Changes in the histochemical properties and meat quality traits of porcine muscles during the growing-finishing period as affected by feed restriction, slaughter age, or slaughter weight[1]

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ABSTRACT: In this study, the degree of contractile and metabolic development of myofibers in porcine LM, rectus femoris (RF), and dark and light portions of the semitendinosus (STD and STL, respectively) was determined, and their impact on meat quality was compared at the same age but different BW (trial 1) or at a given BW but different age (trial 2) in 48 Swiss Large White barrows from 12 litters after the growing and finishing period. The barrows had ad libitum (A) or restricted (R, 80% of A) feed access. In trial 1, at 113 and 154 d of age, 6 barrows in treatment A (62.1 and 99.5 kg of BW, respectively) and 6 siblings in treatment R (51.0 and 86.6 kg of BW, respectively) were slaughtered. In trial 2, a similar protocol was used except that the barrows were slaughtered at 61.3 (104 or 119 d of age, respectively) or 101.3 kg of BW (145 or 167 d of age, respectively). Muscle fibers were stained and classified as slow oxidative (SO), fast oxidative-glycolytic (FOG), or fast glycolytic (FG), and fiber area and distribution were determined. At 113 and 154 d of age, R barrows had smaller ($P \leq 0.04$) SO fibers in the LM, STD, and STL, smaller ($P < 0.01$) FOG fibers in the STL, smaller ($P = 0.03$) FG fibers in the LM, and smaller ($P \leq 0.04$) overall mean area in the LM, STD, and STL. In the STL and RF, R barrows had fewer ($P \leq 0.06$) FG and more ($P \leq 0.08$) FOG fibers than A barrows at 113 and 154 d of age. Except for smaller FOG fibers in the STD of R compared with A barrows slaughtered at the same BW, the myofiber size did not differ ($P \geq 0.11$). However, the LM tended to have fewer ($P = 0.06$) SO and more ($P < 0.01$) FG fibers, and the STD had more ($P < 0.01$) FOG fibers in R barrows. Regardless of whether R barrows were slaughtered at the same age or the same BW as the A barrows, shear force values and cooking losses were greater ($P \leq 0.08$) in the STD and STL of R barrows. These findings revealed that myofiber hypertrophy was impaired by feed restriction in barrows compared at the same age, but differences in myofiber size vanished at the same BW. By contrast, restricted nutrient supply affected myofiber maturation depending on the age and BW, but the impact differed between muscles. The absence of changes in myofiber type distribution among the younger-lighter and older-heavier barrows indicated that myofiber maturation was already completed in the younger-lighter barrows. Although changes in meat quality traits were affected by the feeding regimen, they were not related to myofiber characteristics.

Key words: feed restriction, maturation, meat quality, myofiber, pig

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INTRODUCTION

The myofiber number in porcine muscle is determined prenatally (Stickland and Goldspink, 1973); thus, the postnatal increase in muscle mass depends mainly on myofiber hypertrophy. By contrast, metabolic differentiation of myofibers occurs during postnatal development. At birth, myofibers are mostly oxidative, and with increasing age muscle metabolism becomes more glycolytic (Lefaucheur, 2001).

Quantitative and qualitative aspects of postnatal nutrition have a major effect on muscle development by affecting the growth rate and body composition. Harrison et al. (1996) found that severe feed restriction for 4 wk postweaning impaired myofiber hypertrophy and concomitantly increased the number of type I fibers in the red rhomboideus but not in the white LM. A degree of feed restriction from 25 to 55 kg of BW resulted in smaller slow oxidative (**SO**) and fast glyco-

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lytic (**FG**) fibers, fewer FG fibers, and more fast oxidative glycolytic (**FOG**) fibers in the LM (Solomon et al., 1988). In heavier pigs (100 and 130 kg of BW), feed restriction resulted only in a tendency for larger SO myofibers in the LM (Candek-Potokar et al., 1999). With respect to pork quality, greater drip losses, lower tenderness, and reduced i.m. lipid and collagen content were reported after feed restriction (Candek-Potokar et al., 1999; Kristensen et al., 2002).

Thus, it is unclear whether the effect of feed restriction differs at different developmental stages or whether any potential effects depend on the duration and nature of nutrient restriction, or both. Further, it is noted that myofiber differentiation and hypertrophy are most intense up to 4 mo of age (about 60 kg of BW; Lefaucheur and Vigneron, 1986).

Therefore, the effect of an ad libitum vs. restricted feed allowance on contractile and metabolic development of myofibers was examined after the growing and the finishing period at the same age and different BW or at a given BW and different age. To assess the dietary impact on muscle maturation, porcine muscles known to differ in their allometric growth and myofiber composition were examined.

MATERIALS AND METHODS

Animals and Treatments

The Swiss Federal Committee for Animal Care and Use approved all procedures involving animals.

Trial 1. Swiss Large White barrows (n = 24; mean BW = 20.7 ± 0.67 kg) originating from 6 litters were randomly assigned within litter to 4 treatment groups. The barrows had ad libitum (**A**) or restricted (**R**; 80% of ad libitum) access to a standard growing-finishing diet for the entire experimental period. The feed restriction level was designed to achieve an ADG of 750 g from 20 to 100 kg of BW as outlined in the Swiss feeding recommendation for pigs (Boltshauser et al., 1993). From the beginning of the experiment to 60 kg of BW, the barrows were offered a grower diet (Table 1). At 113 ± 2.4 d of age, 6 barrows (1 per litter) of the ad libitum (**A-113**) and 6 of their siblings of the restricted group (**R-113**) were slaughtered. The slaughter weight of the A-113- and R-113 barrows averaged 62.1 ± 1.82 and 51.0 ± 1.81 kg, respectively. The remaining 12 barrows were offered a finisher diet (Table 1) from 60 kg of BW until slaughter at 154 ± 2.6 d of age. The BW of the ad libitum (**A-154**) and restricted (**R-154**) group averaged 99.5 ± 2.45 kg and 86.6 ± 2.48 kg, respectively.

Trial 2. Swiss Large White barrows (n = 24; mean BW = 19.78 ± 0.67 kg) originating from 6 litters were randomly assigned within litter to 4 treatment groups. Barrows had ad libitum or restricted access to the same growing (beginning of the experiment to 60 kg of BW) and finishing (60 to 100 kg of BW) diets used in trial 1. The feeding regimen for the barrows in the R group was the same as in trial 1. Littermates from both feeding regimen treatments were slaughtered at 61.3 ± 0.99 kg of BW (**A60**, n = 6 and **R60**, n = 6) or 101.3 ± 1.48 kg of BW (**A100**, n = 6 and **R100**, n = 6). The ages at slaughter of the A60, R60, A100, and R100 barrows were 104 ± 3.9, 119 ± 4.2, 145 ± 4.5, and 167 ± 4.1 d, respectively.

In both trials, barrows were reared in individual pens (2.6 m^2/pig) on a concrete floor. Barrows from the R groups were fed individually twice a day and had free access to water. The total daily feed allowance was adjusted weekly according to the individual pig BW (Boltshauser et al., 1993). Barrows of the ad libitum groups were weighed, and feed disappearance was recorded weekly. Feed was withheld from the barrows 12 h before transportation to the research station abattoir. Slaughter and dissection were carried out according to the Swiss Pig Performance Testing Station (MLP, Sempach, Switzerland) meat cutting standards, as previously described by Bee et al. (2004).

Table 1. Ingredient composition of the growing and finishing diets (as-fed basis)

	Diet	
Item	Growing	Finishing
Ingredient, %		
Barley	23.700	26.640
Wheat	59.300	58.600
Corn	—	2.000
Potato protein	7.600	4.200
Flaxseed cake	1.100	—
Rape meal	5.000	4.800
Animal fat (50% lard and 50% tallow)	—	0.452
NaCl	0.350	0.348
Dicalcium phosphate	0.616	0.650
Calcium carbonate	1.360	1.356
Lysine-HCl	0.256	0.242
L-Threonine	0.012	0.012
L-Tryptophan	0.006	—
Pellan[1]	0.300	0.300
Vitamin-mineral premix[2]	0.400	0.400
Nutrient composition, g/100 g of DM		
CP	20.1	16.6
Lysine	1.15	0.89
Crude fat	2.5	2.9
Crude fiber	3.0	3.2
Ca	0.92	0.93
P	0.62	0.62
Calculated energy content		
DE,[3] MJ/kg of DM	15.5	15.4

[1]Pellan = a binder that aids in pellet formation (Mikro-Technik GmbH & Co. KG, Germany).

[2]Supplied the following nutrients per kilogram of diet: 20,000 IU of vitamin A; 200 IU of vitamin D_3; 39 IU of vitamin E; 2.9 mg of riboflavin; 2.4 mg of vitamin B_6; 0.010 mg of vitamin B_{12}; 0.2 mg of vitamin K_3; 10 mg of pantothenic acid; 1.4 mg of niacin; 0.48 mg of folic acid; 199 g of choline; 0.052 mg of biotin; 52 mg of Fe as $FeSO_4$; 0.16 mg of I as $Ca(IO)_3$; 0.15 mg of Se as Na_2Se; 5.5 mg of Cu as $CuSO_4$; 81 mg of Zn as ZnO_2; and 15 mg of Mn as MnO_2.

[3]Calculated according to the following formula: DE, MJ/kg = [18.974 × CP (g/g of DM)] + [33.472 × crude fat (g/g of DM)] + [16.611 × NFE (g/g of DM)] – [21.216 × crude fiber (g/g of DM)] + [16.611 × NFE (g/g of DM)]. NFE = nitrogen-free extracts.

