Free-range rearing of pigs during the winter: Adaptations in muscle fiber characteristics and effects on adipose tissue composition and meat quality traits[1]

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ABSTRACT: This research aimed to determine whether outdoor free-range rearing during the winter (average ambient temperature of 5°C) vs. indoor housing (22°C) affects meat quality, muscle metabolic traits, and muscle fiber characteristics. Forty Large White gilts and barrows were blocked by weight within each gender (20 per gender) and allotted randomly into two groups of pigs, with one reared indoors (IN) in individual pens (2.6 m^2) and the other reared outdoors (OUT) from December to March in a 0.92-ha pasture. Both groups had free access to the same grower-finisher diet from 23 to 105 kg. At slaughter, adipose (backfat [BF] and omental fat [OF]) and muscle tissues (longissimus muscle [LM], rectus femoris [RF], and semitendinosus [ST]) were obtained from the right side of each carcass. Muscle fibers were stained and classified on the basis of stain reaction as slow-oxidative (SO), fast oxidative-glycolytic (FOG), and fast glycolytic (FG); fiber area and distribution were determined. Also assessed were carcass characteristics, initial and ultimate pH, L*a*b* values, drip loss percent, glycolytic potential (GP), and intramuscular lipid content, as well as the fatty acid profile of each muscle and adipose tissue. The OUT pigs had lower ($P < 0.05$) ADG and leaner ($P < 0.05$) carcasses than IN pigs. Rearing environment did not ($P > 0.63$) affect the intramuscular lipid content of the ST, but intramuscular lipid content was lower ($P < 0.01$) in the LM and tended to be higher ($P = 0.06$) in the RF of OUT than in those of IN pigs. In the BF outer layer of the OUT pigs, the higher PUFA content was compensated by both a lower ($P < 0.01$) saturated and monounsaturated fatty acid (MUFA) content, whereas in the OF, LM, and dark portion of the ST, only the percentage of MUFA was decreased ($P < 0.01$). In all tissues of the OUT pigs, the linolenic acid content was higher ($P < 0.01$) and the n–6:n–3 ratio was lower ($P < 0.01$). The GP of all muscles was higher ($P < 0.01$), and the ultimate pH of the RF and ST was lower ($P < 0.01$), in OUT compared with IN pigs. Lightness (L*) values were lower ($P < 0.01$) in the LM. Percentages of drip loss were higher ($P < 0.05$) in the LM and light portion of the ST of OUT than in those of IN pigs. The LM and RF of OUT pigs had more ($P < 0.01$) FOG and fewer ($P < 0.01$) FG fibers than muscles of IN pigs. Results suggest that rearing pigs outdoors increases aerobic capacity of glycolytic muscles but has little concomitant influence on meat quality traits.

Key Words: Adipose Tissue, Fatty Acids, Free Range Husbandry, Meat Quality, Muscle Fibers, Pigs

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Introduction

An increasing number of farms rear pigs according to alternative production forms, such as free-range systems, because of the growing consumer demand for meat that was not produced intensively. Compared to conventional production systems, the growing pig reared outside is subjected to a variety of changing environmental influences and is allowed to perform more extensive physical activities (Enfält et al., 1997; Lebret et al., 2002). Various studies have compared the effect of rearing environment on growth performance, carcass characteristics, adipose tissue, and meat quality (Enfält et al., 1997; Nilzén et al., 2001; Gentry et al., 2002), and, in general, housing pigs outdoors has been reported to result in lower growth rates, less backfat, and darker meat color compared with confinement-reared pigs.

Relatively little has been reported on the effects of the rearing environment on muscle fiber types and muscle metabolism. Lefaucheur et al. (1991) demon-

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strated that constant exposure to cold increased the proportion of type I fibers and oxidative metabolism in slow red porcine muscles, whereas muscle energy (oxidative and glycolytic) metabolism was reduced in warm environments (Rinaldo and Le Dividich, 1991). Furthermore, physical training is known to increase the oxidative capacity of skeletal muscles directly involved in the exercise (Petersen, 1997). However, findings on muscle fiber adaptations during exercise training are not comparable with effects of spontaneous exercise occurring in outdoor environments or free-range systems (Petersen et al., 1998b). Hence, the present study was undertaken to evaluate the effect of rearing environment (free-range vs. indoor confinement rearing in individual pens) and ambient temperature (5 vs. 22°C) on growth performance, carcass characteristics, adipose tissue composition, muscle fiber characteristics, muscle metabolic traits, and meat quality traits of three muscles differing in functional role and anatomical location.

Materials and Methods

Animals and Treatments

The experiment was conducted from December through March 2001 and involved 40 Swiss Large White pigs (20 barrows and 20 gilts) originating from 10 litters. From weaning until the start of the experimental period, pigs were group penned (four pigs per pen) and had ad libitum access to a conventional starter diet. At an average weight of 23.3 ± 0.8 kg, pigs were blocked by weight (within gender), and equally assigned, at random, to either of the following two treatments: 1) reared indoors (**IN**) in individual pens (2.6 m^2/pig) on a concrete floor in environmentally controlled buildings (22°C and 60 to 70% relative humidity) or 2) kept outdoors (**OUT**) on a 0.92-ha pasture. Outdoor-reared pigs had access to two 4 × 2 × 1.4 m igloos (Agroprodukte Reinhard, Rüti, Switzerland) with barley straw bedding. To force pigs to exercise, igloos were placed 180 m from the feeder and water. Temperature and humidity in the igloos and outside (placed near the feeder) were measured online (Escort Messtechnik AG, Aesch, Switzerland). The temperature during the 101-d trial averaged 5°C (−8 to 22°C) and 80% (34 to 100%) relative humidity near the feeder (Figure 1) and 8°C (−7 to 27°C) and 82% (22 to 100%) relative humidity inside the igloos.

From 23 to 60 kg BW, and from 60 to 105 kg BW, both groups had ad libitum access to the same grower and finisher diets (Table 1). The diets were pelleted (4.5-mm diameters) at 60°C. Pigs were weighed and feed disappearance was recorded weekly. When pigs achieved a BW of 105 kg, they were slaughtered at the research station abattoir. Pigs fed outdoors were brought inside the abattoir holding pens 16 h before slaughter to ensure that no additional feed was consumed by the pigs.

Table 1. Composition of the growing and finishing diet, as-fed basis

Item	Growing	Finishing
Ingredients, %		
Barley	20.00	24.30
Wheat	63.50	65.20
Corn	—	1.40
Potato protein	10.80	2.90
Animal fat	1.38	2.12
NaCl	0.426	0.460
Dicalcium phosphate	1.364	1.286
Calcium carbonate	1.136	1.226
Lysine·HCl	0.484	0.338
DL-Methionine	0.060	—
L-Threonine	0.122	0.070
L-Tryptophan	0.028	—
Pellan[a]	0.300	0.300
Vitamin-mineral-premix[b]	0.400	0.400
Calculated composition		
DE, MJ/kg[c]	14.0	14.0
NFE, %[d]	59.3	63.0
CP, %	18.0	13.5
Crude fat, %	2.5	2.5
Crude fiber, %	2.5	2.5
Ash, %	5.4	5.3
Lysine, %	1.22	0.78
Ca, %	0.87	0.87
P, %	0.65	0.63

[a]Binder that aids in pellet formation.
[b]Supplied the following nutrients per kilogram of diet: 20,000 IU vitamin A, 200 IU vitamin D_3, 39 IU vitamin E, 2.9 mg riboflavin, 2.4 mg vitamin B_6, 0.010 mg vitamin B_{12}, 0.2 mg vitamin K_3, 10 mg pantothenic acid, 1.4 mg niacin, 0.48 mg folic acid, 199 g choline, 0.052 mg biotin, 52 mg Fe as Fe-sulfate, 0.16 mg I as $Ca(IO)_3$, 0.15 mg Se as Na_2Se, 5.5 mg Cu as $CuSO_4$, 81 mg Zn as ZnO_2, and 15 mg Mn as MnO_2.
[c]Calculated according to the following formula: DE = 18.974 × CP (g/g DM) + 33.472 × crude fat g/g DM) + 16.611 x NFE (g/g DM). (g/g DM) − 21.216 crude fiber (g/g DM) + 16.611 × NFE (g/g DM).
[d]Nitrogen-free extract: DM − ash − CP − crude fat − crude fiber.

