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EFFECT OF SOME BIOLOGICAL AND ZOOTECHNICAL FACTORS ON APPEARANCE OF GIANT FIBRES IN THE RABBIT. CONSEQUENCES ON MUSCLE FIBRE TYPE, MORPHOLOGY AND MEAT QUALITY

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ABSTRACT: Three experiments were carried out to investigate the contribution of some factors on the frequency of appearance and on histochemical and morphological traits of giant fibres (GF), and the effect of the GF presence on muscle fibre type and morphology and on meat quality. Experiment 1 tested the effect of the type of muscle (*biceps femoris* - BF, *gastrocnemius medialis* - GM, *soleus* - SOL, *semimembronosus proprius* - SMP, *longissimus lumborum* - LL, *psoas major* - PM). Experiment 2 considered the age at slaughter (5, 8 and 11 weeks) and feeding restriction (*ad libitum*: until 5 weeks of age, followed by slaughter; L-H: 70% *ad libitum* from 5 to 8 weeks of age, then 90% from 8 to 11 weeks; H-L: the opposite). Experiment 3 took into account the sire genetic origin (INRA9077, INRA3889, Hy+), the dietary energy concentration (H diet: 11.99 MJ DE/kg DM; L diet: 9.67 MJ DE/kg DM) and the age at slaughter (69, 74 or 84 days) at equal body weight (2.5 kg). On all muscles considered, GF were always classified into the 3 fibre types (αW, αR and βR) even though one or more fibre types were not present into the normal fibres of a given muscle. The type of muscle influenced (P<0.001) the appearance of GF (BF> GM = SOL = SMP > LL > PM). The frequency of appearance of GF was reduced as age increased (P<0.05). Animals with GF exhibited the highest pHu (BF: 5.83 *vs* 5.76, P<0.05), percentages (BF: 5.3 *vs* 3.6%, P<0.10) and cross-sectional area (LL: 1643 *vs* 1243μm^2, P<0.01) of βR fibres. Increasing numbers of GF in BF muscle also led to an increase in percentage of αR fibres (P<0.05), aldolase activity (P<0.01), and pHu (P<0.05).

RESUME: Effet des facteurs biologiques et zootechniques sur l'apparition des fibres musculaires géantes chez le lapin. Conséquences sur typage et surface des fibres musculaires et sur la qualité de la viande.
Dans le but d'étudier la contribution de plusieurs facteurs sur la fréquence d'apparition et sur les caractéristiques istochimiques et morphologiques des fibres géantes (GF) et l'effet de leur présence sur le typage et la morphologie des fibres musculaires et sur la qualité de la viande, 3 expérimentations ont été conduites. L'expérimentation 1 a évalué l'effet du type de muscle (*biceps femoris* - BF, *gastrocnemius medialis* - GM, *soleus* - SOL, *semimembronosus proprius* - SMP, *longissimus lumborum* - LL, *psoas major* - PM). L'expérimentation 2 a considéré l'âge à l'abattage (5, 8 et 11 semaines) et le rationnement alimentaire (*ad libitum*: jusqu'à l'âge de 5 semaines, suivi par l'abattage; L-H: 70% du *ad libitum* de 5 à 8 semaines, puis 90% de 8 à 11 semaines; H-L: l'opposé). L'expérimentation 3 a étudié l'effet du type génétique (INRA9077, INRA 3889, Hy+), la concentration énergétique de l'aliment (H: 11.99 MJ ED/kg MS; L: 9.67 MJ ED/kg MS) et l'âge à l'abattage (69, 74, 84 jours) à poids vif égal (2.5 kg). Dans tous les muscles, GF ont été toujours classifiées dans les 3 types de fibres (αW, αR and βR) même si les fibres normales d'un muscle donné ne présentaient pas un ou l'autre type de fibre. Le type de muscle a influencé significativement (P<0.001) l'apparition des GF chez les 13 animaux considérés dans l'expérimentation 1 (BF>GM=SOL=SMP>LL>PM). La fréquence d'apparition des GF a été réduite en augmentant l'âge à l'abattage (P<0.05). Les animaux avec GF ont présenté valeurs de pHu (m. BF: 5.83 *vs* 5.76, P<0.05), pourcentages (m. BF: 5.4 *vs* 3.7%, P<0.10) et dimensions (m. LL: 1643 *vs* 1243μm^2, P<0.01;) des fibres βR, les plus élevés. En augmentant le nombre des GF, la pourcentage des fibres αR (P<0.05), l'activité de l'aldolase (P<0.01) et le pH (P<0.05) sont augmentés.