Tissue Preparation at Slaughter

Within 40 min after exsanguination, 3 muscles were removed from the right side of each carcass. The torso muscle removed was the LM; the hind-limb muscles removed were the semitendinosus (**ST**) and the rectus femoris (**RF**). Weight, girth, and length of the ST, weight and length of the RF, and the LM cross-sectional area were determined after muscle excision. Muscle samples for histochemical analyses were excised from the central region of the RF, center of the dark (**STD**) and light (**STL**) portions of the ST, and anterior to the 10th-rib location of the LM. One piece (approximately $1 \times 1 \times 3$ cm) of each muscle was immediately placed on a labeled flat stick, rolled in talcum powder, immediately frozen in liquid nitrogen, and stored at –80°C.

From the same samples used for histochemical analyses, two 1.5-cm-thick LM chops were cut at the 12th-rib level, and 2 slices (approximately 70 g each) were obtained from the RF, STD, and STL. From the muscle samples, pH and drip loss percentages were determined. Muscle pH was measured using a pH meter (pH196-S, WTW, Weilheim, Germany) equipped with an electrode (Eb4, WTW) and a temperature probe. Initial pH was measured immediately after the muscle samples were removed (within 40 min of exsanguination), and ultimate pH was obtained 24-h postmortem at the 12th-rib level of the LM and the excised RF, STD, and STL of each left carcass side. Drip loss percentage was measured as the amount of purge formed during storage of the chops at 2°C for 24 h, expressed as a percentage of the initial chop weight (Honikel, 1998). After drip loss measurements were made, the samples were vacuum-packed and stored at –20°C until Warner-Bratzler shear force was determined. To assess thawing loss, frozen samples were thawed for 24 h at 2°C. Subsequently, the chops were kept at room temperature for 1 h and then cooked on a grill plate (Beer Grill AG, Zurich, Switzerland) at 190–195°C to an internal temperature of 69°C, and cooking losses were measured.

Shear force was determined on the cooked samples previously cooled to ambient temperature using the original Warner-Bratzler device (model 3000, G-R Electric MFG Co., Manhattan, KS). For the LM and RF, 8 cores of 1.27-cm diam. were obtained, whereas the STD and STL were cut into 8 strips of $10 \times 10 \times 50$ mm. The maximum shear force for 8 cores or strips per muscle sample, sheared across the fiber direction, was recorded. In addition, on the day of slaughter, approximately 70 g of the LM, RF, STD, and STL was collected, lyophilized, pulverized, vacuum-packaged, and stored at –20°C until DM, CP, and i.m. lipid content were quantified according to the AOAC methods (1995).

Histochemical Analyses

Frozen muscle samples were equilibrated to –25°C, cut from the stick, and trimmed to facilitate transverse sectioning. Samples were mounted on a cryostat chuck with a few drops of tissue-freezing medium (Tissue-Tek, Sakura Finetek Europe, Zoeterwoude, the Netherlands), and 10-μm-thick sections were cut using a Cryotome (Shandon Inc., Pittsburgh, PA). Sections were mounted on glass microscopic slides and were allowed to air-dry for 30 min. Then, sections were treated with a combination of succinic dehydrogenase and acid myofibrillar ATPase, according to the multiple-staining procedure of Solomon and Dunn (1988).

Stained sections were observed under transmitted light at a total magnification of 125× with an Olympus BX50 microscope (Olympus Optical Co., Hamburg, Germany) equipped with a high-resolution digital camera (ColorView12, Soft Imaging System GmbH, Münster, Germany). Muscle fibers were then classified as SO, FOG, and FG based on the staining reaction. The SO fibers showed the darkest, whereas FG displayed the lightest staining intensity. Three random fields, at different locations within a slide of each muscle sample, were captured with the high-resolution digital camera, and a minimum of 250 muscle fibers per field were analyzed with the analySIS 3.0 image analysis software (Soft Imaging System GmbH). To minimize the incidence of measuring intrafasicular terminations of myofibers in the LM and RF, only fibers larger than 700 μm^2 were included in calculations. Fiber type distribution was calculated as the percentage of each fiber type to the total of all fibers measured.

Statistical Analysis

Data were analyzed with the MIXED procedure (SAS Inst. Inc., Cary, NC). The model used for the analyses of growth performance, carcass composition, chemical composition of muscle tissues, muscle fiber characteristics, and meat quality traits included the feeding regimen and slaughter age (trial 1) or slaughter weight (trial 2) and their respective interactions as fixed effects and litter as the random effect. When the interactions were statistically significant at $P < 0.10$, least squares means were separated using the PDIFF option.

RESULTS

Growth Performance and Carcass Measurements (Trial 1)

Trial 1 assessed the effects of feeding regimen (restricted vs. ad libitum) on barrows slaughtered at the same age. As designed, feed restriction reduced ADFI in both the growing ($P < 0.01$) and finishing period ($P < 0.06$; Table 2). For the growing period, this feed restriction reduced ($P < 0.01$) ADG with no effect on feed efficiency (G/F), whereas in the finishing period the feed restriction had no effect on ADG but did result in greater feed efficiency ($P < 0.02$). These effects are

Table 2. Effect of feeding regimen on growth performance and carcass composition of pigs slaughtered at the same age (trial 1)

	Feeding regimen[1]					*P*-value[2]		
Item	A-113	R-113	A-154	R-154	SEM	FR	SA	FR × SA
Growing period								
Time on feed, d	48.2[a]	48.2[a]	46.7[a]	60.2[b]	1.59	<0.01	<0.01	<0.01
ADG, kg	0.86	0.63	0.86	0.67	0.023	<0.01	0.35	0.34
ADFI, kg	1.87	1.41	1.83	1.44	0.047	<0.01	0.92	0.39
G:F	0.46	0.45	0.47	0.46	0.011	0.39	0.24	0.73
Finishing period								
Time on feed, d	—	—	42.2	28.5	2.34	<0.01	—	—
ADG, kg	—	—	0.91	0.90	0.016	0.61	—	—
ADFI, kg	—	—	2.59	2.37	0.068	0.06	—	—
G:F	—	—	0.35	0.38	0.006	0.02	—	—
Carcass measurement								
HCW, kg	49.8	40.1	83.0	69.7	1.67	<0.01	<0.01	0.30
Carcass length, cm	85	80	97	94	0.9	<0.01	<0.01	0.12
Lean percentage,[3] %	56.7	60.3	54.9	58.9	0.78	<0.01	0.03	0.74
Loin, %	25.2	27.0	25.3	26.3	0.41	<0.01	0.46	0.29
Shoulder, %	12.5	12.8	11.6	12.3	0.44	0.07	0.02	0.56
Ham, %	19.0	20.4	17.9	20.3	0.40	<0.01	0.11	0.19
Belly, %	17.1	15.3	18.1	16.7	0.33	<0.01	<0.01	0.49
Omental fat,[4] %	1.0	0.7	1.5	0.9	0.09	<0.01	<0.01	0.25
Subcutaneous fat,[5] %	11.5	9.8	13.7	11.2	0.46	<0.01	<0.01	0.37
10th rib fat, mm	10.0	7.5	19.3	12.9	1.32	<0.01	<0.01	0.10
	Morphometric muscle measurement[6]							
LM area, cm^2	43.7	36.5	65.7	57.5	1.91	<0.01	<0.01	0.77
RF weight, g	245	197	371	359	12.5	0.03	<0.01	0.17
RF length, mm	124	117	149	150	29.1	0.32	<0.01	0.17
ST weight, g	277	236	475	419	16.5	0.01	<0.01	0.65
ST length, mm	161	149	193	184	5.1	0.06	<0.01	0.73
ST girth, mm	186	174	229	215	4.8	<0.01	<0.01	0.79

[a,b]Within a row, means for experimental treatments without a common superscript differ ($P < 0.05$).
[1]A-113 = ad libitum access to feed, slaughtered d 113 of age and 62.1 kg of BW; A-154 = ad libitum access to feed, slaughtered at 154 d of age and 99.5 kg of BW; R-113 = restricted access to feed, slaughtered d 113 of age and 51.0 kg of BW; and R-154 = restricted access to feed, slaughtered at 154 d of age and 86.6 kg of BW.
[2]Probability values for feeding regimen (FR), slaughter age (SA), and their interaction.
[3]Sum of denuded shoulder, back, and ham weights as a percentage of cold carcass weight.
[4]Omental fat weight expressed as a percentage of cold carcass weight.
[5]Sum of external fat from the shoulder, back, and ham expressed as a percentage of cold carcass weight.
[6]RF = rectus femoris and ST = semitendinosus.

somewhat confounded by time of feed. At the time of slaughter of the 113-d barrows, the A-154 group was switched to the finisher diet, but the R-154 group remained on the grower diet for about 13 more days (nutrient specifications are based on BW rather than age, and it took those 13 d for the group to reach 60 kg of BW). Thus, there was a difference in time of feed in the finishing period ($P < 0.01$) due to feed restriction.

With regard to the carcass measurements (Table 2), there were no interactions related to the factors of feed restriction and slaughter age. Feed restriction resulted in carcasses that were lighter ($P < 0.01$), shorter ($P < 0.01$), and leaner ($P < 0.01$), with greater ($P < 0.01$) percentages of loin and ham and lower ($P < 0.01$) percentages of belly. Regarding slaughter age, carcasses from the older barrows (154 d of age compared with those at 113 d of age) were heavier ($P < 0.01$), longer ($P < 0.01$), and less lean ($P < 0.03$) with lower ($P = 0.02$) percentages of shoulder and greater ($P < 0.01$) percentages of belly. With regard to the fat measures (omental and subcutaneous percentages and 10th rib fat depth), feed restriction resulted in less fat ($P < 0.01$) and older slaughter age resulted in more fat ($P < 0.01$).

