
MYOD1 C489T Exon 1	CC-CT	0.14 ± 0.09	ns	ns	ns	ns	ns	0.79 ± 0.45
	CT-TT	0.15 ± 0.14						1.00 ± 0.45
	CC-TT	0.29 ± 0.15*						1.79 ± 0.72*
MYOD1 G566C Exon 1	GG-GC	ns	ns	ns	0.22 ± 0.10*	2.31 ± 0.98*	1.60 ± 0.51*	1.75 ± 0.49**
MYF5 A65C 5'region	AA-AC	ns	0.15 ± 0.11*	0.13 ± 0.11	ns	2.26 ± 1.11*	ns	1.11 ± 0.55*
	AC-CC		-0.08 ± 0.16	-0.40 ± 0.16*		-5.29 ± 1.61*		-0.25 ± 0.81
	AA-CC		0.07 ± 0.18	-0.27 ± 0.18		-3.03 ± 1.87		0.86 ± 0.93
MYF5 C613T 5'region	CC-CT	ns	ns	ns	ns	5.92 ± 1.98*	ns	ns
MYF5 C2931T Exon3	CC-CT	ns	0.23 ± 0.13	ns	ns	ns	ns	ns
	CT-TT		-0.36 ± 0.17*					
	CC-TT		-0.13 ± 0.15					

* P<0.05; **P<0.01; ns - P>0.05

WH - weight of ham; WL - weight of loin; LW - width of loin eye; LH - height of loin eye; LA - loin eye area; MCVC - meat content in valuable carcass cuts; MCC - meat content in carcass

Table 4. Frequency of individual MYOD1 genotypes within groups of Polish Large White (PLW) and Polish Landrace (PL) pigs of highest (>63%) and lowest (<56 %) carcass meat content as well greatest (>62cm2) and smallest (<50cm2) loin eye area.

Gene/ gene region	Mutation	Genotype	Frequency of MYOD1 genotypes within pig groups of different carcass meat content						Frequency of MYOD1genotypes within pig groups of different loin eye area					
			PLW			PL			PLW			PL		
			<56%	>63%	P	<56%	>63%	P	<49 cm^2	>62 cm^2	P	<49 cm^2	>62 cm^2	P
MYOD1/ 5' UTR	G302A	GG	26.1	16.7	ns	18.2	64.0	**	20.0	52.3	*	20.0	45.9	*
		GA	47.8	33.3	ns	63.6	36.0	ns	60.0	47.7	ns	48.0	48.7	ns
		AA	26.1	50.0	ns	18.2	0.0	*	20.0	0.0	*	32.0	5.4	**
MYOD1/ Exon1	C489T	CC	13.0	37.5	ns	20.0	65.2	**	23.8	40.0	ns	13.8	51.4	**
		CT	65.2	50.0	ns	60.0	26.1	*	47.6	53.3	ns	65.5	35.1	*
		TT	21.7	12.5	ns	20.0	8.7	ns	28.6	6.7	*	20.7	13.5	ns
	G566C	GG	52.2	93.8	**	72.0	95.7	*	47.8	76.6	*	21.9	67.6	***
		GC	43.5	6.2	*	20.0	4.3	***	43.4	23.4	ns	71.8	29.4	**
		CC	4.3	0.0	ns	8.0	0.0	ns	8.8	0.0	ns	6.2	3.0	ns

* - P<0.05; ** - P<0.01; *** - P<0.001; ns - P>0.05

PL pigs with loin eye area exceeding 62 cm^2 as compared with animals in which the value of this trait lower than 49 cm^2. A similar tendency was also observed among PLW pigs.