Avoiding all unnecessary stress, pigs were walked approximately 100 m to the stunning area, and allowed a ten-minute rest period. Thereafter, a pig was electrically stunned every 10 min using the head-only electric stun tong apparatus (BTR 100 AVS, Freund Maschinenfabrik Gmbh & Co. KG, Paderborn, Germany). Pigs were subsequently exsanguinated, scalded, mechanically dehaired, eviscerated, and weighed. Thirty minutes after exsanguination, the left side of each carcass entered the air-chilling system (3°C) for 24 h.

Tissue Preparation at Slaughter

Within 40 min after exsanguination, three muscles were removed from the right side of each carcass. The torso muscle included the LM, and the hind-limb muscles included the semitendinosus (**ST**) and rectus femoris (**RF**). Weight, girth, and length of the ST; weight of the RF; and the LM area were determined after excision. Muscle samples for histochemical and biochemical analyses were excised from the central region of the RF, the 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 cm × 1 cm × 3 cm) of each muscle was immediately fixed 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 and biochemical analyses, two 1.5-cm-thick LM chops were cut at the 12th-rib level, and two slices (approximately 70 g each) were obtained from the RF, STD, and STL. From the muscle samples, pH, color, and drip loss percent 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 muscle samples were removed (within 40 min of exsanguination), and ultimate pH was obtained after 24-h drip loss determination. Following a 10-min bloom period, L* (higher value indicates a lighter color), a* (higher value indicates a redder color), and b* (higher value indicates a more yellow color) values for the LM, RF, STD, and STL were measured using a Chroma Meter (CR-300; Minolta, Dietikon, Switzerland) and illuminant D_{65}. Three replicate measures were performed on each muscle sample, resulting in six measurements per muscle. Percentage of drip loss was measured as the amount of purge formed during storage of chops at 2°C for 24 h as a percentage of the initial chop weight (Honikel, 1998). Subsequently, the muscle samples were freeze-dried, pulverized, vacuum-packaged, and stored at −20°C until chemical analysis. Samples of backfat in the region of the 10th and 12th dorsal vertebrae and omental fat (**OF**) were collected from each carcass. The backfat samples were immediately separated into the outer (**BFO**) and inner (**BFI**) layers. All fat samples were vacuum-packaged and stored at −20°C until determination of the fatty acid profile.

Quantitative Carcass Measures

Dissections of the carcasses were carried out 24 h postmortem according to fabrication standards of the Swiss Pig Performance Testing Station (Rebsamen et al., 1995). Briefly, left carcass sides were fabricated into the major primal cuts (shoulder, loin, ham, and belly) and were trimmed free of all external fat. The total weight of the three cuts, as well as of each cut, was expressed as a percentage of the cold left-side weight. Accordingly, carcass fat percent was calculated as the proportion of total weight of the dissected external fat from the loin, shoulder, and ham to the cold left side.

Chemical Analysis

Crude fat and DM of adipose tissues and muscle samples, as well as the CP of muscle samples, were quantified according to the AOAC methods (1995). Fatty acid profiles of the adipose tissue and muscles were determined by gas chromatography of the methyl esters as previously described (Bee, 2001).

Biochemical Analyses

Muscle samples collected at slaughter were assayed for glycogen, glucose, glucose-6-phosphate, and lactic acid (Bee, 2002). Glycolytic potential (**GP**), reported in micromoles per gram of wet tissue, was calculated according to the formula of Monin and Sellier (1985): GP = [2 × (glycogen + glucose + glucose-6-phosphate)] + [lactic acid].

Using the same samples, the activities of 3-hydroxyacyl-CoA-dehydrogenase (**HAD**), lactate dehydrogenase (**LDH**), and citrate synthase (**CS**) were determined as indicators of fatty acid oxidation, anaerobic, and aerobic capacities, respectively. Enzymes were assayed in triplicate as described by Essén et al. (1980), except that the NAD^+/NADH reactions were measured by spectrometry (340 nm) instead of fluorometry, and enzyme activities were expressed in micromoles per minute per gram of wet muscle.

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. Sections were then treated with the combination of succinic dehydrogenase and acid myofibrillar ATPase according to the multiple staining procedure of Solomon and Dunn (1988). Stained sections were observed at 125× with a BX50 microscope in transmitted light mode (Olympus Optical Co., Hamburg, Germany) equipped with a high-resolution digital camera (ColorView12, Soft Imaging System GmbH, Münster, Germany). Muscle fibers were classified as slow oxidative (**SO**), fast oxidative-glycolytic (**FOG**), and fast glycolytic (**FG**) based on the stain reaction. The SO fibers showed darkest and the FG displayed the lightest staining intensity. Three random fields, at different location within a slide of each muscle sample, were captured as TIFF files, and a minimum of 250 muscle fibers 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 measured fibers.

Statistical Analysis

Data were analyzed with the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). The model used for the

Table 2. Growth performance, carcass characteristics, and morphometric muscle measurements of barrows and gilts reared either indoors or outdoors

	Indoors		Outdoors			*P*-values[a]	
Item	Barrow	Gilt	Barrow	Gilt	SEM	T	G
Growth performance							
Time on feed, d	83	91	97	105	4.0	<0.01	0.04
ADG, kg	1.01	0.91	0.86	0.78	0.031	<0.01	0.03
Total feed disappearance, kg[b]	196.7	186.6	218.1	235.2	6.27	<0.01	0.58
Gain:feed	0.42	0.43	0.38	0.35	0.012	<0.01	0.26
Carcass measurements							
Hot carcass weight, kg	86.4	86.0	85.9	87.5	1.33	0.68	0.75
Lean, %[c]	55.3	57.3	56.9	58.2	0.66	0.04	<0.01
Loin, %	24.8	26.8	26.7	27.2	0.54	0.05	0.02
Shoulder, %	11.9	11.9	12.4	12.4	0.16	<0.01	0.91
Ham, %	19.2	20.2	18.6	20.2	0.41	0.35	0.02
Belly, %	17.0	16.9	17.2	16.9	0.27	0.68	0.44
Omental fat, %[d]	1.6	1.1	1.4	0.9	0.13	0.09	<0.01
Subcutaneous fat, %[e]	13.9	12.7	12.5	11.5	0.44	<0.01	0.02
10th-rib fat, mm	21.1	20.5	21.3	16.7	1.28	0.15	0.04
Morphometric muscle measurements[f]							
LM area, cm^2	53.6	57.8	54.3	54.7	1.55	0.43	0.20
RF weight, g	366	373	364	394	12.6	0.26	0.27
ST weight, g	440	472	432	449	10.5	0.15	0.03
ST length, mm	224	231	230	232	5.5	0.49	0.50
ST girth, mm	219	225	210	218	3.8	0.06	0.09