Additionally, the carcasses of barrows with restricted feed access had smaller ($P < 0.01$) LM areas, lighter ($P = 0.03$) RF muscles, lighter ($P = 0.01$) and shorter ($P = 0.06$) ST muscles with a reduced ($P < 0.01$) girth than the carcasses of barrows with ad libitum access to feed. Carcasses of the older barrows had larger ($P < 0.01$) LM areas, heavier ($P < 0.01$) and longer ($P < 0.01$) RF and ST muscles, and ST muscles with greater ($P < 0.01$) girth.

Muscle Fiber Area and Distribution (Trial 1)

With regard to muscle fiber area, the effects of slaughter age are most readily presented. Barrows

Table 3. Effect of feeding regimen on muscle fiber area (μm^2) of pigs slaughtered at the same age (trial 1)

Muscle[1] and fiber[2] type	Feeding regimen[3]					*P*-value[4]		
	A-113	R-113	A-154	R-154	SEM	FR	SA	FR × SA
LM								
SO	2,391	1,722	3,035	2,768	186.8	0.02	<0.01	0.31
FOG	1,984	2,053	2,617	2,472	171.8	0.79	<0.01	0.46
FG	3,109	2,590	4,036	3,609	200.9	0.03	<0.01	0.82
Mean	2,480	2,107	3,214	2,921	150.9	0.04	<0.01	0.80
RF								
SO	1,646	1,927	2,168	2,234	152.4	0.28	<0.01	0.50
FOG	2,103	2,058	2,980	3,024	182.5	0.99	<0.01	0.82
FG	2,284	2,381	3,404	3,471	204.6	0.70	<0.01	0.94
Mean	2,011	2,122	2,851	2,910	160.9	0.61	<0.01	0.88
STD								
SO	3,031[a]	2,958[a]	5,116[b]	3,824[a]	296.5	0.04	<0.01	0.06
FOG	3,508[a]	3,424[a]	5,371[c]	4,322[b]	239.5	0.02	<0.01	0.04
FG	4,464	4,416	6,601	5,615	491.4	0.14	<0.01	0.18
Mean	3,650[a]	3,582[a]	5,679[c]	4,555[b]	282.6	0.02	<0.01	0.04
STL								
SO	2,916	1,903	3,672	2,696	549.8	0.04	0.11	0.97
FOG	3,289	2,685	4,422	3,752	385.2	<0.01	<0.01	0.87
FG	3,698	3,283	5,264	4,623	321.9	0.07	<0.01	0.69
Mean	3,225	2,583	4,412	3,615	381.3	<0.01	<0.01	0.75

[a–c]Within a row, least squares means for experimental treatments without a common superscript differ ($P < 0.10$).

[1]RF = rectus femoris; STD = dark portion of semitendinosus; and STL = light portion of semitendinosus.

[2]SO = slow oxidative; FOG = fast oxidative-glycolytic; and FG = fast glycolytic.

[3]A-113 = ad libitum access to feed, slaughtered d 113 of age and 62.1 kg of BW; A-154 = ad libitum access to feed, slaughtered at 154 d of age and 99.5 kg of BW; R-113 = restricted access to feed, slaughtered d 113 of age and 51.0 kg of BW; and R-154 = restricted access to feed, slaughtered at 154 d of age and 86.6 kg of BW.

[4]Probability values for feeding regimen (FR), slaughter age (SA), and the interaction.

slaughtered at a later age (154 d of age) had greater fiber area for all fiber types in all muscles ($P < 0.01$) with the exception of SO fibers in the STL where the mean response was similar to that for the other measures, but the SEM was the largest recorded on Table 3 and the slaughter age response only approached a tendency ($P = 0.11$). The effects of feed restriction were observed to be muscle dependent and age dependent. Surprisingly, there were no effects of feed restriction on any fiber type in the RF muscle, although the muscle was lighter and shorter in barrows with restricted feed access. In the STL muscle, all fiber types were reduced in area with feed restriction ($P < 0.01$ to 0.07). In the LM muscle, feed restriction reduced SO and FG fiber area ($P < 0.03$) with no effect on the FOG fibers. In the STD muscle, there was no effect of feed restriction on the FG fibers, and the SO and FOG fibers exhibited an interaction with slaughter age ($P = 0.06$ and 0.04, respectively), whereas feed restriction had no effect when barrows were slaughtered at 113 d of age but reduced fiber area substantially when barrows were slaughtered at 154 d of age.

The percentage fiber type distribution is presented in Table 4. It should be noted that any significant effect observed in 1 fiber type within a muscle must be accompanied by a change in another fiber type specifically because these are percentages. With respect to slaughter age, there were no effects observed in the muscles other than the RF. In the RF muscle, older barrows (154 d of age at slaughter) had fewer FG fibers ($P = 0.05$); this change was accompanied by an increase in FOG fibers ($P = 0.12$) and SO fibers ($P = 0.02$). Based on the probability values, one might conclude that only the SO fibers were affected, but the magnitude of response was almost 2 times greater in the FOG fibers and the significant change in the FG fiber types demands an equal magnitude change in one or more of the other fiber types. This raises the question of whether the interpretation of which fiber type was principally affected when the FG fibers were reduced is being affected principally by the relative magnitude of the SEM for the other 2 fiber types. With regard to feed restriction, the effects were, as with the absolute fiber area in Table 3, muscle dependent. There were no effects of feed restriction on the distribution of fiber types in the LM and STD muscles. In the RF muscle, the effects of feed restriction were much the same as those for the barrows slaughtered at an older age. Feed restriction reduced ($P = 0.06$) the percentage of FG fibers; this reduction was accompanied principally by an increase in the FOG fiber percentage ($P = 0.08$) because the effects of feed restriction on the SO percentage were age dependent (FR × SA interaction, $P = 0.07$) with no increase in those fibers in barrows

Table 4. Effect feeding regimen on muscle fiber distribution (% of total fibers) of pigs slaughtered at the same age (trial 1)

Muscle[1] and fiber[2] type	Feeding regimen[3]				SEM	*P*-value[4]		
	A-113	R-113	A-154	R-154		FR	SA	FR × SA
LM								
SO	8.05	10.71	7.87	7.73	1.478	0.37	0.26	0.32
FOG	24.81	23.00	23.93	26.73	1.592	0.77	0.39	0.18
FG	67.23	66.37	68.28	65.62	1.871	0.37	0.94	0.64
RF								
SO	4.12[a]	3.79[a]	4.59[a]	7.08[b]	0.711	0.15	0.02	0.07
FOG	32.89	34.20	33.76	40.27	2.068	0.08	0.12	0.23
FG	62.99	62.01	61.65	52.65	2.471	0.06	0.05	0.13
STD								
SO	29.11	30.16	33.04	28.85	2.846	0.50	0.57	0.26
FOG	37.74	37.51	35.18	39.46	1.522	0.13	0.81	0.10
FG	33.22	32.39	31.85	31.75	2.692	0.86	0.69	0.89
STL								
SO	3.80	6.78	5.25	6.77	2.299	0.21	0.68	0.68
FOG	25.52	32.18	25.53	32.64	3.521	0.03	0.94	0.94
FG	70.20	60.78	68.95	60.11	5.302	0.04	0.81	0.94

[a,b]Within a row, least squares means for experimental treatments without a common superscript differ ($P < 0.10$).

[1]RF = rectus femoris; STD = dark portion of semitendinosus; and STL = light portion of semitendinosus.

[2]SO = slow oxidative; FOG = fast oxidative-glycolytic; and FG = fast glycolytic.

[3]A-113 = ad libitum access to feed, slaughtered d 113 of age and 62.1 kg of BW; A-154 = ad libitum access to feed, slaughtered at 154 d of age and 99.5 kg of BW; R-113 = restricted access to feed, slaughtered d 113 of age and 51.0 kg of BW; and R-154 = restricted access to feed, slaughtered at 154 d of age and 86.6 kg of BW.

[4]Probability values for feeding regimen (FR), slaughter age (SA), and their interaction.

slaughtered at 113 d but an increase at 154 d that accounted for about 30% of the change in the FG fibers. In the STL muscle, feed restriction also reduced FG fiber percentage ($P = 0.04$) with about 70 to 80% of that change being reflected in the FOG fiber percentage ($P = 0.03$) and the remainder reflected in the SO fiber percentage (nonsignificant, $P = 0.21$).

Meat Quality Traits (Trial 1)

An older slaughter age reduced ultimate muscle pH in all muscles ($P = 0.01$ to 0.04) except in the STD (Table 5). This effect of age was not consistently related to effects in initial pH. There was a reduction in initial pH of the LM of barrows slaughtered at 154 d of age, but for other muscles initial pH demonstrated an interaction where ad libitum-fed barrows slaughtered at 154 d had a greater initial pH than ad libitum-fed barrows slaughtered at 113 d whereas feed restricted barrows slaughtered at 154 d had a lower initial pH than their counterparts slaughtered at 113 d [FR × SA interaction for the RF ($P = 0.07$), STD ($P = 0.06$), and STL ($P = 0.03$) muscles]. With regard to the water holding capacity of these muscles (as illustrated by the drip loss, thaw loss, and cooking loss), there were no consistent patterns. For drip loss, the only effect noted was an interaction ($P = 0.02$) in the STD where feed restriction of barrows slaughtered at 154 d resulted in greater drip loss. For thaw loss, there was a tendency ($P = 0.11$) for feed restriction to result in greater loss. And for cooking loss, feed restriction resulted in greater losses in the LM ($P < 0.01$), STD ($P = 0.02$), and STL ($P = 0.08$) muscles. Slaughter age did not affect these water losses except in the STD where slaughter at 154 d resulted in less water loss than slaughter at 113 d ($P = 0.06$). There was a clear effect of an older slaughter age to reduce the shear force (i.e., for the muscle to be more tender) in the STL ($P = 0.04$) and in the RF ($P = 0.06$) with a tendency in the LM ($P = 0.11$) muscle; feed restriction resulted in an increase in the shear force (i.e., a less tender muscle) for the LM ($P < 0.01$), STD ($P = 0.05$), and the STL ($P = 0.03$) muscle.

