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Original article

Development of intra- and intermuscular adipose tissue in growing Large White and Meishan pigs

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Abstract — Lipogenic enzyme activities of porcine intra- and intermuscular adipose tissues were determined in growing lean (Large White) and fat (Meishan) pigs. The activities of acetyl-CoA-carboxylase (ACX), malic enzyme (ME) and glucose-6-phosphate dehydrogenase (G6PDH) were compared in both breeds and at both adipose sites. All three enzyme activities were much lower in the intramuscular adipose tissue than in the intermuscular site. Although the lipogenic activity of the intramuscular adipose site was low, it appeared, however, to possess adequate levels of enzymes for in situ lipid synthesis. The highest differences in lipogenic enzyme activities between Meishan and Large White pigs were found in intramuscular adipose tissue, and essentially concerned the activity of malic enzyme which was much higher in Meishan pigs. A close relationship between ME activity and lipid content of intramuscular adipose tissue was observed in both breeds. It was concluded that ME appeared to be a major factor affecting the incidence of higher intramuscular fat in the pig.

pig / intramuscular adipose tissue / lipogenic enzyme / meat quality

Résumé — Développement du tissu adipeux intramusculaire et conséquences sur la qualité de la viande chez les porcs de races Large White et Meishan en croissance. Le potentiel de synthèse d'enzymes lipogéniques des tissus adipeux intra et intermusculaires de porcs a été mesuré chez des porcs maigres (Large White) et gras (Meishan) en croissance. Les activités de l'Acétyl-CoA-carboxylase (ACX), de l'enzyme malique (EM) et de la glucose-6-phosphate déshydrogénase (G6PDH) ont été comparées dans les deux races et les deux types de tissu adipeux. Les trois activités enzymatiques étaient beaucoup plus faibles dans le tissu adipeux intramusculaire que dans le tissu adipeux intermusculaire, et ceci pour les deux races de porc. Cependant, même si la lipogénèse était faible dans le tissu adipeux intramusculaire, celui-ci possédait suffisamment d'enzymes pour assurer sa propre synthèse lipidique. Les différences d'activités lipogéniques les plus marquées entre les deux races de porcs ont été retrouvées au niveau du tissu intramusculaire et concernaient plus particulièrement l'activité de l'enzyme malique, plus élevée chez le porc Meishan que chez le porc Large-White. Nous avons trouvé une relation étroite entre l'activité de l'enzyme malique et le contenu

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lipidique du tissu adipeux intramusculaire, et ce, quelle que soit la race. L'enzyme malique apparaît comme un facteur prépondérant du développement du tissu adipeux intramusculaire chez le porc. © Inra/Elsevier, Paris.

porc / tissu adipeux intramusculaire / enzyme lipogénique / qualité de la viande

1. INTRODUCTION

In swines, the synthesis of adipose tissue triglycerides (TG), the major constituents of fat depot, either proceeds from fatty acids synthesized de novo (especially from diet starch) in the tissue [28] or from fatty acids obtained from circulating TG as a result of adipose tissue lipoprotein lipase activity [34]. The intramuscular adipose tissue is the latest developing adipose site of the pig adipose tissues, the order of the differential gradient being subcutaneous, intermuscular and intramuscular adipose sites [14, 18, 20]. Some authors studying adipose tissues have suggested that not all adipose tissues are similar but that each shows specific development and metabolism in rats [10], in cattle [24] and in pigs [4, 25, 26]. Intramuscular fat is a very important factor affecting organoleptic quality (for review see [5]). Selection against excessive fat and selection according to growth rate (especially in European pigs) have resulted in a decrease in intramuscular fat content, to the detriment of meat quality. Other breeds such as Chinese pigs that have not been selected against fatness nor on the growth rate still possess high quantities of intramuscular fat [2].

The objectives of this study were: 1) to determine the activity levels of selected lipogenic enzymes in porcine intramuscular fat and to compare these values with those of intermuscular fat to see if the intramuscular adipose site possesses a similar lipid synthesising capacity; 2) to compare the potential of lipogenesis in the intramuscular fat of European (Large White) and Chinese (Meishan) breeds of pigs which differ in their intramuscular fat content, in order to define some of the principal factors contributing to deposition of this adipose tissue; and 3) to study meat quality as the amounts of total lipids in two muscles.

2. MATERIALS AND METHODS

2.1. Animals and diet

Ninety female, male and castrated male pigs of each of two breeds of pigs (Large White and Meishan) weighing 20, 40, 60, 80 and 100 kg live weight (six per sex and per weight group for each breed) were studied. The pigs were housed in individual pens in environmentally controlled buildings under normal husbandry conditions. After weaning, the animals were fed a conventional swine diet (4 % lipid, 17 % crude proteins and 0.8 % lysine), according to a weight-based feeding scale, ranging from 1.9 kg for a live weight of 35 kg to 2.8 kg feed·day^{-1} for pigs weighing 75 kg or more. The animals were reared in compliance with national regulations on animal welfare, human care and use of animals in research.