[a]Probability values for rearing environment (T) and gender (G).
[b]Rearing environment × gender interaction ($P < 0.05$).
[c]Sum of denuded shoulder, back, and ham weights as percentage of cold carcass weight.
[d]Omental fat weight expressed as percentage of cold carcass weight.
[e]Sum of external fat from the shoulder, back, and ham expressed as percentage of cold carcass weight.
[f]LM = longissimus muscle; RF = rectus femoris; and ST = semitendinosus.

analyses of growth performance, carcass composition, fatty acid profile of the tissues, muscle metabolic traits, muscle fiber characteristics, and meat quality traits included rearing conditions (**T**), gender (**G**), and T × G interaction as fixed effects and block (based on initial BW) as the random effect. For the carcass characteristics and meat quality traits, warm carcass weight and date of slaughter were used as covariates (when significant), respectively. Least squares means were calculated and considered statistically significant at $P < 0.05$. When significant T × G interactions occurred they were indexed in the tables. One gilt reared outside did not reach the 105 kg BW for slaughter owing to an extremely low growth rate and, therefore, was excluded from the trial.

Results

Growth Performance

The OUT pigs had a higher ($P < 0.01$) feed intake, lower ($P < 0.01$) ADG, lower ($P < 0.01$) feed utilization, and reached slaughter weight 14 d later than the IN pigs (Table 2). The percentages of valuable (loin and shoulder) cuts were increased ($P < 0.05$), whereas the percentage of subcutaneous fat was decreased ($P < 0.01$) in carcasses from OUT pigs compared with carcasses from IN pigs. As expected, gilts grew slower ($P = 0.03$), had higher ($P < 0.03$) percentages of lean and loin, and lower ($P < 0.02$) percentages of omental and subcutaneous fat than barrows. Gilts fed outdoors consumed more feed (treatment × gender interaction; $P < 0.05$) and tended to be less efficient (lower G:F; treatment × gender interaction; $P < 0.10$) than barrows outdoors. However, there were no ($P > 0.10$) treatment × gender interactions for any other performance or carcass characteristic measured.

Muscle Composition and Intramuscular Fatty Acid Profiles

Compared with carcasses from IN pigs, DM and i.m. lipid content of the LM were lower ($P < 0.03$) in carcasses of OUT pigs (Table 3). Moreover, the RF from OUT pigs had higher ($P < 0.06$) DM and i.m. lipid content than the RF from IN pigs. Rearing environment did not ($P > 0.10$) affect the composition of the ST. With the exception of lower ($P = 0.07$) proportions of palmitic acid (16:0) in the LM of OUT pigs compared to IN pigs, the percentage of saturated fatty acids (**SFA**) in the i.m. lipid from the LM, RF, and ST was unaffected ($P > 0.10$) by the rearing conditions. Conversely, the percentage of monounsaturated fatty acids (**MUFA**) was decreased ($P < 0.01$), and the proportion of PUFA was increased ($P < 0.01$), in the LM and STD of OUT pigs compared to the LM and STD of IN pigs. These changes were attributed to lower ($P < 0.01$) proportions of oleic acid (18:1n–7) and higher (P

< 0.01) proportions of linoleic (18:2n–6), eicosadienoic (20:2n–6), linolenic (18:3n–3), and docosapentaenoic (22:5n–3) acids in the LM and STD from OUT than IN pigs. Compared with IN pigs, only the percentages of linolenic and docosapentaenoic acids in the RF and STL increased ($P < 0.06$) in the OUT pigs. In all muscles studied, the relative amount of n–3 fatty acids was increased, resulting in lower ($P < 0.01$) n–6:n–3 in all muscles from OUT pigs compared with those of IN pigs.

In the STL, no ($P > 0.10$) differences in the fatty acid profile were observed between genders; however, gilts had lower ($P < 0.03$) MUFA concentrations in the LM and RF and higher ($P < 0.04$) PUFA concentrations in the LM, RF, and STD than barrows. These differences were attributed to lower ($P < 0.04$) percentages of oleic acid in the LM and RF and higher ($P < 0.04$) proportions of linoleic and arachidonic (20:4n–6) acids in the LM, RF, and STD from gilts than barrows.

Fatty Acid Profile of the Backfat and Omental Fat

The DM was lower ($P < 0.01$) in the BFI and tended to be lower ($P = 0.09$) in the BFO of OUT pigs than IN pigs (Table 4). The effect of rearing environment on the fatty acid profile of the BFO was more pronounced than that of the BFI. Compared to the composition of the i.m. lipids, both MUFA and PUFA concentrations were higher ($P < 0.01$) and SFA proportion was lower ($P < 0.01$) in the BFO of OUT pigs than IN pigs. The proportion of palmitic and stearic (18:0) acids was lower ($P < 0.01$) and the percentages of oleic, eicosenoic (20:1n–7), linoleic, eicosadienoic, linolenic, and docosapentaenoic acids were higher ($P < 0.01$) in the BFO from OUT than IN pigs. Eicosenoic, eicosadienoic, and linolenic acid concentrations were increased ($P < 0.05$) and stearic acid proportion was decreased ($P < 0.01$) in the BFI of OUT pigs; however, total SFA, MUFA, and PUFA percent were not altered ($P > 0.10$) by the rearing environment. The percentage of MUFA was decreased ($P < 0.01$) and the proportion of PUFA was increased ($P < 0.01$) in the OF of OUT pigs compared to the OF of IN pigs. These changes were attributed to higher ($P < 0.01$) proportions of linoleic, eicosadienoic, arachidonic, and linolenic acids and lower ($P < 0.01$) proportion of oleic acid in the OF from IN than OUT pigs. The n–6:n–3 ratio was lower ($P < 0.01$) in the

Table 3. Nutrient content and fatty acid profile of three muscles from barrows and gilts reared either indoors or outdoors