Muscle Chemical Composition (Trial 1)

Feed restriction of barrows resulted in a lower DM content of the LM ($P = 0.02$) and STL ($P = 0.05$) muscles, a lower CP content of the LM ($P = 0.11$) and RF ($P = 0.05$) muscle, and an increase in the i.m. lipid content of the STL ($P = 0.02$; Figure 1). With regard to slaughter age, the DM content of the LM, RF, and STL was greater ($P \leq 0.01$) in barrows slaughtered at 154 d; the CP content of LM ($P < 0.01$) and RF ($P < 0.01$) muscles and the i.m. lipid content of the STL ($P = 0.06$) were also greater in older barrows. The composition of the STD was subject to an interaction for DM content ($P < 0.01$) and i.m. lipid content ($P = 0.03$) where the value was elevated for ad libitum fed barrows slaughtered at 154 d with no differences among the other treatments.

Table 5. Effect of feeding regimen on meat quality traits of pigs slaughtered at the same age (trial 1)

	Feeding regimen[2]					*P*-value[3]		
Muscle[1]	A-113	R-113	A-154	R-154	SEM	FR	SA	FR × SA
LM								
Initial pH	6.27	6.34	6.16	6.14	0.051	0.67	0.01	0.41
Ultimate pH	5.59	5.60	5.43	5.41	0.041	0.99	<0.01	0.61
Drip loss, %	4.01	4.53	4.36	4.52	0.407	0.34	0.63	0.61
Thaw loss, %	12.46	13.50	10.65	14.67	1.654	0.11	0.84	0.33
Cooking loss, %	13.04	19.55	14.43	17.04	1.273	<0.01	0.64	0.12
Shear force, kg	3.94	4.76	3.41	4.31	3.937	<0.01	0.11	0.90
RF								
Initial pH	6.00[a]	6.27[ab]	6.35[b]	6.23[ab]	0.152	0.45	0.13	0.07
Ultimate pH	5.66	5.77	5.57	5.56	0.052	0.28	<0.01	0.21
Drip loss, %	3.12	3.02	3.09	4.16	0.353	0.20	0.14	0.12
Thaw loss, %	13.90	14.90	12.24	13.89	1.151	0.28	0.28	0.79
Cooking loss, %	19.34	19.75	18.58	22.46	1.413	0.17	0.52	0.26
Shear force, kg	4.16	4.21	3.78	3.86	0.168	0.71	0.06	0.91
STD								
Initial pH	6.02[ab]	6.20[b]	6.15[ab]	5.91[a]	0.103	0.77	0.47	0.06
Ultimate pH	5.86	5.81	5.81	5.65	0.067	0.15	0.14	0.46
Drip loss, %	3.84[a]	3.70[a]	3.61[a]	4.72[b]	0.533	0.08	0.14	0.02
Thaw loss, %	10.46	16.25	11.46	11.35	2.724	0.32	0.49	0.30
Cooking loss, %	22.09	25.56	20.29	22.77	1.140	0.02	0.06	0.68
Shear force, kg	3.54	4.14	3.11	3.91	0.328	0.05	0.34	0.76
STL								
Initial pH	5.81[a]	6.07[b]	5.94[ab]	5.79[a]	0.134	0.53	0.40	0.03
Ultimate pH	5.70	5.68	5.63	5.53	0.054	0.25	0.04	0.52
Drip loss, %	4.46	4.01	3.90	5.10	0.548	0.51	0.64	0.15
Thaw loss, %	12.06	17.88	12.98	14.92	3.131	0.24	0.75	0.55
Cooking loss, %	21.98	23.52	19.82	23.56	1.425	0.08	0.48	0.46
Shear force, kg	3.86	4.31	3.46	3.89	0.180	0.03	0.04	0.98

[a,b]Within a row, least squares means for the experimental treatments without a common superscript differ ($P < 0.10$).

[1]RF = rectus femoris; STD = dark portion of semitendinosus; and STL = light portion of semitendinosus.

[2]A-113 = ad libitum access to feed, slaughtered d 113 of age and 62.1 kg of BW; A-154 = ad libitum access to feed, slaughtered at 154 d of age and 99.5 kg of BW; R-113 = restricted access to feed, slaughtered d 113 of age and 51.0 kg of BW; and R-154 = restricted access to feed, slaughtered at 154 d of age and 86.6 kg of BW.

[3]Probability values for feeding regimen (R), slaughter age (SA), and their interaction.

Growth Performance and Carcass Measurements (Trial 2)

Trial 2 assessed the effects of feeding regimen (restricted vs. ad libitum) on performance and carcass characteristics when barrows were slaughtered at the same BW but differing age. As designed, feed restriction reduced ADFI in the growing ($P < 0.01$) and finishing period ($P < 0.01$; Table 6). For both periods, this feed restriction reduced ($P < 0.01$) ADG with no effect on feed efficiency (G:F). Surprisingly, in the growing period A and R barrows slaughtered at 60 kg tended to ingest more ($P = 0.08$) feed, and because ADG was not different ($P = 0.26$), feed efficiency was lower (G:F; $P < 0.01$) compared with the A100- and R100-barrows. Because only the feeding treatment was in effect at this point, this observation is an artifact of the allotment and does not represent a biological response.

With regard to the carcass measurements (Table 6), carcasses from the heavier barrows (100 kg slaughter weight) were heavier ($P < 0.01$) and longer ($P < 0.01$) with lower ($P = 0.02$) percentages of ham and greater ($P < 0.01$) percentages of belly. Feed restriction resulted in carcasses that were longer ($P = 0.08$). An interaction existed for lean percentage ($P = 0.03$) with feed restriction resulting in a greater lean percentage in barrows slaughtered at 60 kg with no difference in those slaughtered at 100 kg. With regard to the fat measures (omental and subcutaneous percentages and 10th-rib fat depth), barrows slaughtered at 100 kg had greater ($P < 0.01$) omental fat and 10th-rib fat depth, whereas feed restriction resulted in less ($P < 0.06$) omental fat. There was an interaction for subcutaneous fat ($P = 0.02$) wherein the expected reduction associated with feed restriction was greater in barrows slaughtered at 60 kg than in those slaughtered at 100 kg.

Carcasses of the heavier barrows had larger ($P < 0.01$) LM areas, heavier and longer ($P < 0.01$) RF and ST ($P < 0.01$ and 0.02, respectively) muscles, and ST muscles with greater ($P < 0.01$) girth. Additionally, the carcasses of barrows with restricted feed access had shorter ($P = 0.06$) RF muscles than the carcasses of barrows with ad libitum access to feed.

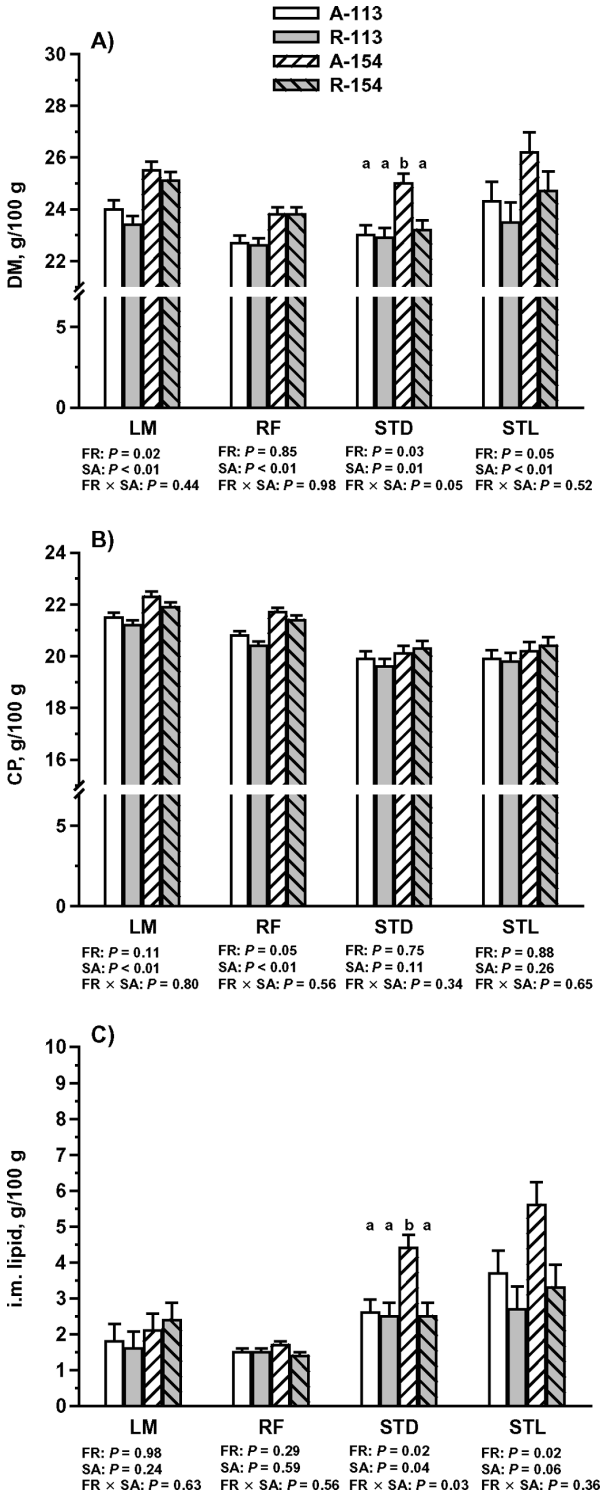

Figure 1. Effect of feeding regimen on DM (A), CP (B), and i.m. lipid (C) content of the LM, rectus femoris (RF), and dark (STD) and light (STL) portion of the semitendinosus muscle of pigs fed ad libitum or restricted-fed that were slaughtered at d 113 (A-113 and R-113, respectively) or 154 (A-154 and R-154, respectively) of age. For each muscle, the probability values for feeding regimen (FR), slaughter age (SA), and the FR × SA interaction, and SEM are reported. [a,b]For the DM and i.m. lipid content in the STD, least squares means for the experimental treatments without a common superscript differ ($P < 0.05$).