DISCUSSION

The *MYOD1* and *MYF5* genes belong to the *MyoD* family, coding for myogenic regulatory factors. Both of those genes were selected as potential candidate genes affecting carcass meatiness due to their role in muscle development. Moreover, on pig chromosome 2, QTL for lean meat content was mapped in the region encompassing the *MYOD1* locus (Lee et al., 2003). In our earlier study, an analysis was made of the relation between the polymorphism in non-coding regions of both genes *MYOD1* and *MYF5* and carcass traits (Cieślak et al., 2000, 2002; Kurył et al., 2002). The observed significant or highly significant effect of genotype at these loci on the meat content in ham, loin and carcass was shown to depend on the pig breed or line. Thus, it was suggested that mutations of the analysed genes could not be accepted as causing the differences in the value of carcass traits observed between various *MYOD1* or *MYF5* genotypes. On the other hand, those results rendered it possible to assume that causative mutations could be localized in other regions of the *MYOD1* and *MYF5* genes. te Pas et al. (1999) failed to find a significant relation between the polymorphism identified in intron 1 of the porcine *MYF5* gene and several performance traits obtained for Yorkshire pigs (birth weight, growth rate, weight at slaughter corrected for slaughter age, carcass meat weight, mean back fat thickness from 4 ultrasonic measurements between shoulder and last rib).

Recently, we identified new polymorphisms (SNPs, single nucleotide polymorphisms) in the coding and 5'-flanking regions of the porcine *MYOD1* and *MYF5* genes (Urbański and Kurył, 2004a,b). The *G*566*C* mutation in exon 1 of the *MYOD1* gene leads to a replacement of arginine with proline, whereas the *C*2931*T* transition in exon 3 of the *MYF5* gene results in a change of the amino acid sequence Leu→Pro, which may affect the functional properties of both proteins. Another four SNPs were found in the 5'-flanking regions of both genes. The analysis presented here shows a significant association between individual *MYOD1* and *MYF5* genotypes and the recorded carcass traits. Homozygotes of the "wild" alleles for mutations of the *MYOD1* gene appeared to be more profitable than the remaining genotypes. These relations were similar in all the pig breeds analysed. On the other hand, homozygotes of the wild allele for transition *A*65*C* in the 5'-flanking region of *MYF5* gene seemed to be unprofitable as regards loin eye size, but beneficial for loin weight and carcass meat content in both analysed

pig breeds. The share of homozygotes of the "wild" alleles for all SNPs identified in the *MYOD1* gene was significantly higher in the group of PLW and PL pigs showing a high carcass meat content (>63%) and greatest loin eye area (>62cm^2) than in the group with a low value of these traits (<56 and 49 cm^2, respectively).

In the present study, heterozygotes in terms of a mutation of the *MYOD1* and *MYF5* genes demonstrated the highest or lowest values for given carcass traits when compared with both homozygous genotypes. This phenomenon has been observed for certain human genes and is termed negative- or positive heterosis (Comings and MacMurray, 2000). These authors suggested that if the regulation of the gene is dose dependent, the presence of a regulatory sequence in a heterozygous state could modify the gene function.

In summarizing the results presented in this study, it should be emphasized that if a particular *MYOD1* or *MYF5* gene variant had a beneficial effect on the value of any trait, it was observed in both tested breeds. No opposite effects of the same gene variant on a particular trait in different breeds were observed, as has been reported in an earlier study concerning the relation between slaughter traits and polymorphisms in non-coding regions of the *MyoD* genes (Cieślak et al., 2000). This makes it possible to conclude that the effect of the mutations in the *MYOD1* and *MYF5* genes analysed in this study is similar to that characteristic for causal mutations. Linkage between the analysed SNPs herein and an unknown gene mutation affecting carcass traits should also be taken into consideration.

CONCLUSIONS

The presented results indicate that identifying the genotype concerning point mutations in the coding and 5'-flanking regions of the porcine *MYOD1* and *MYF5* genes may be useful for selection aimed at improving the value of traits characterizing carcass meat deposition. Moreover, the fact that the relationship between genotype and trait value showed a similar tendency irrespectively of the breeds tested indicates that the associations observed in the present study may also be true for other pig breeds.

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