	Indoors		Outdoors			*P*-values[a]	
Item	Barrow	Gilt	Barrow	Gilt	SEM	T	G
Longissimus muscle							
DM, g/100 g	26.9	26.6	26.7	25.9	0.22	0.03	0.06
Crude fat, g/100 g of wet tissue	2.6	2.2	2.2	1.6	0.24	<0.01	0.11
16:0[b]	24.86	23.84	24.20	23.60	0.312	0.07	0.05
18:0	11.45	11.11	11.38	11.13	0.294	0.93	0.43
16:1n–7	4.54	4.36	2.28	3.93	0.181	0.03	0.22
18:1n–7	47.24	46.42	45.68	43.31	0.627	<0.01	0.02
18:2n–6	6.36	8.01	8.21	10.19	0.630	<0.01	0.03
20:2n–6[c]	0.17	0.17	0.20	0.25	0.018	<0.01	0.06
20:4n–6	1.72	2.40	2.10	3.26	0.273	<0.01	0.02
18:3n–3	0.31	0.36	0.45	0.47	0.024	<0.01	0.25
22:5n–3	0.26	0.36	0.41	0.56	0.057	<0.01	0.05
SFA[d]	38.07	36.58	37.22	36.14	0.612	0.16	0.12
MUFA[e]	52.71	51.63	50.82	48.11	0.668	<0.01	0.02
PUFA	9.16	11.78	12.03	15.68	1.011	<0.01	0.02
n–6:n–3 ratio	14.48	13.90	9.32	9.46	0.409	<0.01	0.62
Rectus femoris							
DM, g/100 g	24.4	23.8	24.7	24.9	0.22	<0.01	0.32
Crude fat, g/100 g of wet tissue	1.4	1.4	1.6	1.4	0.93	0.06	0.10
16:0	21.88	21.26	21.90	21.69	0.252	0.28	0.19
18:0	10.08	9.94	10.00	10.01	0.191	0.97	0.79
16:1n–7	4.27	4.05	4.08	3.69	0.183	0.07	0.20
18:1n–7	41.91	40.90	42.06	39.14	0.752	0.27	0.03
18:2n–6	13.08	14.37	13.48	15.51	0.635	0.17	0.04
20:2n–6[c]	0.30	0.29	0.24	0.34	0.033	0.85	0.12
20:4n–6	4.13	4.79	3.73	4.79	0.307	0.46	0.03
18:3n–3	0.65	0.65	0.74	0.80	0.032	<0.01	0.44
22:5n–3	0.56	0.65	0.63	0.75	0.058	0.06	0.08
SFA[d]	33.28	32.46	33.27	33.02	0.414	0.39	0.31
MUFA[e]	47.08	45.75	47.03	43.71	0.869	0.21	0.03
PUFA	19.59	21.78	19.77	23.26	1.023	0.36	0.03
n–6:n–3 ratio[c]	12.76	12.16	9.77	10.67	0.410	<0.01	0.77

(continued)

Table 3 *continued.* Nutrient content and fatty acid profile of three muscles from barrows and gilts reared either indoors or outdoors

	Indoors		Outdoors			*P*-values[a]	
Item	Barrow	Gilt	Barrow	Gilt	SEM	T	G
Semitendinosus (dark portion)							
DM, g/100 g	26.2	24.9	27.1	25.4	0.82	0.26	0.12
Crude fat, g/100 g of wet tissue	5.3	3.7	5.5	3.7	0.91	0.87	0.15
16:0	24.09	23.10	23.87	23.63	0.333	0.56	0.15
18:0	11.75	11.03	11.42	11.45	0.262	0.86	0.27
16:1n–7	4.14	4.17	4.12	3.80	0.178	0.19	0.47
18:1n–7	47.14	46.72	45.82	44.03	0.524	<0.01	0.13
18:2n–6	7.50	8.97	8.65	10.34	0.296	<0.01	0.04
20:2n–6	0.26	0.32	0.32	0.36	0.027	<0.01	0.05
20:4n–6	1.34	1.83	1.44	1.95	0.172	0.41	0.03
18:3n–3	0.45	0.51	0.63	0.68	0.041	<0.01	0.32
22:5n–3	0.19	0.26	0.26	0.32	0.033	<0.01	0.09
SFA[d]	37.75	35.94	37.28	37.01	0.584	0.53	0.16
MUFA[e]	52.24	51.83	50.96	48.81	0.610	<0.01	0.13
PUFA	10.04	12.26	11.73	14.14	0.794	<0.01	0.04
n–6:n–3 ratio	13.68	13.79	9.78	10.78	0.382	<0.01	0.15
Semitendinosus (light portion)							
DM, g/100 g	26.0	26.4	27.3	26.3	0.52	0.16	0.65
Crude fat, g/100 g of wet tissue	4.4	4.5	4.7	3.8	0.55	0.63	0.51
16:0	24.14	25.73	23.42	23.34	1.071	0.17	0.55
18:0	11.43	12.24	11.02	10.87	0.640	0.20	0.66
16:1n–7	4.20	4.64	4.12	4.16	0.282	0.33	0.49
18:1n–7	48.56	43.67	48.51	47.61	2.183	0.40	0.27
18:2n–6	6.41	7.78	7.24	7.95	0.417	0.11	0.09
20:2n–6	0.24	0.28	0.28	0.30	0.022	0.18	0.18
20:4n–6	1.18	1.49	1.26	1.57	0.133	0.36	0.12
18:3n–3	0.40	0.48	0.54	0.51	0.037	<0.01	0.52
22:5n–3	0.18	0.23	0.25	0.28	0.021	<0.01	0.26
SFA[d]	37.43	39.99	36.28	35.99	1.799	0.18	0.59
MUFA[e]	53.72	49.38	53.68	52.79	1.910	0.41	0.24
PUFA	8.69	10.67	10.05	11.11	0.603	0.04	0.10
n–6:n–3 ratio[c]	12.43	11.49	8.51	9.67	0.381	<0.01	0.82

[a]Probability values for rearing environment (T) and gender (G).
[b]Fatty acids are expressed as g/100 g total fatty acids. Fatty acids were designated by the number of carbon atoms followed by the number of double bonds. The position of the first double bond relative to the methyl(n) end of the molecule was also included.
[c]Rearing environment × gender interaction ($P < 0.05$).
[d]SFA = saturated fatty acids.
[e]MUFA = monounsaturated fatty acids.

adipose tissues from OUT pigs than IN pigs. Compared to the barrows, gilts had less ($P < 0.01$) DM in the BF, but not in the OF. Furthermore, total PUFA proportions were higher in the BFO ($P < 0.04$) and BFI ($P = 0.06$) of gilts than barrows.

Muscle Metabolites and Enzyme Activities

Regardless of the gender, the GP and the concentrations of glycolytic intermediates (glycogen + glucose + glucose-6-phosphate) of all muscles, as well as the concentration of lactic acid in the STL, were markedly higher ($P < 0.01$) in OUT pigs than IN pigs (Figure 2). The LDH activity was higher ($P = 0.05$) in the LM but not ($P > 0.10$) in the RF and ST of OUT pigs compared with IN pigs (Table 5). Activities of CS and HAD were higher ($P < 0.05$) in the RF, STD, and STL of OUT pigs than IN pigs, and these activities tended to be higher ($P < 0.10$) in the LM of OUT pigs compared to IN pigs. The treatment × gender interaction ($P < 0.05$) indicated that gilts reared outdoors had higher ($P < 0.05$) CS activity in the LM (5.3 vs. 2.9 $\mu mol \cdot min^{-1} \cdot g^{-1}$ wet muscle) and RF (9.7 vs. 4.9 $\mu mol \cdot min^{-1} \cdot g^{-1}$ wet muscle) compared with gilts reared indoors.