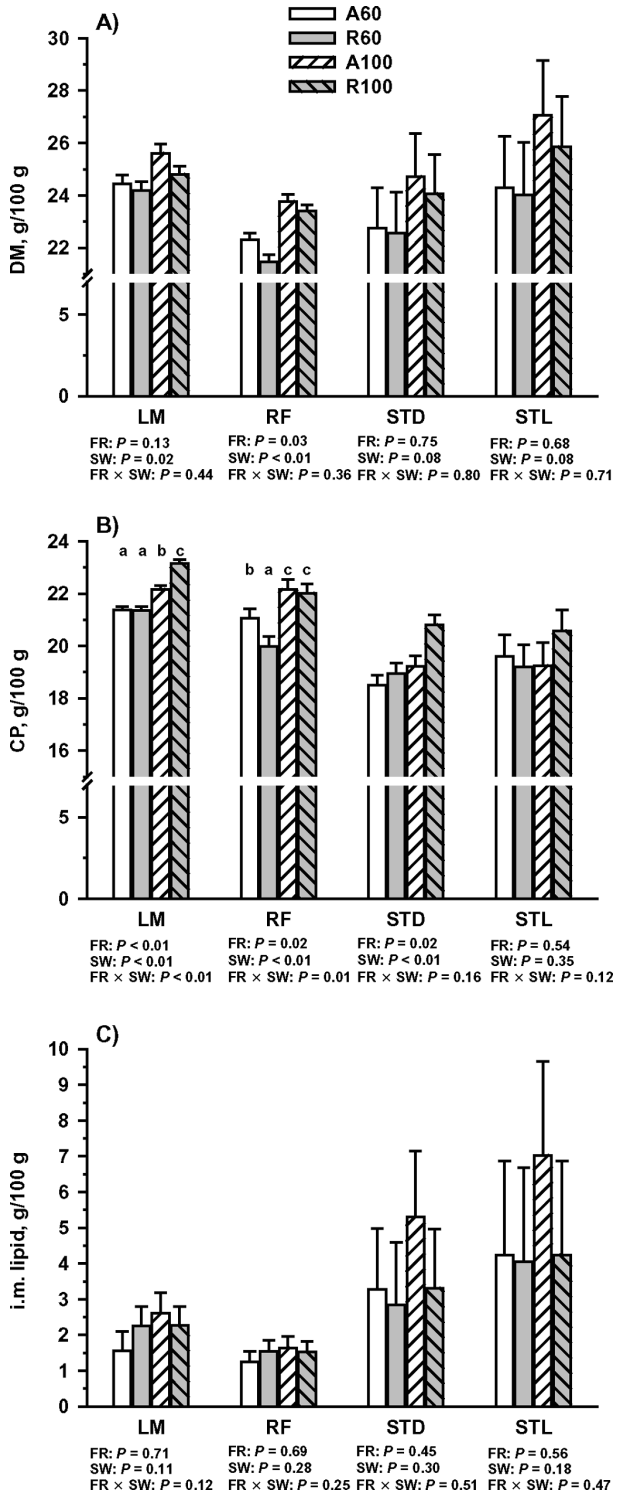

Figure 2. Effect of feeding regimen on DM (A), CP (B), and i.m. lipid (C) content of the LM, rectus femoris (RF), and dark (STD) and light (STL) portion of the semitendinosus muscle of pigs fed ad libitum or restricted-fed that were slaughtered at 61.3 kg of BW (A60 and R60, respectively) or 101.3 kg of BW (A100 and R100, respectively). For each muscle, probability values for feeding regimen (FR), slaughter weight (SW), and the FR × SW interaction, and SEM are reported. [a–c]For the CP content in the LM and RF, least squares means for the experimental treatments without a common superscript differ ($P < 0.05$).

Table 6. Effect of feeding regimen on growth performance and carcass composition of pigs slaughtered at the same BW (trial 2)

	Feeding regimen[1]					*P*-value[2]		
Item	A60	R60	A100	R100	SEM	FR	SW	FR × SW
Growing period								
Time on feed, d	48.3	61.4	47.6	59.5	2.38	<0.01	0.57	0.80
ADG, kg	0.85	0.69	0.90	0.70	0.032	<0.01	0.26	0.42
ADFI, kg	1.91	1.55	1.86	1.44	0.045	<0.01	0.08	0.44
G:F	0.45	0.44	0.49	0.48	0.014	0.40	<0.01	0.93
Finishing period								
Time on feed, d	—	—	47.4	53.6	1.65	0.02	—	—
ADG, kg	—	—	0.95	0.80	0.033	<0.01	—	—
ADFI, kg	—	—	2.96	2.46	0.076	<0.01	—	—
G:F	—	—	0.33	0.32	0.013	0.26	—	—
Carcass measurements								
HCW, kg	47.5	47.5	82.6	83.4	0.83	0.66	<0.01	0.60
Carcass length, cm	83	85	98	100	1.1	0.08	<0.01	0.75
Lean percentage,[3] %	56.3[a]	59.7[b]	55.2[a]	54.8[a]	0.83	0.08	<0.01	0.03
Loin, %	25.5	26.9	25.5	25.5	0.65	0.27	0.28	0.25
Shoulder, %	12.9[b]	14.0[c]	13.0[b]	11.8[a]	0.26	0.89	<0.01	<0.01
Ham, %	18.1	18.9	16.8	17.5	0.43	0.13	<0.01	0.84
Belly, %	16.2	16.2	17.3	17.7	0.61	0.83	<0.01	0.63
Omental fat,[4] %	1.2	0.8	1.7	1.6	0.12	0.06	<0.01	0.27
Subcutaneous fat,[5] %	13.5[b]	10.3[a]	14.7[b]	13.9[b]	0.73	<0.01	<0.01	0.02
10th rib fat, mm	13.8	11.9	21.7	17.0	1.90	0.15	<0.01	0.37
	Morphometric muscle measurement[6]							
LM area, cm^2	37.1	38.1	57.1	62.9	2.18	0.12	<0.01	0.26
RF weight, g	219	216	359	371	14.8	0.77	<0.01	0.60
RF length, mm	128	123	146	135	4.1	0.06	<0.01	0.39
ST weight, g	224	246	429	449	13.1	0.10	<0.01	0.95
ST length, mm	172	167	186	180	5.9	0.34	0.02	0.92
ST girth, mm	166	179	221	223	5.7	0.18	<0.01	0.34

[a–c]Within a row, least squares means for the experimental treatments without a common superscript differ ($P < 0.05$).

[1]A60 = ad libitum access to feed, slaughtered at 61.3 kg of BW; A100 = ad libitum access to feed and slaughtered at 101.3 kg of BW; R60 = restricted access to feed and slaughtered at 61.3 kg of BW; and R100 = restricted access to feed and slaughtered at 101.3 kg of BW.

[2]Probability values for feeding regimen (FR), slaughter weight (SW), and their interaction.

[3]Sum of denuded shoulder, back, and ham weights as a percentage of cold carcass weight.

[4]Omental fat weight expressed as a percentage of cold carcass weight.

[5]Sum of external fat from the shoulder, back, and ham expressed as a percentage of cold carcass weight.

[6]RF = rectus femoris and ST = semitendinosus.

Muscle Fiber Area and Distribution (Trial 2)

Feed restriction had limited effects on absolute fiber area (Table 7). There was a tendency ($P = 0.11$) for SO fibers in the LM to be smaller in feed-restricted barrows than those of ad libitum-fed barrows. Also, interactions existed for the FOG in the RF muscle ($P = 0.04$) and the STL muscle ($P = 0.06$) wherein feed restriction resulted in increased fiber area in those barrows slaughtered at 60 kg but reduced fiber area in those barrows slaughtered at 100 kg. An interaction also existed for the FOG in the STD, but this was one of magnitude wherein feed restriction resulted in a reduction in fiber size at both slaughter weights but the effect was much more pronounced at the 60-kg slaughter weight. The effects of slaughter weight on fiber size were as anticipated. The heavier slaughter weight resulted in greater fiber area for all fiber types in all muscles ($P < 0.01$ to 0.05) with the exception of the FOG fibers in the LM ($P = 0.19$).