INTRODUCTION

Giant fibres (GF) have been observed on histochemically stained sections taken from different muscles of turkey (DEFLESSELLE, 1994), chicken (KLOSOWSKA *et al.*, 1979), bovine (SINK *et al.*, 1986) and pigs (ESSÉN-GUSTAVSSON *et al.*, 1994). These fibres usually exhibit oval or round shapes and a large cross-sectional area. They are mainly located in groups or isolated at the periphery of a fascicle (SINK *et al.*, 1986). Overall energy metabolism is generally low in GF (CASSENS *et al.*, 1969) and they are classified as type IIB or type I (CASSENS *et al.*, 1969; HANDEL and STICKLAND, 1986; SOLOMON and EASTRIDGE, 1987). A high percentage of fast-twitch and glycolytic fibres (bovine and pigs), stressful treatments before slaughter, the halothane gene (pigs), Duchenne Muscular Dystrophy (man), and selection for meat production (turkey) are all factors related to an increase in the frequency of GF. Other important factors are the animal, its age and the type of muscle considered. Nevertheless, the effects of these factors are not yet well established. Moreover, the mechanisms leading to the appearance of GF in *post mortem* muscles are still not well understood. GF could be interpreted as an indicator of a disturbed metabolism and abnormal contraction of myofibres during *rigor mortis* development (KLOSOWSKA and KLOSOWSKI, 1985). An other hypothesis is that GF develop in relation to metabolic stress-situations occurring at slaughter. In pigs, the appearance of GF has been related to the presence of the halothane gene

Table 1 : Effect of type of muscle (n=6) and animal (n=13) on the frequency of appearance, average frequency per unit size and fibre type distribution of giant fibres (GF) (Experiment 1)

	LL	PM	BF	GM	SOL	SMP	P[1]		RSD
							Muscle	Animal	
Animals with GF[2]	2	1	11	7	7	7	***		
Number of GF/mm^2	0.05	0.27	0.28	0.33	0.39	0.07	n.s.	n.s.	0.40
Fibre type distribution of GF (%) :									
- βR	100.0	88.9	72.5	29.3	55.1	-	n.s.	n.s.	39.8
- αR	0	11.1	3.67	69.3	30.4	-	n.s.	n.s.	22.8
- αW	0	0	23.9	1.33	14.5	-	n.s.	n.s.	29.9

[1] Level of significance : *** : P<0.001 [2]chi-square test

(SOLOMON *et al.*, 1990, 1991) and metabolic stress-situations that speed up glycogenolysis, subsequent lactate accumulation and pH fall in muscle (ESSÉN-GUSTAVSSON *et al.*, 1994). In rabbits, the presence of GF in *post mortem* skeletal muscles has never been studied. The purpose of the present study was to characterise GF in rabbit muscles and investigate possible factors leading to their appearance.

MATERIAL AND METHODS

Animals and experimental design

Experiment 1

Thirteen INRA1077 male rabbits were fed *ad libitum* a commercial diet from weaning (28 days) to slaughter at 80 days of age (slaughter weight: 1567±146 g). Fifteen minutes after slaughter, the following six muscles were taken from each rabbit - *biceps femoris* (BF), *gastrocnemius medialis* (GM), *soleus* (SOL), *semimembronosus proprius* (SMP), *longissimus lumborum* (LL, 3rd – 7th lumbar vertebra), and *psoas major* (PM, 3rd – 7th lumbar vertebra). The muscles were frozen in isopentane cooled by liquid nitrogen. Samples were stored at –80°C until histochemical analysis.

Experiment 2

At weaning, 50 hybrid rabbits were divided into 5 groups (labelled blocks, table 2). Block 1 was fed *ad libitum* with a commercial diet until slaughter at 5 weeks of age. The remaining rabbits were fed the same diet until slaughter, but with different restriction levels. Rabbits coming from blocks 2 and 3 received 70% and 90% of *ad libitum*, respectively, from 5 to 8 weeks of age; the animals belonging to blocks 4 and 5 received 70% and 90% of *ad libitum*, respectively, up to 8 weeks. At 8 weeks, the , restriction levels were reversed until slaughter at 11 weeks of age.

