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Original article

Microstructure of skeletal muscles of growing calves fed silage-based *vs* hay-based diets. I. Fibre diameters

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Summary — Samples of musculus longissimus dorsi, semimembranosus and semitendinosus were obtained post-slaughter from 2-week, 3-month and 10-month-old bull calves. The 2-week-old calves were fed milk only. All the remaining animals were fed grass silage or hay *ad lib* and a restricted amount of concentrate from 2 weeks of age onwards. Muscle fibres were differentiated according to Ziegan into fast-twitch glycolytic, fast-twitch oxidoglycolytic and slow-twitch oxidative fibres (FTG, FTO and STO, respectively). In all calves, marked fibre growth took place between 3 and 10 months of age. From the 2nd week to the 3rd month, growth was observed virtually only in the FTG fibres, irrespective of feeding. Feeding calves with a silage-based *vs* hay-based diet resulted in thicker muscle fibres for each type of fibre. Significant linear regression coefficients have shown the fibre diameters to be clearly related to live weight gain resulting from DM intake that was higher in the silage-based diet.

calf / skeletal muscle fibre / silage / hay

Résumé — Microstructure des muscles squelettiques chez les veaux à l'ensilage ou au foin. I. Diamètre des fibres musculaires. *Après l'abattage de veaux âgés de 2 semaines, de 3 mois et de 10 mois on a prélevé des échantillons de muscles : longissimus dorsi, semimembranosus et semitendinosus. Les veaux âgés de deux semaines ont été nourris au lait. Les veaux restants recevaient de l'ensilage d'herbe ou du foin à volonté et une quantité limitée de concentré. D'après la méthode de Ziegan (1979) on a distingué des fibres musculaires glycolytiques et oxydatives glycolytiques à contraction rapide (FTG et FTO) et des fibres oxydatives à contraction lente (STO). Chez tous les taurillons de 3 à 10 mois, on a constaté l'augmentation rapide du diamètre des fibres musculaires, mais chez les animaux de 2 semaines à 3 mois, on a observé seulement l'augmentation du diamètre des fibres FTG, indépendamment du régime alimentaire. Les fibres musculaires étaient plus épaisses chez les veaux nourris à l'ensilage que chez ceux nourris au foin. Les coeffi-*

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cients significatifs de la régression linéaire indiquent que le diamètre des fibres musculaires est lié à la vitesse d'accroissement du poids vif des animaux analysés. C'est le résultat d'une ingestion plus grande de matière sèche par les animaux à l'ensilage.

veau / fibre musculaire / ensilage / foin

INTRODUCTION

Animal growth is influenced by genetic and nutritive factors (Breewinkle *et al,* 1979; Seideman and Crouse, 1986). Increasing age and increase in live weight are accompanied by an increase in muscle fibre diameter and changes in the percentage of enzymatically differentiated fibre types (Kłosowski *et al,* 1988). Basically, skeletal muscles are composed of white (fast-twitch glycolytic, FTG), red (slow-twitch oxidative, STO) and intermediate (fast-twitch oxidoglycolytic, FTO) fibres. The thinnest fibres are generally the STO and FTO, whereas the FTG are the thickest. Thus within a given muscle the proportion between individual fibre types may affect both its size and metabolism. There are inter-individual and inter-muscle differences in the distribution of different fibre types, as well as their share in the total muscle weight. Kłosowski and Kłosowska (1984) and Kłosowski *et al* (1988) reported that the faster the animals' growth as affected by feeding, the larger the fibre diameter and higher the percentage of FTG fibers. In growing calves reared on hay-free low-concentrate diets based on grass silage, satisfactory gains have been reported (Marsh, 1975, 1976; Bartholomew *et al,* 1981; Bidwell-Porębska *et al,* 1987; Piotrowski *et al,* 1988) with no simultaneous mention of any detrimental effect on the animals' health. However, Rumsey *et al* (1987) found differences in carcass characteristics (lean score for colour, firmness and shrinkage, fat over the ribeye, longissimus muscle area, estimated kidney, pelvic and heart fat, USDA yield grade and USDA quality grade) between steers fattened on concentrate-based *vs* silage-only diets. Moreover, Pellegrini *et al* (1982) have reporting results obtained in 3 animals only, and suggested that feeding heifers exclusively on maize silage led to myopathia and muscular dystrophy. Investigations presented here constitute an attempt at evaluating the possible relation between diet and fibre diameter in different muscles of growing calves.