With regard to the distribution of fiber types within the various muscles, feed restriction resulted in an increase ($P < 0.01$) in FG fibers, which was offset by a decrease ($P = 0.06$) in SO fibers in the LM muscle compared with those barrows that were ad libitum-fed (Table 8). Despite the greater percentage of the large FG fibers in R barrows, average mean fiber area of the LM was not greater ($P = 0.89$; Table 7), which can be explained by the smaller size as well as the lower percentage of SO fibers in R barrows. Feed restriction also increased FOG fibers ($P < 0.01$) in the STD muscle compared with those barrows that were ad libitum-fed, and the increase was not associated with any significant effects on the other 2 fiber types, which suggests that both fiber types absorbed some of the change (the largest numerical effects were in the FG fibers). The effects of slaughter weight on fiber type distribution were generally dependent on the feeding treatment. In the RF muscle, the interaction ($P < 0.01$) demonstrated a decrease in FG fibers in feed-restricted

Table 7. Effect of feeding regimen on muscle fiber area (μm^2) of pigs slaughtered at the same BW (trial 2)

Muscle[1] and fiber[2] type	Feeding regimen[3]				SEM	*P*-value[4]		
	A60	R60	A100	R100		FR	SW	FR × SW
LM								
SO	2,522	2,124	3,395	2,740	454.4	0.11	<0.01	0.55
FOG	2,529	2,365	2,720	2,846	298.5	0.95	0.19	0.57
FG	3,417	3,344	4,161	4,115	256.5	0.81	<0.01	0.96
Mean	2,717	2,655	3,295	3,295	220.7	0.89	<0.01	0.88
RF								
SO	1,469	1,712	2,238	2,068	140.3	0.79	<0.01	0.14
FOG	2,178[a]	2,438[ab]	3,375[c]	2,887[bc]	174.3	0.50	<0.01	0.04
FG	2,790	2,805	3,469	3,389	271.1	0.90	0.03	0.86
Mean	2,146	2,318	3,027	2,781	156.1	0.81	<0.01	0.18
STD								
SO	3,458	2,818	4,801	4,338	397.3	0.16	<0.01	0.82
FOG	4,207	3,171	4,871	4,721	277.0	0.04	<0.01	0.11
FG	4,417	4,444	5,824	6,403	399.2	0.48	<0.01	0.44
Mean	4,017	3,499	5,147	5,172	298.3	0.40	<0.01	0.35
STL								
SO	3,332	2,674	4,173	3,769	438.0	0.22	0.03	0.77
FOG	3,332[a]	3,878[a]	5,224[b]	4,119[ab]	422.3	0.50	0.02	0.06
FG	3,764	4,552	4,964	5,015	403.1	0.29	0.05	0.35
Mean	3,476	3,701	4,787	4,301	335.3	0.69	<0.01	0.28

[a–c]Within a row, least squares means for the experimental treatments without a common superscript differ ($P < 0.10$).

[1]RF = rectus femoris; STD = dark portion of semitendinosus; and STL = light portion of semitendinosus.

[2]SO = slow oxidative; FOG = fast oxidative-glycolytic; and FG = fast glycolytic.

[3]A60 = ad libitum access to feed, slaughtered at 61.3 kg of BW; A100 = ad libitum access to feed and slaughtered at 101.3 kg of BW; R60 = restricted access to feed and slaughtered at 61.3 kg of BW; and R100 = restricted access to feed and slaughtered at 101.3 kg of BW.

[4]Probability values for feeding regimen (FR), slaughter weight (SW), and their interaction.

Table 8. Effect of feeding regimen on muscle fiber distribution (% of total fibers) of pigs slaughtered at the same BW (trial 2)

Muscle[1] and fiber[2] type	Feeding regimen[3]				SEM	*P*-value[4]		
	A60	R60	A100	R100		FR	SW	FR × SW
LM								
SO	13.45	6.50	10.69	8.62	2.316	0.06	0.89	0.29
FOG	23.99	21.91	24.03	21.19	1.785	0.29	0.84	0.82
FG	62.50	71.53	65.24	70.16	2.358	<0.01	0.77	0.38
RF								
SO	6.91	5.14	5.57	5.37	1.075	0.35	0.59	0.46
FOG	37.56[b]	31.98[b]	24.51[a]	33.89[b]	2.339	0.41	<0.01	<0.01
FG	56.35[a]	62.57[a]	70.93[b]	60.30[a]	3.125	0.45	<0.01	<0.01
STD								
SO	29.75	27.79	27.26	26.73	5.078	0.80	0.72	0.89
FOG	29.83	34.93	30.40	37.97	1.722	<0.01	0.29	0.46
FG	40.42	37.28	42.34	35.30	4.977	0.30	0.99	0.69
STL								
SO	3.59[a]	15.12[b]	5.93[a]	4.58[a]	3.084	0.14	0.12	0.02
FOG	31.71	28.45	24.29	28.91	3.531	0.85	0.30	0.24
FG	64.78	55.05	70.26	65.50	5.291	0.18	0.06	0.54

[a,b]Within a row, least squares means for the experimental treatments without a common superscript differ ($P < 0.05$).

[1]RF = rectus femoris; STD = dark portion of semitendinosus; and STL = light portion of semitendinosus.

[2]SO = slow oxidative; FOG = fast oxidative-glycolytic; and FG = fast glycolytic.

[3]A60 = ad libitum access to feed, slaughtered at 61.3 kg of BW; A100 = ad libitum access to feed and slaughtered at 101.3 kg of BW; R60 = restricted access to feed and slaughtered at 61.3 kg of BW; and R100 = restricted access to feed and slaughtered at 101.3 kg of BW.

[4]Probability values for feeding regimen (FR), slaughter weight (SW), and their interaction.

barrows at 100 kg of BW that was totally accounted for by an increase in FOG fibers; the exact opposite effects were observed at the 60-kg slaughter weight. In the STL muscle, barrows slaughtered at 100 kg had a greater percentage of FG fibers ($P = 0.06$) than those slaughtered at 60 kg. This increase was associated with a decrease in FOG fibers in ad libitum-fed barrows but was associated with a decrease in SO fibers in the feed-restricted barrows.

Meat Quality Traits (Trial 2)

There were few effects observed on muscle pH. No effects were observed on ultimate pH, and for initial pH the only effects observed were a tendency ($P = 0.08$) for barrows slaughtered at 100 kg to have a greater value in the RF than barrows slaughtered at 60 kg and a tendency for an interaction ($P = 0.07$) in the LM muscle. Feed restriction had no effect in those barrows slaughtered at 60 kg, but barrows slaughtered at 100 kg of BW that were feed-restricted had a lower value than those fed ad libitum (Table 9). Feed restriction of barrows did not affect moisture losses (drip loss, thaw loss, or cooking loss) in the LM muscle. However, it significantly increased drip losses in the RF ($P < 0.01$) and STD ($P = 0.03$), cooking loss ($P = 0.02$) in the STD and STL, and tended to increase thaw loss in the STD ($P = 0.07$). The heavier slaughter weight of 100 kg reduced thaw loss ($P < 0.01$) and cooking loss ($P = 0.05$) in the LM, thaw loss in the RF ($P < 0.01$), drip and thaw loss in the STD ($P < 0.01$), and drip loss ($P = 0.08$) and thaw loss ($P < 0.01$) in the STL. A tendency for an interaction ($P = 0.09$) existed relative to cooking loss in the STD, where heavier slaughter weight was associated with a reduction in cooking loss in barrows fed ad libitum but not in restricted-fed barrows. The shear force of restricted-fed barrows was greater in the STD ($P = 0.06$) and the STL ($P < 0.01$). In the LM an interaction existed ($P = 0.06$) for shear force where barrows that were feed restricted had a greater shear force at 60 kg of slaughter weight but not at 100 kg of slaughter weight. The heavier slaughter weight was associated with a lower shear force in the STD compared with that of barrows slaughtered at 60 kg.

Muscle Chemical Composition (Trial 2)

Feed restriction of barrows resulted in a lower DM content of the RF ($P = 0.03$) muscle and a lower CP content of the STD ($P = 0.02$) muscle (Figure 2). With regard to slaughter weight, the DM content of the LM ($P = 0.02$), RF ($P < 0.01$), STD ($P = 0.08$), and STL was greater ($P = 0.08$) in barrows slaughtered at 100 kg as was the CP content of the STD ($P < 0.01$) muscle. The CP composition of the LM was subject to an interaction ($P < 0.01$) where feed restriction had no effect in barrows slaughtered at 60 kg but increased CP content in barrows slaughtered at 100 kg. An interaction was also observed in CP content of the RF ($P < 0.01$), but it was different in that feed restriction had no impact at 100-kg slaughter weight and actually reduced CP content in barrows slaughtered at 60 kg.

DISCUSSION

In the current study, barrows slaughtered at the same age but different BW (trial 1) as a result of feed restriction had slower growth and greater feed efficiency at the end of the growing (113 d of age) and finishing (154 d of age) periods. This resulted, on average, in 2.1% units lower adipose and 3.8% units greater lean tissue deposition. The lack of the feeding regimen × slaughter age interactions on carcass measurements indicated that restriction affected carcass composition in a similar way at 113 and 154 d of age. Oksbjerg et al. (2002) observed differences in the same order of magnitude in the carcass composition of older pigs (170 d of age) and heavier pigs with restricted (113 kg of slaughter weight) compared with ad libitum access to the diet (135 kg of slaughter weight). It has to be pointed out that A barrows in trial 1 grew slower than in trial 2, which can be partly explained by the lower voluntary feed intake. A possible explanation for the lower growth rate is that this trial was carried out during the summer time, and ambient temperature was on average 4°C greater in trial 1 than trial 2 (20 vs. 24°C). Surprisingly, in trial 2, barrows of the restricted group were not leaner than barrows of the ad libitum group at 100 kg of BW. This is in contrast to the expected effects of feed restriction on lean and adipose tissue accretion (Lebret et al., 2001). Compared with R-154 barrows in trial 1, R100 barrows in trial 2 grew slower (ADG = 0.76 vs. 0.90 kg; $P < 0.01$) and were less efficient (G:F = 0.35 vs. 0.38; $P = 0.02$) from 60 to 86 kg of BW (the average slaughter weight of the R-154 barrows). These findings suggested that lean tissue deposition at 154 d of age was lower in barrows of the restricted group in trial 2 than in trial 1 although in both trials feeding regimen and the composition of the experimental diet were the same.