2.2. Data collection

The pigs were slaughtered after electronarcosis. Samples were taken from the *Semimembranosus* (ham) and *Supraspinatus* (shoulder) muscles and from two intermuscular adipose tissues located near these two muscles. All samples were frozen in liquid N_2 and stored at –80 °C until analysed.

2.3. Enzyme assays

The lipogenic enzyme activities of intra- and intermuscular adipose tissues were determined. Weighed quantities of adipose tissue (1–1.5 g)

were homogenised in 0.25 M sucrose buffer and centrifuged at 30 000 *g* for 40 min. Supernatants were analysed for malic enzyme (ME, EC 1.1.1.40) and glucose-6-phosphate-dehydrogenase (G6PDH, EC 1.1.1.49) using modifications [13] of the methods of Fitch et al. [11] and Hsu and Lardy [15], respectively. NADPH formation was measured at 37 °C by absorbance at 340 nm. Acetyl-CoA-carboxylase (ACX, EC 6.4.1.2) was assayed by the HCO_3^- fixation method [6–8]. ME and G6PDH activities were expressed as micromoles of NADPH produced per min per g adipose tissue. Acetyl-CoA-carboxylase activity was expressed as nmol bicarbonate incorporated per min per g adipose tissue. We have chosen to express our results 'per g of tissue' instead of 'per mg proteins'. This latter mode of expression does not apply in muscles whose proteins are mainly myofibrillar ones. The mode of expression 'per g tissue' makes sense when the aim is to investigate the lipogenic activity in the muscle on its whole, as is the case in our study.

2.4. Lipid content of adipose tissues

Lipids were extracted from the intramuscular adipose tissues at 20, 60 and 100 kg body weight by chloroform/methanol (2:1), according to the procedure of Folch et al. [12].

2.5. Statistical analysis

Data were processed by variance analysis, using the general linear model procedure of SAS [32]. The model included the main effects of breed, site, sex and weight and their interactions. Multiple comparisons of the means were performed, when appropriate, using Bonferonni's test. Pearson coefficients of correlation between enzyme activities and intramuscular fat content were calculated overall (all data irrespective of breed and weight) or within breed.

3. RESULTS AND DISCUSSION

The effects of sex on lipogenesis were mostly non-significant. Therefore, the data from the three sex groups were pooled for each breed (18 animals per weight group).

The average ages of Large White [LW] and (Meishan [MS]) pigs weighing 20, 40, 60, 80 and 100 kg (live weight) were 60–63 and (80–83) days, 95–100 and (112–115) days, 130–136 and (146–150) days, 160–168 and (184–188) days, 185–195 and (245–260) days, respectively.

Comparison of the two breeds at equal weight was difficult because of major physiological differences between them: MS pigs are noted for their poor growth [3, 16] and early sexual maturity compared with European breeds (about 3 months for MS pigs compared with about 5–6 months for LW ones) [9, 29, 35]. If the two breeds are to be compared at equal weight, the MS pigs would therefore always be older than the LW ones. In the present study, MS pigs reached their sexual maturity at about 40 kg live weight compared with about 100 kg live weight in the case of LW pigs. If the two breeds are compared at the same age, they would therefore exhibit different body weights. The most relevant comparison seems to be at equal weights, because live weight is more important in pig production than age.

3.1. Enzyme activities

The activities of ACX, ME and G6PDH are presented in *tables I* and *II* for LW and MS pigs, respectively.

ACX catalyses the first step in fatty acid biosynthesis. There is considerable evidence to suggest that this enzyme has a key role in the regulation of fatty acid biosynthesis in animal tissues and ACX is generally considered as a rate-limiting enzyme for lipogenesis in animals [27] and especially in pigs [23, 33]. ACX activity in LW pigs was lower in the *Semimembranosus* than in the *Supraspinatus* muscle. The evolution in enzyme activity was very similar in both intermuscular adipose tissues, with a peak of 40 kg body weight in LW pigs. ACX activity in MS pigs presented a peak at 20 kg body weight and decreased thereafter in the four adipose tissues studied.

Table I. Lipogenic enzyme activities in Large White pigs.