MATERIAL AND METHODS

Animals

The data were collected on 25 Polish Friesian bull calves born in the autumn and reared during the winter months. All the animals were brought to the Jastrzebiec Experimental Farm at the age of approximately 10 days, and placed in a heated, old-fashioned calf-shed. Until the calves reached 14 days of age, milk only was provided (10% live weight). On day 14, 5 randomly selected calves (henceforth referred to as "newborn" calves) were slaughtered and muscle tissue samples were taken. The remaining 20 calves received 300 g of concentrate daily, with milk provided as before. On the 42nd day of life, the calves were weaned and the daily concentrate allowance was increased to 1 000 g/head. This level of concentrate feeding was maintained until the age of 91 days. Vitamin and mineral mixtures (Polfamix® and Tetamix®, Polfa, Poland) were added to the concentrate according to the manufacturer's instructions.

On day 14, the calves were randomly assigned to one of the following groups: group I: meadow hay cut into 3–5-cm long chaff; group

II: grass silage prepared with Acidol II (acetic, sulphuric, phosphoric acid and water, 16:1:1:2, 4 kg/ton of fresh material).

Silage or hay were provided *at libitum* until day 91, when 5 calves from each group were slaughtered and muscle tissue samples were taken. These animals are henceforth referred to as "younger" calves.

The remaining animals, henceforth referred to as "older" calves, still received 1 000 g/head of concentrate per day. Silage or hay were again offered *ad libitum*, as follows: group Ia (2nd half of group I), natural length meadow hay until slaughter; group IIa (2nd half of group II), grass silage prepared with Acidol II until the 5th month, and then maize silage until slaughter.

Animals from group I and Ia will henceforth be referred to as hay diet (HD) fed, and those from groups II and IIa as silage diet (SD) fed calves.

The older calves were slaughtered and muscle samples were taken at approximately 250 kg (242–256) live weight (LW). This meant that due to the different daily weight gains, animals from group Ia were slaughtered at an average age of 338 days (325–350) and those from group IIa at 305 days (298–309). However, 2 calves from group IIa died before reaching the weight of 250 kg – one broke a leg, the other did not survive an acute bloat. Thus the results refer to 5 animals in group Ia and only 3 in group IIa.

Muscle sampling and preparation

The following muscles were sampled: musculus longissimus dorsi (LD) from the lumbar region, at the level of the processus transversus of L2, m semimembranosus (SM) and m semitendinosus (ST) from the medial portion. Single tissue samples were taken from all the slaughtered calves (right side of carcass) approximately 1 h *post-mortem* and were immediately frozen in liquid nitrogen and sectioned in a cryostat. Ten-μm thick sections were subjected to double reaction for activity of NADH tetrazolium oxidoreductase and myosin ATPase after acid preincubation (Ziegan, 1979). Sections were stained with hematoxylin – eosin according to Van Gieson (Dubowitz *et al,* 1973). Fast-twitch glycolytic (FTG), slow-twitch oxidative (STO) and fast-twitch oxidoglycolytic (FTO) fibres were obtained as light brown, dark brown and blue, respectively. The smallest diameters (Brooke, 1970) of fibres belonging to each type were determined by measuring 200 fibres/muscle/animal on a lanameter. Moreover, the muscle tissues were carefully examined for the presence of any pathologies.

Statistics

A 1-way analysis of variance was applied using the least-squares method. The relationship between LW gains and fibre diameter was estimated by the linear regression as:

$$y = \mu + \beta (x - \bar{x})$$

where: y = expected mean fibre diameter;

μ = mean fibre diameter;

β = regression coefficient;

x = obtained LW gain;

$\bar{x}$ = mean LW gain.