Because skeletal muscle fiber hyperplasia ceases before birth in pigs, the increase in size and length of muscle fibers determines postnatal muscle growth (Rehfeldt et al., 2000; Lefaucheur, 2001). Ultimately, postnatal muscle growth depends on the rate of satellite cell proliferation and differentiation as well as on the net protein gain (Mesires and Doumit, 2002; Oksbjerg et al., 2004). The efficiency of these processes is in part determined by the amount and balance of nutrient intake during a defined period of time. The present results on morphometric muscle measurements showed that at the same age R barrows had 14% smaller LM area, 11 and 13% lighter RF and ST muscles, respectively, and 6% shorter ST with 6% smaller girth than A barrows. Similarly, Oksbjerg et al. (2002) and Therkildsen et al. (2004) reported 11 and 17% lighter ST muscles in 170- (113 kg of BW) and 140-

Table 9. Effect of feeding regimen on meat quality traits of pigs slaughtered at the same BW, trial 2

	Feeding regimen[2]					*P*-value[3]		
Muscle[1]	A60	R60	A100	R100	SEM	FR	SW	FR × SW
LM								
Initial pH	6.30[ab]	6.32[ab]	6.50[b]	6.12[a]	0.121	0.18	0.99	0.07
Ultimate pH	5.66	5.62	5.64	5.65	0.071	0.81	0.94	0.67
Drip loss, %	4.77	4.60	4.00	4.32	0.473	0.86	0.26	0.60
Thaw loss, %	12.16	11.33	8.35	7.93	0.932	0.45	<0.01	0.74
Cooking loss, %	20.44	19.85	18.62	17.11	1.323	0.44	0.05	0.68
Shear force, kg	4.32[a]	5.37[b]	4.36[a]	4.21[a]	0.309	0.15	0.07	0.06
RF								
Initial pH	6.46	6.31	6.58	6.62	0.122	0.65	0.08	0.41
Ultimate pH	5.72	5.78	5.79	5.76	0.072	0.80	0.73	0.53
Drip loss, %	2.79	3.52	2.65	3.37	0.177	<0.01	0.39	0.99
Thaw loss, %	13.32	15.85	10.23	11.51	1.270	0.14	<0.01	0.52
Cooking loss, %	18.83	19.92	16.82	18.77	1.055	0.13	0.11	0.61
Shear force, kg	4.61	4.94	4.81	4.73	0.234	0.58	0.97	0.36
STD								
Initial pH	6.14	6.22	6.13	6.29	0.103	0.34	0.76	0.68
Ultimate pH	5.93	5.80	6.03	5.99	0.113	0.44	0.19	0.69
Drip loss, %	3.41	4.26	2.92	3.14	0.231	0.03	<0.01	0.18
Thaw loss, %	13.85	15.51	7.96	9.99	1.012	0.07	<0.01	0.85
Cooking loss, %	24.29[ab]	25.44[b]	20.32[a]	26.29[b]	1.403	0.02	0.26	0.09
Shear force, kg	3.65	4.17	3.00	3.65	0.305	0.06	0.06	0.82
STL								
Initial pH	6.17	6.05	6.03	6.08	0.154	0.83	0.70	0.54
Ultimate pH	5.75	5.67	5.90	5.72	0.094	0.14	0.26	0.56
Drip loss, %	3.47	3.96	3.10	3.32	0.288	0.22	0.08	0.65
Thaw loss, %	12.78	12.85	8.39	10.71	0.914	0.25	<0.01	0.19
Cooking loss, %	20.33	23.67	17.90	23.13	1.509	0.02	0.23	0.43
Shear force, kg	3.23	4.61	3.34	4.00	0.311	<0.01	0.28	0.12

[a,b]Within a row, least squares means for the experimental treatments without a common superscript differ ($P < 0.10$).

[1]RF = rectus femoris; STD = dark portion of semitendinosus; and STL = light portion of semitendinosus.

[2]A60 = ad libitum access to feed, slaughtered at 61.3 kg of BW; A100 = ad libitum access to feed and slaughtered at 101.3 kg of BW; R60 = restricted access to feed and slaughtered at 61.3 kg of BW; and R100 = restricted access to feed and slaughtered at 101.3 kg of BW.

[3]Probability values for feeding regimen (FR), slaughter weight (SW), and their interaction.

(75 kg of BW) d-old pigs, respectively, with restricted compared with ad libitum feed allowance. The lower total DNA and RNA content found in the aforementioned studies in the ST of pigs in the restricted compared with the ad libitum group suggested lower satellite cell proliferation and protein synthesis, respectively (Oksbjerg et al., 2002; Therkildsen et al., 2002). However, delayed muscle growth seems to depend on the limited nutrient supply during a specific period or to be related to the BW, or both, because when barrows were slaughtered at the same BW (trial 2), the dietary induced differences in muscle morphometry vanished except for the 10% heavier ST in R compared with A barrows. As for the carcass measurements, the lack of interactions for feeding regimen × slaughter age or slaughter weight pointed out that in the muscles included in this study the differences in weight, length, and area due to the feeding regimen were similar after the growing and finishing periods.

With the histochemical staining procedure used in this study 3 muscle fiber types (SO, FOG, and FG) can be differentiated. However, results of recent studies revealed the existence of 4 muscle fiber types in the LM of pigs at 100 kg of BW, each one expressing a distinct myosin heavy chain isoform (I, IIa, IIx, and IIb; Lefaucheur et al., 2002; Toniolo et al., 2004). Lefaucheur et al. (2002) reported that compared with IIb, IIx muscle fibers display also a moderate succinic dehydrogenase staining. Thus, the FOG fibers reported in this study actually contain 2 distinct populations of myofibers (IIa and IIx). Therefore, the current results do not allow to estimate to what extent age, BW, and feed restriction determined the size and the distribution of the IIa and IIx fibers and how the factors under investigations affected muscle fiber conversion, which follows the obligatory pathway of myosin heavy chain transition (I ↔IIa ↔ IIx ↔ IIb; Schiaffino and Reggiani, 1994; Toniolo et al., 2004).

With respect to the muscle fiber characteristics, the major finding of the current study was that alterations in nutrient intake significantly modified the phenotype of myofibers. The dietary impact on myofiber size and distribution differed when comparisons were made at the same age or at the same BW. Furthermore, the

feeding regimen effect varied between and within muscles, was fiber type-specific, and seemed only partially related to the contractile or metabolic properties of the muscle. Consistent with the observed changes in morphometric measurements, SO, FOG, and FG fibers of the muscles under investigation increased in size with increasing age, BW, or both, and the increases in size were similar in magnitude for the 3 fiber types. Conversely, Ono et al. (1995) and Candek-Potokar et al. (1999) found from 60 to 90 kg of BW and from 100 to 130 kg of BW, respectively, a more distinct increase in SO and FOG than in FG fiber size. Ono et al. (1995) concluded that the FG fibers mature earlier than SO and FOG fibers, and that the latter 2 fiber types accounted for the largest part of muscle growth after 60 kg of BW. Except for the RF, myofiber type distribution remained unchanged from 113 to 154 d of age or from 60 to 100 kg of BW, regardless of the feeding regimen. Thus, metabolic differentiation occurred at an earlier stage of muscle development and confirms results from Ono et al. (1995).

When barrows were slaughtered at the same age, feed restriction significantly delayed overall myofiber hypertrophy in the LM and ST but not in the RF. One reason for the lack of dietary impact on the RF myofiber size could be the fact that allometric growth coefficient of the RF (0.99) is lower than of the LM (1.12) and the ST (1.04; Davies, 1974). Thus, the LM and to some extent also the ST, displaying greater postnatal allometric growth ratios, may be regarded as retarded muscles, relative to the RF that have already decelerated its growth. Based on these results, one could hypothesize that feed restriction had no effect on postnatal muscle fiber growth in the RF or that delay of myofiber hypertrophy occurred at an earlier developmental stage and was already compensated at 113 d of age. The latter explanation might be more plausible because the lighter muscle weight and lower CP content of the RF in R barrows at 113 and 154 d of age compared with the RF of their siblings in the ad libitum group suggested that overall muscle growth was impaired by feed restriction. The differing dietary intake impact on myofiber growth was clearly evidenced when the RF and ST myofiber size were compared at the same age. Whereas the allometric growth ratios of the RF and ST were similar, myofibers of the STL were smaller, and based on the myofiber distribution, muscle metabolism was less glycolytic in barrows of the restricted compared with the ad libitum group. By contrast in the STD, the predominantly oxidative part of the ST, feeding regimen did not affect muscle fiber size up to 113 d of age, whereas hypertrophic growth of SO and FOG fibers was delayed afterwards (d 153 of age). These observations revealed that within muscle the sensitivity toward exogenic factors markedly differed. It is well established that the concentration of various hormones known for their involvement in myofiber growth and differentiation are under nutritional regulation (Cassar-Malek et al., 1998). White et al. (2000) found greater proportions of fibers with high oxidative activity after a period of severe feed restriction in various porcine muscles, and these changes were closely related to decreased levels of plasma thyroid hormones. The dietary impact was greater in white (LM) compared with red muscles (diaphragm). The discrepancy in hormonal responsiveness among muscles seemed to be related to muscle-specific differences in thyroid hormone receptor isoforms expression (White et al., 2001). Also a determinant role in postnatal muscle growth is played by the insulin-like growth factor system (Oksbjerg et al., 2004). It was suggested that endocrine and local changes in the IGF-I system might contribute to changes in muscle growth seen by various feeding levels or feeding strategies. For instance Therkildsen et al. (2004) reported that mild feed restriction markedly lowered the IGF-I concentration and concomitantly ST weight. According to Bramfeld et al. (1996), expression of IGF-I mRNA was lower in the ST but not the LM when dietary protein supply was decreased. The close relationship between IGF-I concentration, muscle development, and myofiber growth was evidenced by results obtained with transgenic pigs, which expressed IGF-I only in skeletal muscle (Pursel et al., 2004). Transgenic overexpression of IGF-I elicited a pronounced increase in myofiber size in various muscles (Bee et al., 1997).