Muscle Fiber Area and Distribution

The effect of the rearing environment on the cross-sectional area of the three fiber types was minimal. Outdoor-reared pigs tended to have smaller ($P < 0.10$) SO (2,722 vs. 3,455 μm^2) and overall mean area (3,878 vs. 4,391 μm^2) in the STL than did the IN pigs. The treatment × gender interaction ($P < 0.05$) indicated that gilts reared indoors had smaller FG fibers in the RF than barrows reared indoors (3,256 vs. 4,213 μm^2) and outdoors (4,509 vs. 4,202 μm^2). Regardless of the rearing environment, gilts had smaller ($P = 0.02$) FOG fibers (2,748 vs. 3,203 μm^2) and mean fiber areas

Table 4. Dry matter content and fatty acid profile of the outer- and inner backfat and omental fat from barrows and gilts reared either indoors or outdoors

	Indoors		Outdoors			*P*-values[a]	
Item	Barrow	Gilt	Barrow	Gilt	SEM	T	G
Backfat outer layer							
DM, g/100 g	89.7	88.4	89.4	86.7	0.62	0.09	<0.01
16:0[b]	25.05	24.33	23.52	23.49	0.294	<0.01	0.30
18:0	13.47	12.85	11.64	11.87	0.325	<0.01	0.56
16:1n–7	3.03	3.13	3.20	3.12	0.142	0.55	0.97
18:1n–7	44.52	45.00	46.51	46.04	0.375	<0.01	0.98
20:1n–7	0.80	0.78	0.88	0.90	0.043	0.03	0.98
18:2n–6	8.90	9.55	9.61	10.09	0.245	0.02	0.03
20:2n–6	0.42	0.44	0.50	0.51	0.021	<0.01	0.33
20:4n–6	0.22	0.24	0.23	0.25	0.015	0.56	0.08
18:3n–3	0.77	0.84	0.97	0.95	0.033	<0.01	0.53
SFA[c]	40.72	39.42	37.34	37.49	0.486	<0.01	0.33
MUFA[d]	48.83	49.42	51.17	50.56	0.404	<0.01	0.98
PUFA	10.44	11.21	11.55	12.03	0.297	<0.01	0.04
n–6:n–3 ratio[e]	10.71	10.58	8.61	9.44	0.223	<0.01	0.19
Backfat inner layer							
DM, g/100 g	90.6	88.8	87.2	83.3	0.01	<0.01	<0.01
16:0	23.68	25.07	24.75	25.16	1.423	0.67	0.57
18:0[e]	17.15	15.44	14.81	15.14	0.544	<0.01	0.30
16:1n–7	2.51	2.55	2.55	2.55	0.132	0.88	0.88
18:1n–7	44.21	44.09	45.28	44.01	1.118	0.64	0.58
20:1n–7	0.94	0.81	1.03	1.03	0.074	0.02	0.46
18:2n–6	7.69	8.21	7.80	8.26	0.236	0.72	0.07
20:2n–6	0.39	0.39	0.42	0.43	0.023	0.05	0.81
20:4n–6	0.17	0.19	0.16	0.19	0.015	0.41	0.02
18:3n–3	0.66	0.70	0.73	0.78	0.034	0.01	0.20
SFA[c]	43.06	42.53	41.39	42.16	1.256	0.41	0.93
MUFA[d]	47.97	47.86	49.31	47.97	1.143	0.51	0.56
PUFA	9.02	9.60	9.24	9.83	0.276	0.39	0.06
n–6:n–3 ratio	10.72	11.03	9.84	9.73	0.263	<0.01	0.74
Omental fat							
DM, g/100 g	87.7	86.4	88.3	88.2	0.01	0.23	0.57
16:0	28.48	27.89	28.15	28.53	0.293	0.48	0.78
18:0[e]	19.96	19.51	18.69	19.31	0.424	0.09	0.85
16:1n–7	2.26	2.33	2.32	2.19	0.116	0.70	0.80
18:1n–7	38.02	38.08	36.45	35.04	0.485	<0.01	0.27
20:1n–7[e]	0.65	0.56	0.59	0.59	0.032	0.60	0.27
18:2n–6	6.83	7.70	9.14	9.60	0.368	<0.01	0.13
20:2n–6	0.28	0.29	0.33	0.33	0.016	<0.01	0.49
20:4n–6	0.19	0.21	0.23	0.25	0.013	<0.01	0.23
18:3n–3	0.63	0.73	1.05	1.06	0.050	<0.01	0.26
SFA[c]	50.81	49.71	49.28	50.37	0.521	0.34	0.99
MUFA[d]	41.21	41.31	39.80	38.18	0.535	<0.01	0.25
PUFA	7.98	8.99	10.91	11.43	0.427	<0.01	0.13
n–6:n–3 ratio	10.62	10.61	8.16	8.25	0.233	<0.01	0.86

[a]Probability values for rearing environment (T) and gender (G).
[b]Fatty acids are expressed as g/100 g total fatty acids. Fatty acids were designated by the number of carbon atoms followed by the number of double bonds. The position of the first double bond relative to the methyl(n) end of the molecule was also included.
[c]SFA = saturated fatty acids.
[d]MUFA = monounsaturated fatty acids.
[e]Rearing environment × gender interaction ($P < 0.05$).

(2,919 vs. 3,261 μm^2; $P = 0.06$) in the RF than barrows. Compared with IN pigs, the LM and RF of OUT pigs had more ($P < 0.01$) FOG and fewer ($P < 0.01$) FG fibers; however, the proportion of SO fibers was not ($P > 0.10$) affected by rearing environment (Figure 3). There was a tendency for the STL of OUT pigs to have fewer ($P = 0.09$) SO fibers than IN pigs.

Meat Quality Traits

The LM and STL of OUT pigs had higher ($P < 0.05$) percentages of drip loss than the LM and STL of IN pigs (Table 6). Compared to IN pigs, the LM from OUT pigs was darker (lower L* value; $P < 0.01$) and the RF from OUT pigs had a more yellow color (higher b*