All the animals were weighted before slaughtering and the BF muscles were immediately dissected. One BF muscle was frozen in isopentane cooled by liquid nitrogen and stored at –80°C until histochemical analysis. The other was used for ultimate pH (24 h *post mortem*, pHu) and L*a*b* colour measurements (OUHAYOUN and DALLE ZOTTE, 1996). It was then ground with a Dangoumau ball mill and stored at –80°C until the final determination of enzyme activities characteristic of the glycolytic (aldolase) and oxidative (NADP-isocitrate dehydrogenase: ICDH) energetic pathways (BACOU, 1972).

Experiment 3

Fifty rabbits coming from one dam strain (INRA 1067; adult body weight 3.6 kg) and 3 sire strains (INRA9077: adult b.w. 4.1 kg; Hy+: 5.1 kg; INRA3889: 3.1 kg) were used. At weaning, half of the INRA9077 and Hy+ sired rabbits were fed the H diet (11.99 MJ DE/kg DM), the other half the L diet (9.67 MJ DE/kg DM). The INRA3889 sired rabbits were fed with the H diet only. The rabbits of the 5 groups (blocks) were slaughtered when the group average body weight reached 2.5 kg (table 5). Immediately after slaughter, the LL muscle was taken and treated as described for experiment 1. Growth performance, carcass composition, meat physicochemical and LL histochemical traits are reported elsewhere (DALLE ZOTTE and OUHAYOUN, 1998).

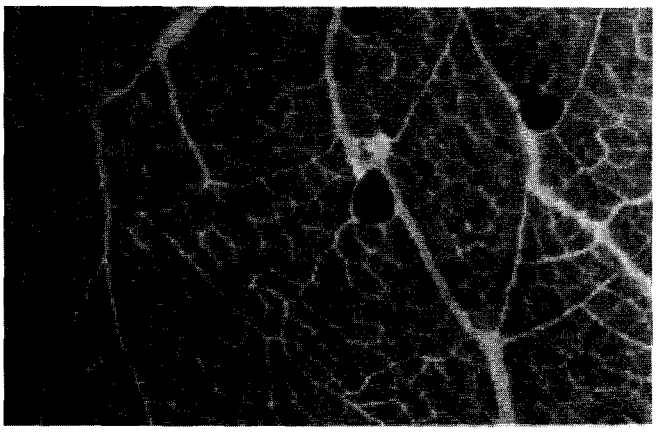

Figure 1 : Example of fibre cross-sections stained with azorubine. The GF's result more markedly stained than normal fibres.

Table 2 : Effect of age and feed restriction combination (block) on slaughter weight, frequency of appearance, average frequency per unit size and fibre type distribution of GF in BF muscle (Experiment 2)

Block	1	2	3	4	5	P(1) block	RSD
Slaughter age (days)	35	56	56	77	77		
Feed restriction	*ad libitum*	70%	90%	70-90%	90-70%		
Number of rabbits	10	10	10	10	10		
Slaughter weight (g)	1064^{A}	1536^{B}	1814^{C}	2413^{E}	2216^{D}	***	72.4
Animals with GF	8	6	8	6	5		
Number of GF/mm²	0.67	0.65	0.47	0.17	0.16	P<0.10	0.42
Fibre type distribution of GF (%):							
- βR	77.1	73.6	61.2	45.8	80.0	n.s.	37.7
- αR	6.3	16.7	16.7	12.5	0	n.s.	27.8
- αW	16.7	9.7	22.1	41.7	20.0	n.s.	31.6

(1)Level of significance : *** or A, B, C, D, E : P<0.001

Muscle analysis

For histochemical analyses, six serial cross-sections from each muscle were obtained with a cryostat at -20°C. One section was stained with azorubine (reference stain). Four sections were processed for the mATPase activity after acid or alkaline pre-incubation (GUTH and SAMAHA, 1970). The sixth was stained for succino-dehydrogenase (SDH) activity (NACHLAS *et al.*, 1957). Computerised image analysis (BUCHE, 1990) was used to type the fibres according to ASHMORE and DOERR (1971). For each muscle fibre type (βR, αR and αW) the respective percentage and mean cross-sectional area was determined.

On each section stained with azorubine the giant fibres (GF) were counted and their average frequency per unit size of muscle section calculated (figure 1). Using the combined information from the other stained serial cuts, the GF fibre type distribution was determined.