Except for the smaller FOG fibers in the STD of R60 and R100 barrows, the effect of feed allowance on muscle fiber size vanished when barrows were slaughtered at the same BW. In older and heavier (100 or 130 kg of BW) pigs Candek-Potokar et al. (1999) also found no effect of feed restriction on myofiber size development. By contrast, mild feed restriction in the growing period (25 to 55 kg of BW) inhibited SO and FG fiber hypertrophy in the LM (Solomon et al., 1988). The latter findings could be explained by the fact that myofiber development is more prone to reduced nutrient supply at an earlier development stage because hypertrophic growth is 4 times greater from 20 to 60 than from 60 to 90 kg of BW (Ono et al., 1995). The lack of effect of feed restriction on the size of most myofiber types at 60 as well as at 100 kg of BW could be due to the fact that in the current study total nutrient intake was similar in both experimental groups during the growing and finishing period. These results may lead to the conclusion that hypertrophy of most myofibers depended more on the total than on the daily nutrient intake.

In the pig, results of several studies suggest that dietary feed restriction can delay muscle maturation as evidenced by changes in the muscle fiber distribution and that the extent of the effects differs among muscles during postnatal growth. Lefaucheur et al. (2003) reported markedly greater percentages of muscle fibers expressing the type I myosin heavy chain isoform and lower lactate dehydrogenase activity, indicative for the lower glycolytic potential, in 7-d-old

piglets after dietary restriction (30% of control). In that study the dietary impact was more evident in the LM than in the rhomboideus muscle. Also in 2-mo-old pigs, feed restriction (50% of control) for 4 wk resulted in a significantly greater percentage of slow fibers in the rhomboideus muscle (Harrison et al., 1996), whereas the dietary effect was less pronounced in the LM and absent in the soleus muscle. Higher percentages of SO muscle fibers in the LM of restricted-fed barrows (80% of control) were reported at 55 kg of BW (Solomon et al., 1988) and to a lesser extent at 100 and 130 kg of BW (Candek-Potokar et al., 1999). Accordingly, the present data revealed that at the same BW (different age) and to some extent also at the same age (different BW), FOG fibers were selectively preserved in muscles with a low allometric growth ratio such as the RF and ST in restricted-fed barrows. However, contrary to the aforementioned results, we found a markedly lower proportion of oxidative fibers in the LM of feed-restricted barrows at 60 as well as at 100 kg of BW. Because feed restriction had no effect on the fiber type distribution of the late maturing LM when barrows were slaughtered at the same age, one could deduce that the variation in the metabolic activity of the LM reflected the differences in age rather than in nutritional status.

In both trials we observed a weight-related small but significant increase in the CP (0.8 to 2 g/100 g of tissue) and DM (0.6 to 1.7 g/100 g of tissue) content of the LM and RF without any changes in the i.m. lipid concentration. These findings are in agreement with results of previous studies with gilts, barrows, and boars (70 up to 130 kg of carcass weight) reporting increases in the DM and CP with increasing carcass weight without a concomitant change in the i.m. lipid concentration of various muscles (Beattie et al., 1999; Correa et al., 2006; Fischer et al., 2006b). By contrast, Candek-Potokar et al. (1998) found in the LM of barrows slaughtered at 130 compared with 100 kg of BW greater protein and i.m. lipid and lower water content. A similar relationship was also observed in trial 1 of this study in the STL and in part in the STD. A possible reason for the discrepancy among the aforementioned results might be due to differences in the genetic potential for growth, lean tissue deposition, or both, of the pigs used in the different studies. For instance regarding the growth potential, growth rates of barrows with ad libitum-feed access in the study of Fischer et al. (2006a) were 119 g/d greater (902 vs. 783 g) than in the study presented by Candek-Potokar et al. (1998). Furthermore, the results reported by d'Souza et al. (2004) suggested that the weight-related effect on the chemical muscle composition differ among muscles. In the weight range of the carcasses from 45 to 79 kg, the i.m lipid content in the LM and supraspinatis muscle were unaltered whereas the lipid content of the biceps femoris increased from 45 to 66 kg.

Restricted feeding has been reported to be associated with decreased i.m. lipid content of the LM (Wood et al., 1996; Candek-Potokar et al., 1998; Gondret and Lebret, 2002), which in the current study, could not be confirmed for the LM and RF. Reduced lipid content in restricted-fed barrows was observed only in the STD (154 d) and STL (113 and 154 d) when slaughtered at the same BW as their siblings with ad libitum-feed access. Although not significant, a similar feeding regimen-related pattern for the i.m. lipid content was observed also in both portions of the ST in trial 2. Compared with trial 1, in lighter and heavier A and R barrows the lipid content of the STD and STL was on average 1% greater and more variable as indicated by the large SEM. The reason for this variability within feeding level and slaughter weight is unknown. Nevertheless, the present results suggested that compared with the other muscles under investigation the ST was more prone to increased lipid deposition under ad libitum feeding condition. Furthermore, the differences in the i.m. lipid content were not related to changes in the muscle fiber type distribution. Because of the fact that oxidative muscle fibers contain larger amounts of triglycerides than the glycolytic ones (Essen-Gustavsson et al., 1994), one could have expected large differences in the i.m. lipid content based on the differences in the myofiber type distribution between the STD and STL. The lack of any phenotypic relationship between muscle fiber composition and lipid content has also been shown in other studies (Larzul et al., 1997; Candek-Potokar et al., 1999; Eggert et al., 2002). These results confirm that the lipids stored intracellularly account only for a small portion of the i.m. lipid content, whereas the major part of the lipids originates from adipocytes interspersed between myofibers. Furthermore, these data confirm that dietary manipulation can affect to some extent the muscle lipid content without a clear impact on muscle fiber characteristics as suggested by Lefaucheur (2001).

Regarding meat quality, shear force values in the STD, STL, and LM of barrows with restricted compared with ad libitum access to feed were consistently greater regardless of whether measurements were carried out at the same age or at the same BW. However, it is unlikely that differences in tenderness were caused by differences in the myofiber size because myofibers were smaller in R compared with A barrows in trial 1 but not in trial 2. Furthermore, dietary induced changes in the myofiber type distribution were not consistent with the changes in shear force values. The lack of accordance between myofiber characteristics and tenderness of pork confirm findings of recent studies (Eggert et al., 2002; Ryu and Kim, 2005). Therefore, the present results indicated that the extent of tissue accretion/protein turnover per se rather than morphological differences in the muscles determined the extent of postmortem muscle tenderization. Although, the lower shear force values were associated with lower i.m. lipid concentrations in the STD (trial 2; slaughtered at the same BW) and STL (trial 1; slaughtered at the same age) but not in the LM, the lack of

distinct accordance between the shear force values and the i.m. lipid content was in agreement with previous findings reporting low (Wood et al., 1999) or no (Candek-Potokar et al., 1999) correlations among those traits. According to Wheeler et al. (2000), sarcomere length, connective tissue content, and proteolysis of myofibrillar proteins account for most, if not all, of the explainable variation observed in tenderness, and their relative contribution is muscle dependent. Early postmortem proteolysis of myofibrillar components, in which the calpain proteolytic system plays a key role, seems to be affected by nutrient supply. Kristensen et al. (2002) reported significantly lower shear force values in the LM of gilts slaughtered at the same age (165 d) with ad libitum compared with restricted-feed access and the differences were associated by the greater proteolytic potential (expressed as the μ-calpain:calpastatin activity ratio) of the muscle at slaughter. In a recent study carried out with pigs with the same genetic background as in the present experiment, the LM and the STD of restricted-fed barrows slaughtered at the same BW were less tender compared with their siblings with ad libitum-feed access (Bee et al., 2006). In accordance to Wheeler et al. (2000), these differences were paralleled by lower postmortem proteolysis (Bee et al., 2006). In addition cooking losses determined in the ST and partly also in the LM coincided with changes in shear force values. These findings are consistent with recent evidence that degradation of cytoskeletal proteins may result in increased shrinking of the overall muscle cell, which is ultimately translated into the extent of water-holding capacity (Huff-Lonergan and Lonergan, 2005).

In conclusion, the present findings pointed out that mild feed restriction, which still permitted barrows to grow, impaired myofiber hypertrophy depending primarily on the BW. Thus, similar myofiber size can eventually be found when restricted-fed barrows have the same BW, but are older, than barrows with ad libitum feed access. By contrast, restricted nutrient supply delayed muscle maturation as evidenced by a greater percentage of oxidative myofibers in early maturing muscles with a low allometric growth ratio. However, the lack of distinct changes in the myofiber type distribution among the younger and lighter barrows and their older and heavier siblings indicated that myofiber transition toward an increased glycolytic metabolism was already completed in the younger and lighter barrows. The observed differences in meat quality traits suggested an involvement of the dietary induced differences in the growth rate but were barely associated with changes in myofiber characteristics. When meat quality traits were affected by the age at slaughter the effect was positive. However, the lower water-holding capacity during thawing and cooking and the greater shear force values, indicating lower tenderness, suggested that even mild feed restriction had a detrimental impact on meat quality.

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