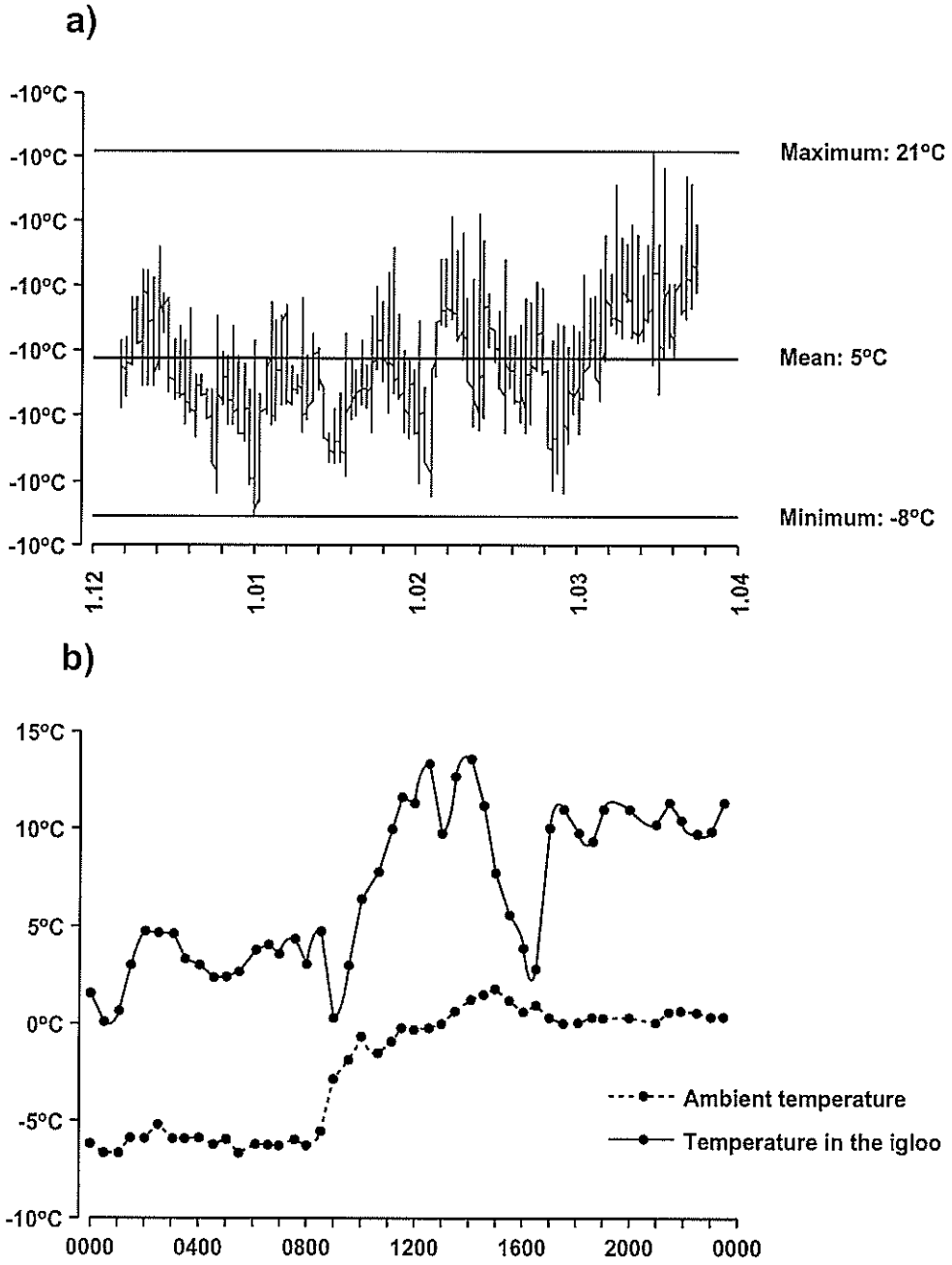

Figure 1. Outdoor temperatures assessed near the feeder during the experimental period (a), and a 1-d temperature profile assessed in the igloo and near the feeder (b).

value; $P < 0.01$). Even though initial pH was not ($P > 0.10$) different among muscles, ultimate (24 h) pH of the RF and ST from OUT pigs was lower ($P < 0.01$) than that of IN pigs.

Discussion

When comparing outdoor vs. indoor environments, two confounding factors affect results obtained in these studies: 1) the amount of activity performed by the pigs and 2) the environmental influences. Both can account for the observed differences but they cannot be easily separated. In the present study, we observed that even though pigs reared indoors and outdoors had free access to the same diets, those reared outdoors consumed 15% more feed and grew 17% slower. Compared with indoor rearing in narrow single pen, OUT pigs had the possibility to move around and to forage

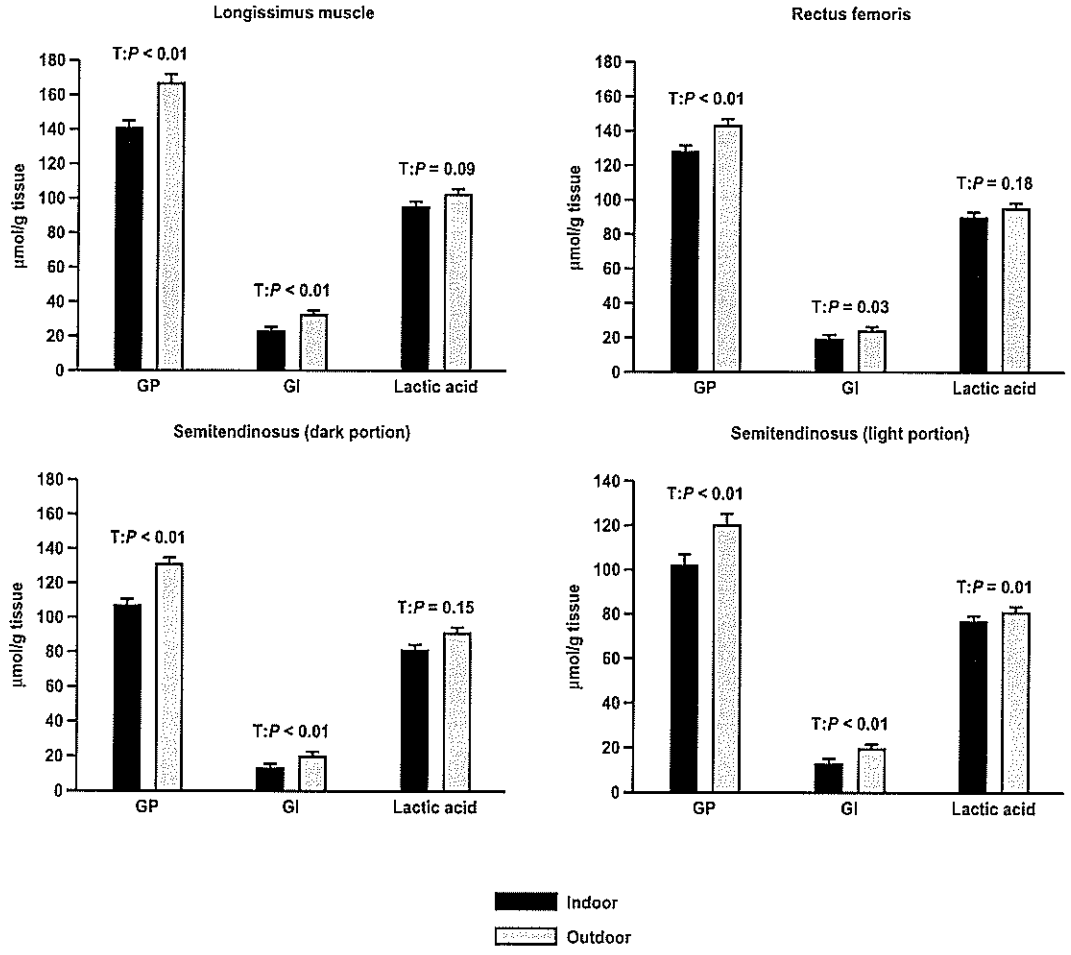

Figure 2. Glycolytic potential (GP), glycolytic intermediates (GI = sum of glycogen, glucose-6-phosphate and glucose), and lactic acid concentration (µmol/g of wet tissue) in the longissimus, rectus femoris, and semitendinosus (dark and light portions) muscles 30 min postmortem in pigs reared either indoors or outdoors.

Table 5. Metabolic traits of three muscles from pigs reared either indoors or outdoors

Item[a]	Indoors	Outdoors	SEM	*P*-values[b]
Longissimus muscle				
LDH	3,328	3,565	81.7	0.05
CS[c]	3.6	4.9	0.48	0.06
HAD	0.21	0.29	0.034	0.10
Rectus femoris				
LDH	2,607	2,517	68.4	0.35
CS[c]	5.6	8.2	0.91	0.04
HAD	0.24	0.48	0.056	<0.01
Semitendinosus (dark portion)				
LDH	1,741	1,801	78.1	0.58
CS	8.0	12.5	1.42	0.01
HAD	0.35	0.69	0.110	0.03
Semitendinosus (light portion)				
LDH	2,126	2,192	87.6	0.59
CS	4.2	5.7	0.58	0.04
HAD	0.12	0.18	0.020	0.05

[a]LDH = lactate dehydrogenase; CS = citrate synthase; and HAD = 3-hydroxyacyl-CoA-dehydrogenase. Enzyme activities are expressed as $\mu mol \cdot min^{-1} \cdot g^{-1}$ wet muscle.
[b]Probability values for rearing environment.
[c]Rearing environment × gender interaction ($P < 0.05$).