Weight (kg)	Ham (Inter. A. T.)[1]	*Semimembranosus* muscle	Shoulder (Inter. A. T.)[1]	*Supraspinatus* muscle
		Acetyl-CoA-carboxylase[2]		
20	9.20[a]	1.52[a]	20.62[a]	1.76[ab]
40	26.10[b]	1.55[a]	29.64[b]	2.14[a]
60	11.84[a]	1.60[a]	17.81[a]	1.78[ab]
80	10.48[a]	1.38[a]	8.22[c]	2.06[a]
100	9.41[a]	1.18[b]	8.42[c]	1.49[b]
RSD[3]	5.39	0.42	6.96	0.51
Weight effect	$P < 0.001$	$P < 0.01$	$P < 0.001$	$P < 0.001$
		Malic enzyme[4]		
20	2.00[abc]	0.14[a]	2.29[abc]	0.16[ab]
40	2.61[a]	0.16[ab]	2.59[ac]	0.15[b]
60	2.38[ab]	0.21[bc]	2.64[a]	0.22[ad]
80	2.21[ab]	0.24[c]	2.83[a]	0.24[de]
100	1.83[bc]	0.26[c]	1.94[bc]	0.28[e]
RSD	0.59	0.06	0.65	0.06
Weight effect	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
		Glucose-6-phosphate dehydrogenase[4]		
20	3.10[a]	0.05[a]	4.07[a]	0.10[a]
40	3.36[a]	0.04[a]	4.16[a]	0.06[b]
60	2.28[b]	0.04[a]	2.42[b]	0.05[b]
80	1.68[bc]	0.03[a]	1.96[bc]	0.04[b]
100	1.43[c]	0.04[a]	1.47[c]	0.04[b]
RSD	0.77	0.02	0.67	0.03
Weight effect	$P < 0.001$	NS	$P < 0.001$	$P < 0.001$

[1] Intermuscular adipose tissue; [2] nmol HCO_3^-·min^{-1}·g^{-1}; [3] residual standard deviation; [4] µmol NADPH·min^{-1}·g^{-1}. Means within a column lacking a common superscript letter differ ($P < 0.05$).

ME and G6PDH are recognised to be the main enzymes involved in supplying NADPH for the reductive biosynthesis of fatty acids [36, 37]. Malic enzyme activities were similar in muscles in each breed. They increased with age in LW pigs and were relatively constant in MS ones. ME activities were relatively similar in both intermuscular adipose sites in each breed.

In LW pigs, G6PDH activities in both muscles were similar and constant while the activities decreased with ageing in both intermuscular adipose sites. In the intra- and intermuscular adipose tissues of MS pigs, G6PDH activities were high at 20 kg body weight and decreased thereafter. G6PDH activity was much lower than ME activity in the intramuscular adipose tissues of both breeds while G6PDH activity was higher than ME activity in the early period and lower than ME activity in the later period at the intermuscular adipose sites. These results concerning intermuscular adipose tissue are in accordance with a previous study [25]. Comparison of results for ME and G6PDH activities in inter- and intra-

muscular adipose tissue suggests that the latter adipose site might behave differently to other adipose sites, with regards to its metabolic activity, and this agrees with the previous work of Lee and Kauffman [18].

All three enzyme activities in muscle were lower than those of intermuscular adipose tissue in both breeds ($P < 0.001$). These findings indicate that although the intramuscular site exhibited low activity compared to other adipose tissues, it possessed substantially adequate levels of enzymes which would account for in situ lipid synthesis and deposition. These results confirmed previous studies [17, 19] and contradicted the hypothesis of Leites [21] and Allen et al. [1] who postulated that the major factor involved in regulating the accumulation of fatty acids in intramuscular adipose tissue might be the degradative process rather than the synthetic one.

Overall, ME activity in the muscles was higher in MS compared to LW pigs ($P < 0.01$), whereas ACX activity was lower in MS pigs ($P < 0.001$). G6PDH activity was relatively similar in both breeds. The highest differences in lipogenic enzyme activities between MS and LW pigs were found in intramuscular adipose tissue, and essentially concerned malic enzyme for which the activity was much higher in MS pigs ($P < 0.001$).