Daily LW gains and corresponding fibre diameters were arranged pairwise and analysed with no reference to feeding system or age at slaughter. Moreover, the relationship between fibre diameter and daily gains was examined as related to age, feeding system and interaction between the two. Daily LW gains were calculated from 14 or 42 days (weaning) of age.

RESULTS

Intake and LW gains

An attempt at eliminating the effect of the milk feeding period was made by presenting live weight gains not only for the entire experimental period (14 days to slaughter), but also within the weight range of 42 days to slaughter.

The LW gains in both younger and older animals were higher in SD fed than in HD fed calves (table I). This corresponds to higher dry matter (DM) intake in animals kept on SD. As the concentrate offered at

Table I. Mean daily intake and daily live weight (LW gains).

Age range	*Younger calves*		*Older calves*	
	HD fed	*SD fed*	*HD fed*	*SD fed*
14 days of age till slaughter				
LW gain (g)	447	506	617	713
Intake DM (g/day)	1 003	1 155	3 075	4 599
CP (g/day)	205	233	501	478
GE (MJ/day)	18.5	22.0	59.5	86.9
CP/GE	11.1	10.6	8.4	5.5
42 days of age till slaughter				
LW gain (g)	393	534	617	736
Intake DM (g/day)	1 140	1 391	3 279	4 944
CP (g/day)	222	265	532	510
GE (MJ/day)	19.4	24.8	63.6	94.3
CP/GE	11.5	10.7	8.4	5.4

a strictly limited level was always fully consumed, the difference in DM intake reflects the consumption of forages.

In the younger calves the intake of crude protein (CP) and gross energy (GE) was also slightly higher in the SD fed group. In the older animals the daily intake of GE was considerably higher, while the intake of CP was lower in the SD than in the HD fed group (table I). This was caused by introducing maize silage in the place of grass silage at the age of 5 months, which of course, also affected the CP/GE ratio (g CP/1 MJ GE).

Fibre diameter

In all SD fed calves (pooled data for younger and older calves) the mean fibre diameters were always higher by 2–5 μm than those found in all (similarily pooled) HD fed animals (tables II–IV). According to a 1-way analysis of variance, these differences appeared non-significant only for FTO and both oxidative fibres (BO) in SM muscle (table III). Differences between the feeding systems in younger calves showed a pattern identical to that observed in older animals (tables II–IV), being non-significant for FTG in all muscles, and also for FTO in LD and STO in SM muscle. For BO fibres, the effect of the feeding system was found to be significant in each of the 2 age groups considered.

Similarly, a 1-way analysis of variance indicated that all younger calves (pooled data for SD and HD fed) had mean fibre diameters 12–28 μm smaller (tables II–IV) than the older (similarly pooled) animals; the differences were found to be significant in all muscles and for all types of fibre. The relations between younger calves and newborn calves were less definite. Nevertheless, FTG and STO were found to be thinner and FTO to be thicker in newborn calves (tables II–IV); for STO fibres in both LD and SM muscles the respective differences were not found to be significant.

Since the SD calves had, in almost all cases, significantly greater fibre diameters and higher LW gains than HD fed animals

Table II. Mean fibre diameters (μm) m longissimus dorsi. Fibre types: FTG: fast twitch glycolytic; STO: slow twitch oxidative; FTO: fast twitch oxidoglycolytic; BO: both oxidative; AT: all types.

Age group and feeding		*FTG*	*STO*	*FTO*	*BO*	*AT*
Newborn calves	Milk only	22.8 ABDE	20.4 AE	19.5 ABDE	20.0 AB[ab]	21.7 ABD
Younger calves	Silage diet	27.7 D	21.7 CE	16.6 D	18.8 D[a]	21.9[a]
	Hay diet	25.5 E	19.7 C	14.8 E	16.8 D[b]	19.0[a]D
Older calves	Silage diet	49.9	33.6 D	28.1	30.9 E	37.2[b]
	Hay diet	49.4	31.7 D	28.2	30.0 E	36.5[b]
Total silage diet fed calves		38.3 F	27.7 F	22.6 F	25.6 F	30.4 E
Total hay diet fed calves		33.4 F	24.5 F	20.1 F	22.1 F	26.1 E
Total younger calves		26.6 AC	20.6 B	15.8 AC	17.8 AC	20.5 AC
Total older calves		49.7 BC	32.8 AB	28.1 BC	30.6 BC	36.8 BC

Within columns, means bearing the same letters differ significantly (capitals $P < 0.01$; small letters: $P < 0.05$).