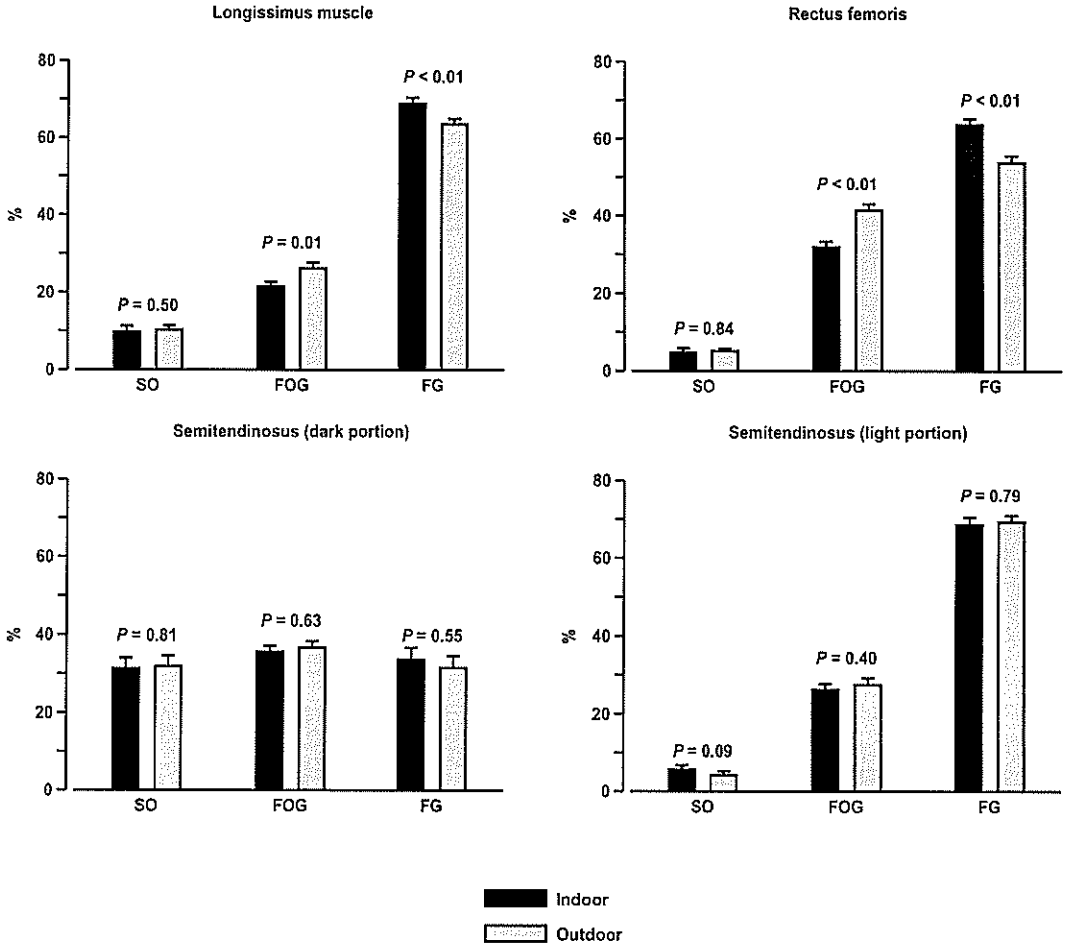

Figure 3. Distribution of the muscle fiber types (SO = slow oxidative; FOG = fast-oxidative glycolytic; and FG = fast-glycolytic) in the longissimus, rectus femoris, and semitendinosus (dark and light portions) muscles of pigs reared either indoors or outdoors.

for food, thereby allowing them to be more active. However, under controlled experimental conditions, increased activity did not affect growth rate when feed was supplied ad libitum (Enfält et al., 1993; Petersen et al., 1998b). The other plausible reason for the slower growth could result from the higher nutrient requirements due to increased heat production in order to maintain body temperature. During the experimental period of this study, ambient temperature was, on average, 12 (in the igloo) to 15°C (near the feeder) below the thermoneutral zone. Lopez et al. (1991) reported 27% lower growth rates and 5% higher feed intake of finishing pigs subjected to a cold diurnal temperature (−5 to 8°C) for 21 d compared with a constant, thermoneutral temperature of 20°C. However, Derno et al. (1995) observed a reduction in heat production over time due to processes of acclimatization of the pigs to the cold environment. Gilts reared outside consumed more feed compared to barrows, whereas no gender differences occurred in the IN group. This finding seems reasonable because gilts are generally leaner than barrows. Thus, energy requirements to maintain body temperature are even more increased when ambient temperature is below the critical temperature (Lopez et al., 1991).

In agreement with results of various other studies (Stoll, 1995; Enfält et al., 1997; Petersen et al., 1998b), pigs fed outdoors were leaner than their contemporaries fed indoors. The higher lean percent in OUT pigs vs. IN pigs was a result of increased loin and shoulder weights, yet the weight of the ham did not differ among treatments. Thus, it was not surprising that the weights of the two ham muscles (ST and RF) were similar for the two treatments, confirming the results of Enfält et al. (1997). However, those authors found that the total weight of three glycolytic muscles (biceps femoris, semimembranosus, and gluteus medius) of the ham were heavier in pigs reared outside rather than inside. The greater percentage of the loin was not reflected by either an increase in LM or a reduction in backfat depth in carcasses from OUT pigs. In addition, Sather et al. (1997) revealed that higher weight

Table 6. Meat quality traits determined in three muscles from pigs reared either indoors or outdoors

Item	Indoors	Outdoors	SEM	*P*-values[a]
Longissimus muscle				
Drip loss, %	1.85	2.00	0.055	0.03
L*	48.8	47.3	0.33	<0.01
a*	8.2	8.5	0.30	0.49
b*	6.3	6.3	0.18	0.86
Initial pH	6.3	6.3	0.06	0.52
Ultimate pH	5.5	5.5	0.01	0.97
Rectus femoris				
Drip loss, %	1.47	1.44	0.050	0.48
L*	45.1	44.6	0.48	0.45
a*	10.8	12.0	0.40	0.06
b*	7.0	7.9	0.23	<0.01
Initial pH	6.6	6.4	0.06	0.09
Ultimate pH	5.7	5.6	0.03	0.01
Semitendinosus (dark portion)				
Drip loss, %	1.55	1.74	0.088	0.16
L*	45.0	44.7	0.52	0.71
a*	13.9	14.0	0.41	0.86
b*	8.5	8.5	0.19	0.51
Initial pH	6.0	6.0	0.05	0.40
Ultimate pH	5.9	5.7	0.04	<0.01
Semitendinosus (light portion)				
Drip loss, %	1.50	2.11	0.1886	0.05
L*	52.4	51.9	1.34	0.80
a*	10.0	9.7	0.36	0.55
b*	7.7	7.6	0.26	0.75
Initial pH	5.9	6.0	0.07	0.21
Ultimate pH	5.7	5.6	0.03	<0.01

[a]Probability values for rearing environment.

of primal cuts from pigs reared outside resulted from increased bone and muscle mass and lower i.m. fat content.