Statistical analysis

Analysis of variance was performed using the GLM procedure of SAS (SAS Institute, 1990) with different fixed effects; muscle, animal and muscle x animal interaction in experiment 1, combined effects of "diet-age", presence/absence of GF and their interactions in experiment 2, and combined effects of "diet-sire genetic origin-age", presence/absence of GF and their interactions in experiment 3. In experiments 2 and 3, the number of GF was used as a covariate. Least square means were calculated for all the effects involved in the models. Variability was expressed as residual standard deviation (RSD) for each character.

Table 3 : Effect of GF presence and age x feed restriction combination (block) on fibre type distribution, fibre cross-sectional area and physicochemical traits of BF muscle (n= 50) (Experiment 2)

	GF		Probability (1)		RSD
	No	*Yes*	Presence of GF	Block effect	
Fibre type distribution (%):					
- βR	3.6	5.3	P<0.10	***	2.9
- αR	27.4	26.4	n.s.	***	4.6
- αW	69.0	68.3	n.s.	***	5.1
Fibre cross-sectional area (µm²):					
- βR	970	1040	n.s.	***	252
- αR	896	1017	n.s.	***	239
- αW	1483	1518	n.s.	***	279
Aldolase (IU/g)	701.5	729.1	n.s.	***	54.4
ICDH (IU/g)	5.49	5.55	n.s.	***	0.68
Aldolase/ICDH	136.0	143.9	n.s.	***	20.9
pHu(2)	5.76	5.83	*	***	0.08
L*(2)	57.7	57.6	n.s.	P<0.10	2.6
a*(2)	5.2	5.7	n.s.	n.s.	2.2
b*(2)	3.3	3.3	n.s.	n.s.	1.8

(1)Level of significance : *: P<0.05 ; *** : P<0.001 (2) Only blocks 2 to 5

RESULTS AND DISCUSSION

Classification of Giant Fibres (GF)

Giant fibres were always found isolated and randomly distributed in muscles. In all experiments, GF were mainly classified as βR while the remaining ones were shared between the αW and αR fibre types. In the pig, GF fibres were identified as type IIB (comparable to αW fibres) (SOSNICKI, 1987), as mainly (60%) type I (comparable to βR) (HANDEL and

Table 4 : Effect of GF number (GFn) on fibre type distribution, fibre cross-sectional area and physicochemical traits of BF muscle (n= 50) (Experiment 2)

	Regression Coefficient GFn	P[1] Regr. Coeff. GFn	Interaction GFn x block	RSD
Fibre type distribution (%):				
- βR	0.15	n.s.	n.s.	2.84
- αR	-0.20	n.s.	n.s.	4.52
- αW	0.05	n.s.	n.s.	5.08
Fibre cross-sectional area (μm^2)				
- βR	15.8	n.s.	n.s.	232.4
- αR	17.0	*	n.s.	208.2
- αW	9.4	n.s.	n.s.	256.1
Aldolase (IU/g)	5.95	**	*	50.09
ICDH (IU/g)	-0.01	n.s.	n.s.	0.66
Aldolase/ICDH	1.89	*	*	19.04
pHu[2]	0.01	*	n.s.	0.08
L*[2]	0.10	n.s.	n.s.	2.66
a*[2]	-0.06	n.s.	n.s.	2.33
b*[2]	-0.07	n.s.	n.s.	1.82

[1]Level of significance : *: P<0.05 ; ** : P<0.01 [2] Only blocks 2 to 5

STICKLAND, 1986) or completely as type I (SOLOMON and EASTRIDGE, 1987). In pigs, GF are never classified as αR (or type IIA) muscle fibres. In the rabbit, GF can be typed as βR, αR or αW and the typing does not exactly reflect that of their originating muscle (table 1). In consequence, it can be concluded that every normal muscle fibre type is able to be transformed in GF.

Experiment 1

Twelve out of the 13 animals presented GF in at least one muscle. The type of muscle significantly affected the presence of GF (P<0.001): eleven animals presented GF on BF, meanwhile only 1 or 2 GF are reported in the PM or LL, respectively (table 1). In the rabbit, the incidence of GF was not positively related to the frequency of normal IIB fibres, as reported in pigs (SOLOMON and EASTRIDGE, 1987). Indeed, the muscles exhibiting the highest proportions of αW fibres (*i.e.* 80% in PM m. and 56% in LL m., on average), contained very few GF. Contrary to the results reported in pigs by DUTSON *et al.* (1978), the present experiment shows that the presence of GF in a given muscle, does not imply that GF are also present in the other muscles of the rabbit. The average number of GF/mm^2 decreased according to the type of muscle in the rank order: SOL (0.39) > GM (0.33) > BF (0.28) > PM (0.27) > SMP (0.07) > LL (0.05). Moreover, the three fibre types were always represented in GF of hindleg muscles (SMP m. was not typed) even though some of these muscles do not normally contain the three fibre types. This suggests that when normal fibres transform to GF, they change not only their oxidative pathway, but also their contraction speed. It is the case for SOL m. which normally contains only βR (88%) and αR (12%) fibres (ALASNIER et al., 1996), whereas 15% of GF are αW (table 1). Appearance of GF in a given muscle is associated with modification of the fibre type proportion of that muscle. However, it is not yet clear if it is the GF appearance that induces the abnormal fibre type change or the opposite.