Table III. Mean fibre diameters (μm), m seminebranosus.

Age group and feeding		*FTG*	*STO*	*FTO*	*BO*	*AT*
Newborn calves	Milk only	25.7 ABD[a]	19.9 AC	20.6 ABFG	20.4 ABF[a]	22.3 ABC
Younger calves	Silage diet	27.9 D	19.2	17.9 DF	18.9 DF	21.4[ac]
	Hay diet	26.6[a]	21.8 C	17.2 DG	19.5 D[a]	22.0[a]
Older calves	Silage diet	50.8	35.4	28.1 E	32.0 E	38.4[b]
	Hay diet	50.0	35.4	32.1 E	33.8 E	39.3[b]
Total silage diet fed calves		38.2 E	27.7[a]	23.4	26.0	31.8 D
Total hay diet fed calves		34.9 E	26.8[a]	23.0	25.0	28.8 D
Total younger calves		27.3 AC	20.6 B	17.5 AC	19.2 AC	21.8 AC
Total older calves		50.5 BC	35.4 AB	29.6 BC	32.7 BC	38.8 BC

Within columns, means bearing the same letters differ significantly (capitals: $P < 0.01$; small letters: $P <$-0.05). Abbreviations explained in table II.

Table IV. Mean fibre diameters (μm), m semitendinosus.

Age group and feeding		*FTG*	*STO*	*FTO*	*BO*	*AT*
Newborn calves	Milk only	24.9 ABDE	20.0 ABEF	20.6 ABFG	20.1 AB	21.6 AB
Younger calves	Silage diet	26.8 D	21.5 E	18.5 DF	20.1 D	22.0 D
	Hay diet	26.7 E	21.5 F	17.8 DG	19.5 D	21.8 D
Older calves	Silage diet	54.7	39.7 D	32.8 E	36.6 E	42.9 E
	Hay diet	53.9	37.5 D	30.8 E	34.0 E	40.5 E
Total silage diet fed calves		39.5 F	30.6 G	26.4 H	29.1 F	32.9 F
Total hay diet fed calves		36.3 F	27.2 G	23.3 H	25.6 F	29.6 F
Total younger calves		26.8 AC	21.5 AC	18.2 AC	19.8 AC	21.9 AC
Total older calves		54.4 BC	38.9 BC	32.1 BC	35.7 BC	42.0 BC

Within columns, means bearing the same letters differ significantly (capitals: $P < 0.01$. Abbreviations explained in table II.

a linear regression analysis was made to examine the relationship between the 2 variables mentioned (tables V, VI). A marked positive and highly significant relationship was found for LW gains and diameters of all fibres in LD muscle. For the remaining 2 muscles the relationships were less clear. Nevertheless, the relationship between LW gains and fibre diameters seemed to be more pronounced after the withdrawal of milk from the diet (table V *vs* VI). The interrelationship between fibre diameter and LW gains was in all cases significantly affected by age, and in some cases also by feeding and an interaction between the 2 factors.

Muscle pathologies

The rearing system applied was not found to induce any pathological changes in the muscle tissue of younger calves. Cross-sections of fibres were polygonal. Fibres were closely adjacent to each other, with numerous nuclei beneath sarcolemma and were assembled in bundles separated by thin connective tissue.

In 2 older SD fed calves, some tiny dystrophic fibres were observed. Darker-stained fibres also occurred, with an elliptical cross-section, or wider inter-fibre spaces.

Table V. Relationship between fibre diameter (y, µm) and daily gains of calves (x, kg) as calculated for the period from 14 days of age to slaughter.