3.2. Total lipid content

Table III presents the total lipid content in both muscles of MS and LW pigs, at 20, 60 and 100 kg live weight. The lipid content of the *Supraspinatus* muscle was higher than that of the *Semimembranosus* muscle ($P < 0.05$) in each breed. The amount in lipids increased with age, in both muscles and both breeds ($P < 0.01$ or less). The muscle of MS pigs generally contained higher quantities of lipids than that of LW pigs ($P < 0.01$). These results can be related to the higher organoleptic quality (such as tenderness) of the MS pig meat. These results can also be related to the higher ME activity in the intramuscular adipose tissue of MS pigs. If we consider that the ME activity is an indicator of the lipogenic capacity and activity of adipose tissue, we can conclude that the lipogenesis potential is higher in the intramuscular adipose tissue of MS pigs. The correlation coefficients between the intramuscular content in lipids and ME activity in both muscles was 0.90 and 0.81 in MS and LW pigs, respectively, and 0.81 when both breeds of pigs were taken together. No such correlation between intramuscular adipose tissue lipid content and the two other lipogenic enzyme activities was found in the present study (the correlation coefficients were 0.1 and 0.3 for G6PDH and ACX, respectively, when both breeds of pigs were taken together). This strong association between fat content and ME activity was observed by Martin et al. [22] who described a higher activity of ME in Ossabaw (obese) pigs than in Yorkshire (lean) ones. More recently, Rothfuss et al. [31] and Renard et al. [30] found a high relation between ME activity and fatness in pigs selected against subcutaneous adipose tissue thickness. Malic enzyme therefore appears to be a major factor controlling the incidence of higher intramuscular fat in certain breeds of pigs.

4. CONCLUSION

The organoleptic qualities of pork, especially meat tenderness, are closely related to the amount of intramuscular adipose tissue. Our long-term objective is to control the amount of intramuscular adipose tissue in LW pigs which has been considerably decreased by selection. We must enhance this amount without increasing overall adiposity. One possibility would be to use the Meishan breed in crossbreeding systems to produce tender, juicier and more intensely flavoured meat, although there might be an associated risk of increasing global adiposity in the progeny. Another possibility would

Table II. Lipogenic enzyme activities in Meishan pigs.

Weight (kg)	Ham (Inter. A. T.)[1]	*Semimembranosus* muscle	Shoulder (Inter. A. T.)[1]	*Supraspinatus* muscle
		Acetyl-CoA-carboxylase[2]		
20	14.75^{a}	2.21^{a}	19.62^{a}	2.46^{a}
40	6.33^{b}	1.59^{a}	7.73^{b}	1.93^{bc}
60	5.28^{bc}	1.51^{a}	2.81^{c}	1.83^{bcd}
80	2.97^{cd}	1.49^{a}	2.64^{c}	1.82^{bcd}
100	0.43^{d}	1.49^{a}	1.53^{c}	1.50^{d}
RSD	2.67	0.32	3.35	0.39
Weight effect	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
		Malic enzyme[3]		
20	3.10^{a}	0.34^{a}	3.35^{a}	0.36^{a}
40	3.57^{a}	0.36^{a}	3.69^{a}	0.35^{a}
60	3.40^{a}	0.35^{a}	2.72^{b}	0.36^{a}
80	2.49^{b}	0.40^{a}	2.43^{b}	0.37^{a}
100	1.02^{c}	0.40^{a}	1.14^{c}	0.42^{a}
RSD	0.63	0.13	0.60	0.11
Weight effect	$P < 0.001$	NS	$P < 0.001$	NS
		Glucose-6-phosphate dehydrogenase[3]		
20	5.55^{a}	0.11^{a}	6.32^{a}	0.20^{a}
40	3.69^{b}	0.05^{a}	4.73^{b}	0.09^{b}
60	2.89^{bc}	0.07^{a}	2.51^{cd}	0.09^{b}
80	2.28^{c}	0.05^{a}	2.07^{cd}	0.06^{b}
100	0.80^{d}	0.07^{a}	0.91^{e}	0.06^{b}
RSD	0.94	0.05	0.74	0.08
Weight effect	$P < 0.001$	$P < 0.01$	$P < 0.001$	$P < 0.001$

[1] Intermuscular adipose tissue; [2] nmol HCO_3^-·min^{-1}·g^{-1}; [3] µmol NADPH·min^{-1}·g^{-1}. Means within a column lacking a common superscript letter differ ($P < 0.05$).

Table III. Total lipid content of *Semimembranosus* and *Supraspinatus* muscles, expressed as a percentage.

Weight (kg)	Large White		Meishan	
	Semimembranosus muscle	*Supraspinatus* muscle	*Smimembranosus* muscle	*Supraspinatus* muscle
20	2.13^{a}	2.39^{a}	2.80^{a}	3.21^{a}
60	2.25^{ab}	2.66^{ab}	2.91^{a}	3.37^{a}
100	2.56^{a}	2.96^{b}	3.51^{b}	4.13^{b}
RSD	0.43	0.46	0.35	0.33
Weight effect	$P < 0.01$	$P < 0.01$	$P < 0.001$	$P < 0.001$

Means within a column lacking a common superscript letter differ ($P < 0.05$).

be to study the malic enzyme gene and its regulation in both breeds of pigs, because of the importance of this enzyme in fatness propensity.

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