Experiment 2

Thirty three of the 50 animals presented GF in the BF muscle. Table 2 shows the combined age and feed restriction effects (block) on the appearance and on the fibre type distribution of the GF found in the BF

Table 5. Effect of genotype x dietary energy density x age combination (block) on frequency of appearance, average frequency per unit size and fibre type distribution of GF in LL muscle (Experiment 3)

Block	1	2	3	4	5	P[1] Block	RSD
Sire genetic origin	**INRA9077**	**Hy+**	**INRA3889**	**INRA9077**	**Hy+**		
Adult body weight (kg)	**4.1**	**5.1**	**3.1**	**4.1**	**5.1**		
Diet	**H**	**H**	**H**	**L**	**L**		
Slaughter age (days)	**74**	**69**	**84**	**84**	**74**		
Number of rabbits	10	10	10	10	10		
Animals with GF	4	5	2	1	2		
Number of GF/mm^2	0.12	0.16	0.11	0.08	0.14	n.s.	0.08
Fibre type distribution of GF(%):							
- βR	77.5^b	28.3^a	0	100^b	83.3^b	*	31.1
- αR	0	15.0	0	0	0	n.s.	22.4
- αW	22.5^a	56.7^{ab}	100^b	0	16.7^a	P<0.10	31.5

[1]Level of significance : * or a, b : P<0.05

Table 6 : Effect of GF presence and genotype x dietary energy density x age combination (block) on fibre type distribution and fibre cross-sectional area of LL muscle (n = 50) (Experiment 3)

	GF		P[(1)] Presence of GF	P[(1)] block	RSD
	No	*Yes*			
Fibre type distribution (%):					
- βR	1.8	1.9	n.s.	P<0.10	1.4
- αR	19.7	20.9	n.s.	n.s.	4.2
- αW	78.5	77.2	n.s.	n.s.	4.3
Fibre cross-sectional area (μm²):					
- βR	1243	1643	**	*	412
- αR	1355	1442	n.s.	*	340
- αW	1975	1979	n.s.	*	409

[(1)]Level of significance : *: P<0.05 ; ** : P<0.01

muscle. The number of GF per unit area was slightly influenced by age (P<0.10; table 2). A decrease in the number of GF/mm² as the rabbits aged was observed. The compensatory growth of the early restricted animals (block 4) tended to increase the percentage of fast-twitch glycolytic fibres (αW) to the detriment of the slow twitch ones (βR). The opposite tendencies were observed for the late feeding restriction (block 5).

When animals presented GF, they exhibited a higher percentage of βR normal fibres (5.3 *vs* 3.6; P<0.10) and higher pHu values (5.83 *vs* 5.76; P<0.05) in BF muscle (table 3). The effects of the presence of GF on pHu values are opposite to what is found in halothane homozygote or stressed pigs (ESSÉN-GUSTAVSSON *et al.*, 1994). This different metabolic effect between the pig and rabbit has previously been reported, particularly in response to stress situations (DALLE ZOTTE *et al.*, 1995). The non-significant interaction between presence of GF and block indicate that the fibre type distribution and meat physicochemical traits of animals with or without GF in BF were not significantly different when submitted to the age and feed restriction effects. As the number of GF increased (table 4), the area of αR fibres (P<0.05), the aldolase activity (P<0.01), the aldolase/ICDH ratio (P<0.05) and the pHu (P<0.05) values also increased. Moreover, the aldolase activity and the aldolase/ICDH ratio were significantly influenced by the number of GF x block interaction (P<0.05). The regression coefficient was highly significant in block 4 (77 days of age, feed restriction 70-90%), indicating an increase of 28.3 IU of the aldolase activity for every GF found. To a lesser extent, a similar trend was observed for pHu (block 4: +0.03 pHu unit for every GF found, P<0.05). An increase of the muscular glycolytic energy metabolism causes a decrease of pHu mainly due to lactate accumulation. The presence and, more markedly, the number of GF on aldolase activity and on pHu increases is difficult to explain. Zootechnical factors (*peri-mortem* stress conditions) and/or individual susceptibility to develop GF could have altered this equilibrium in the rabbit, *i.e.* by inactivating the glycolytic enzymes at lower lactate concentrations.