Muscle	*Fibre*	*Regression coefficient*	*Regression equation (given only when regression coefficient was significant)*	*Effect on the relationship between fibre diameter and LW gains of:*		
				Age (A)	*Feeding (F)*	*Interaction (A x F)*
LD	FTG	7.5 *xx*	$y = 38.01 + 7.5\ (x - 0.586)$	*xx*	NS	*x*
	STO	12.3 *xx*	$y = 26.59 + 12.3\ (x - 0.596)$	*xx*	NS	NS
	FTO	11.5 *xx*	$y = 21.97 + 11.5\ (x - 0.592)$	*xx*	NS	*x*
	BO	10.2 *xx*	$y = 24.20 + 10.2\ (x - 0.599)$	*xx*	NS	NS
	AT	8.5 *xx*	$y = 28.72 + 8.5\ (x - 0.600)$	*xx*	*x*	*xx*
SM	FTG	0.3 NS		*xx*	*x*	NS
	STO	5.8 *xx*	$y = 28.02 + 5.8\ (x - 0.587)$	*xx*	NS	*xx*
	FTO	5.8 *xx*	$y = 23.80 + 5.8\ (x - 0.581)$	*xx*	*xx*	*xx*
	BO	0.5 NS		*xx*	*xx*	*x*
	AT	0.3 NS		*xx*	*x*	NS
ST	FTG	5.4 *xx*	$y = 40.44 + 5.4\ (x - 0.581)$	*xx*	NS	NS
	STO	2.3 NS		*xx*	NS	*xx*
	FTO	0.4 NS		*xx*	*x*	NS
	BO	1.7 NS		*xx*	*xx*	*xx*
	AT	1.9 NS		*xx*	*xx*	*xx*

x: significant at $P < 0.05$; *xx*: significant at $P < 0.01$; NS: non significant. Abbreviations explained in table II.

DISCUSSION

Muscle fibre diameters were affected by both feeding system and calves age, particularly for fibres with glycolytic metabolic capacity (FTG). FTG diameter evidently increased with age.

The changes observed in fibre diameters were found to be related not only to age and (or) feeding, but also to individual muscles. This could be attributed to the various functions of muscles and their non-identical growth pattern (Richmond and Berg, 1982).

Mean fibre diameters in LD muscle of newborn calves were similar to those reported by Wegner (1983) and Kłosowski and Kłosowski (1988). However, fibre diameters in LD and SD of younger, *ie* 3-month-old calves (feeding systems pooled) were found to be markedly smaller than those reported by Kłosowski and Kłosowska (1987, 1988) for calves of a similar age. Again, mean fibre diameter of older animals, *ie* 10-month-old calves (feeding systems pooled) were smaller than those quoted by Wegner (1983) and Kłosowski and Kłosowska (1988), who reported 49.4 and 47.6 µm, respectively. Thinner fibres in both younger and older animals, appearing simultaneously with "normal" fibres in newborn calves, could result from the low-concentrate feeding (1 kg daily) maintained up to the 10th month of life. This was reflected in relatively low daily LW

Table VI. Relationship between fibre diameter (y, μm) and daily gains of calves (x, kg) as calculated for the period from 42 days of age to slaughter.