Table 7 : Effect of GF number (GFn) on fibre type distribution and fibre cross-sectional area of LL muscle (n = 50) (Experiment 3)

	Regression Coefficient GFn	P Regr. Coeff. GFn	RSD
Fibre type distribution (%) :			
- βR[a]	0.62	P<0.10	1.37
- αR	0.29	n.s.	4.43
- αW	-0.91	n.s.	4.49
Fibre cross-sectional area (μm²) :			
- βR[b]	82.9	n.s.	429.5
- αR	18.0	n.s.	344.7
- αW	-29.0	n.s.	397.6

[a] block 4, regression coefficient : 3.32 (P<0.05) ; [b] block 1, regression coefficient : 212 (P<0.05)

Experiment 3

Fourteen of the 50 animals had GF in their LL muscles. The highest number of rabbits presenting GF were those fed the H diet (table 5). Youngest rabbits at equal commercial slaughter weight (blocks 1, 2 and 5) and rabbits selected for rapid growth (Hy+ > INRA9077) exhibited more GF/mm². Analogous age and selection effects were found in turkeys (DUPAS, 1992; WILSON *et al.*, 1990). According to SOSNICKI *et al.* (1991), selection for increased muscle size in modern turkey strains, coupled with minimal physical activity, may predispose the animals to muscle abnormalities, such as hypercontracted (hyalinized) muscle fibres, by altering the vascular supply at the terminal capillary bed level.

Table 5 also reports the combined genotype x dietary energy density x age effect (block) on fibre type distribution of GF in LL. The block significantly influenced the proportion of the βR fibres (P<0.05) and, to a lesser extent, the αW fibres (P<0.10) of GF. Block 3 (INRA3889 sired, H diet, 84 days of age) was characterised by the absence of GF fibres typed βR or αR while all the GF were of the βR type in block 4 (INRA9077 sired, L diet, 84 days of age). A small proportion of GF (15%) were classified as αR in block 2. These results seem to indicate a sire genetic origin effect for the presence of oxidative GF (INRA9077 > Hy+ > INRA3889) and a diet effect (more oxidative

GF in animals fed the L diet). Nevertheless, the small number of animals with GF suggests further investigation in this area. .

In animals with GF, the fibre cross-sectional area of βR fibres of LL was larger than that of animals without GF (1643 *vs* 1243μm^2, P<0.01; table 6) reinforcing the trend observed in experiment 2. The GFxblock interaction was never significant.

The increase in the percentage of βR fibres was positively linked to the increase in the number of GF with a general regression coefficient of 0.62 (P<0.10), depending on the significance of the regression coefficient of block 4 (INRA9077 sired; L diet: 3.32; P<0.05) (table 7). As observed in experiment 2, when the number of GF increased, the average area of oxidative fibres increased as well (for every GF found, area of βR and αR fibres increased 82.9 and 18.0μm^2, respectively, n.s.). Block 1 (INRA9077 sired; H diet) exhibited a significant (P<0.05) regression coefficient of the βR fibre area (increase of 212μm^2 for every GF found). This suggests that, if compared to the other sire strains, INRA9077 seemed to be the more susceptible to variations in percentage and area of normal βR fibres as the number of GF increased.

CONCLUSIONS

In the rabbit the main factors that influence the frequency of GF are the type of muscle, the age at slaughter, the energy content of the diet and the genetic origin of the animals. It is probable that, even in the rabbit, individual susceptibility to develop GF exists, derived from both higher fragility of cell membranes and fibre hypercontraction. The presence of the three fibre types in GF seems to support the hypothesis that they are involved in abnormal muscular energy metabolism and contraction speed, whereas the hypothesis that they represent a different fibre type is less probable. The presence of GF significantly increases the percentage and area of βR fibres and the pHu of the muscles. The positive regression coefficients between number of GF and aldolase activity and pHu indicate that high frequencies of GF could have some influence on rabbit meat quality. It has not been disproven that the individual tendency to develop GF could be associated with a tendency towards abnormal muscular energy metabolism of normal fibres, too.

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