Muscle	*Fibre*	*Regression coefficient*	*Regression equation (given only when regression coefficient was significant)*	*Effect on the relationship between fibre diameter and LW gains of:*		
				Age (A)	*Feeding (F)*	*Interaction A x F*
LD	FTG	10.2 xx	$y = 38.00 + 10.2\ (x - 0.557)$	*xx*	NS	*xx*
	STO	10.3 xx	$y = 26.63 + 10.3\ (x - 0.566)$	*xx*	*xx*	NS
	FTO	10.1 xx	$y = 21.95 + 10.1\ (x - 0.558)$	*xx*	NS	*xx*
	BO	8.1 xx	$y = 24.17 + 8.1\ (x - 0.565)$	*xx*	*xx*	*x*
	AT	6.8 xx	$y = 28.69 + 6.8\ (x - 0.566)$	*xx*	*xx*	*xx*
SM	FTG	3.3 NS		*xx*	NS	NS
	STO	4.3 xx	$y = 27.99 + 4.3\ (x - 0.557)$	*xx*	*xx*	*xx*
	FTO	7.9 xx	$y = 23.80 + 7.9\ (x - 0.551)$	*xx*	*xx*	*xx*
	BO	2.1 NS		*xx*	*xx*	*x*
	AT	2.0 NS		*xx*	*xx*	NS
ST	FTG	13.3 xx	$y = 40.35 + 13.3\ (x - 0.556)$	*xx*	*x*	NS
	STO	4.0 x	$y = 30.04 + 4.0\ (x - 0.553)$	*xx*	*x*	*xx*
	FTO	2.4 NS		*xx*	*x*	NS
	BO	3.3 NS		*xx*	*xx*	*xx*
	AT	4.4 xx	$y = 31.79 + 4.4\ (x - 0.562)$	*xx*	*xx*	*xx*

x: significant at $P < 0.05$, *xx*: significant at $P < 0.01$; NS: non significant. Abbreviations explained in table II.

gains in all calves used. SD fed animals (pooled younger and older animals), which consumed more nutrients per day and had higher weight gains, simultaneously had thicker muscle fibres. On the other hand, Moody *et al* (1970) working on growing sheep, reported age and body weight at slaughter to be the factors affecting muscle fibre diameter, while LW gains were found to have no statistically confirmed effect.

Relationship between the fibre diameters and LW gains was confirmed by the positive and significant coefficients of regression, more pronounced in LD muscle (tables V, VI). Thus, the differences in fibre diameters between SD and HD calves should be attributed to their different growth rates, arising obviously from a different intake of nutrients (table I). However, this does not seem to exhaust the problem. Although both the younger and older SD fed calves consumed more DM and GE per day than did the HD fed animals, the older SD consumed simultaneously less CP and thus had a considerably lower CP/GE ratio. In all cases however, the fibre diameters were larger in the SD group. Moreover, the significant influence of the feeding system on the relationship between fibre diameter and LW gain in cases when the coefficient of regression was non-significant could be interpreted as resulting from some specific traits of the diet and not only from the consumption of different quantities of nutrients.

The elliptical and darker stained fibres found in 2 older SD fed calves can be interpreted as being due to super-twitch, which is one of the first manifestations of nutritional myopathia resulting from vitamin E or Se deficiency (Goedegebuure, 1987). According to Pellegrini *et al* (1982) a long-term maize silage feeding of heifers could be responsible for certain pathologies in the muscle structure.

Under the applied nutritional regime (drastically limited concentrate, forage *ad libitum*) marked muscle fibre growth took place between the 3rd and 10th month of age. Virtually only the FTG fibres grew from the 2nd week to the 3rd month of life. In this study, rearing calves on a silage-based *vs* hay-based diet resulted in thicker muscle fibres, the respective differences being significant in LD and ST muscles for each type of fibre; in SM muscle the effect mentioned was not found to be significant either for FTO, or for BO (pooled STO and FTO fibres). Muscle tissue pathologies were found only in 2 out of 5, 10-month-old SD fed calves. This does not indicate any definite detrimental effect of the applied rearing and fattening system on calves' health.

As feeding cattle on silage-only diets is becoming increasingly popular throughout the world, the present study aimed at examining the possible effects of such nutritional regimes on the microstructure of skeletal muscles. The observed differences in muscle fibre growth between HD fed and SD fed animals may arise from differing DM, CP or GE consumption, different CP/GE ratio, or other factors which have not been specified in the present study. However, these differences primarily reflect the applied feeding regime and may be expected in given nutritional conditions. Thus the observed differences in muscular microstructure are also directly connected with the rearing system applied. Results of the linear regression analysis show a close relationship between fibre diameters and LW gains as related to DM intake, but also suggest the possibility of some other specific influence of the diet. Further investigations appear necessary to clarify this point.

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