The i.m. lipid content varied among rearing conditions, with a lower content in the LM and a higher content in the RF of OUT pigs compared to IN pigs. Other studies confirm the variable influence of rearing conditions on i.m lipid content of different muscles (Dufey, 1995; Enfält et al., 1997; Andrés et al., 2001). In the present study, changes in the i.m. lipid content were compensated primarily by higher and lower moisture contents of the LM and RF, respectively, whereas protein content was not affected. By contrast, other research has failed to demonstrate an effect of rearing environment on i.m. lipid content (Enfält et al., 1997; Nilzén et al., 2001). Nilzén et al. (2001) reported a reduction in CP, whereas Enfält et al. (1997) reported increased protein content, in muscle of pigs reared outside.

Diet and amount of deposited fat are major factors influencing the fatty acid composition of i.m. and adipose lipids (reviewed by Nürnberg et al., 1998). Because the basal diet was the same for the two groups, the observed differences in the fatty acid composition of the tissues can be partly explained by different amounts of deposited fat in the tissues. In the LM, the increased PUFA concentration (+26%) is consistent with the lower i.m. lipid content (–26%) of the OUT pigs, indicating that the total amount of deposited PUFA was similar in both treatments. In contrast, the observed increase in PUFA levels in the ST of OUT pigs was not accompanied by any changes in the lipid content. Because HAD activity was significantly increased, suggesting a higher fatty acid oxidation rate, our findings could imply that the PUFA incorporation was more efficient in the ST of the OUT pigs than IN pigs. In agreement with results presented by others (Dufey, 1995; Nilzén et al., 2001), the amount of n–3 fatty acids was higher in all muscles and fat tissues of the OUT pigs than IN pigs. Although the experiment was carried out during the winter, the present results indicate that pigs utilized the available grass that is known to be a rich source of linolenic acid (Wood et al., 1999). From a human health point of view, the higher concentration of both linolenic and docosapentaenoic acids is beneficial because the lack of n–3 fatty acids intake has been linked to various chronic disorders (Williams, 2000). Furthermore, the pronounced increase in n–3, compared to n–6, fatty acids in tissues of OUT pigs resulted in lower n–6:n–3 ratios that approached levels recommended by the Food and Agriculture Organization/World Health Organization (Roche, 1999).

Our findings that the level of unsaturation in the i.m. and adipose tissue lipids was higher for gilts than

for barrows confirmed results of other studies (Warnants et al., 1996; Nilzén et al., 2001). In part, this effect can be attributed to the overall lower lipid content of tissues in gilts (LM, BFI, and BFO). When i.m. lipid content is reduced, the proportion of unsaturated phospholipids is higher and results in an overall increase in PUFA content (Bee, 2002). However, this explanation seems not to be plausible for the RF and ST because no gender differences in i.m. lipid content were noted in these muscles.

Metabolism and fiber composition of skeletal muscles have been reported to be affected by both intensity of physical activity and exposure to a cold environment (Lefaucheur et al., 1991; Petersen et al., 1998a). In the muscles (LM, RF, and ST) studied in the present trial, the potential for aerobic ATP production (CS), as well as the ability to oxidize fatty acids (HAD), was elevated in the OUT pigs; however, the response of glycolytic metabolism (LDH) to rearing environment was restricted to only the LM. Lefaucheur et al. (1991) hypothesized that the increase in oxidative metabolism of cold-exposed (12°C) pigs housed in individual pens resulted from either the elevated secretion and utilization of thyroid hormones (known to be involved in metabolic adaptations of skeletal muscles), or from the heat-producing mechanism of shivering. By contrast, the activity of oxidative enzymes in muscles of pigs subjected to moderate exercise (Enfält et al., 1993) or housed in large pens were unaffected (Petersen et al., 1997).

In the present study, metabolic adaptations were, in part, reflected in the muscle fiber composition. In the LM and RF, outdoor rearing elevated the proportion of FOG fibers at the expense of FG fibers, whereas the percentage of SO fibers was unaffected. These findings are in agreement with earlier studies comparing the impact of physical activity on histological traits (Essen-Gustavsson and Jensen-Waern, 1993; Petersen et al., 1998a; Lebret et al., 2002). Surprisingly, the fiber distribution of the ST (STD and STL), a muscle known to be involved in locomotion, was not influenced by the rearing conditions, even though CS activity was increased. In the same muscle, Petersen et al. (1998a) reported an increase in the proportion of FOG fibers at the expense of slow- and fast-twitch fibers in pigs reared in large pens compared to those housed individually; however, they did not separate the ST into the dark and light portions. A possible reason for the lack of difference among treatments in the STD could be that the percentage of oxidative fibers was already elevated in this part of the muscle. However, this explanation is not plausible for the light portion of the ST.

Meat color and water-holding capacity are affected by biochemical processes during the postslaughter conversion of muscle to meat. The extent of postmortem metabolism and ultimate muscle pH are determined by glycogen content at slaughter (Bendall and Swatland, 1988). In the present study, this relationship was confirmed in the RF, STD, and STL (but not in the LM), where pork from OUT pigs had higher GP and lower ultimate pH values. However, these differences did not affect drip losses in the RF and STD. By contrast, the higher GP in the LM and STL of OUT pigs was consistent with the observed elevation in percentages of drip loss.

In agreement with results of the present study, Sather et al. (1997) reported higher percentages of drip loss in the LM of free-range vs. confinement-housed pigs; however, ultimate pH of the LM and semimembranosus muscle were not affected by rearing environment. Moreover, Enfält et al. (1997) observed lower ultimate pH values, combined with greater percentages of drip loss, in the LM of pigs reared outdoors, whereas neither Warriss et al. (1983) nor van der Wal et al. (1993) could establish any differences between rearing environments on pork quality traits. Low ambient temperature markedly increased the GP and lowered initial and ultimate pH values in the LM; however, GP was decreased, and pH of the semispinalis was unaffected, by decreasing ambient temperature (Lefaucheur et al., 1991). In agreement with earlier studies (Lefaucheur et al., 1991; Petersen et al., 1997; 1998a), the higher GP content in muscles of the OUT pigs was not consistent with muscle fiber type distribution. One would have expected that GP decreases with the increasing proportion of FOG at the expense of FG fibers (as observed in the LM and RF of OUT pigs), yet Henckel et al. (1997) and Larzul et al. (1997) found no phenotypic correlations between GP and fiber-type distribution.

Implications

Compared with individually housed pigs, growth retardation, combined with leaner carcasses and adaptations of muscle metabolism and characteristics, occurred when pigs exposed to a cold environment were finished in a free-range system. Higher concentrations of polyunsaturated fatty acids, caused by the lower fat deposition, may lead to softer fat, increased susceptibility to fatty acid oxidation, and impaired technological properties of outdoor-housed pigs. However, the intake of grass on pasture increased the linolenic acid content, thereby improving the nutritional value of the fat.

Literature Cited

Andrés, A. I., R. Cava, A. I. Mayoral, J. F. Tejeda, D. Morcuende, and J. Ruiz. 2001. Oxidative stability and fatty acid composition of pig muscles as affected by rearing system, crossbreeding and metabolic type of muscle fibre. Meat Sci. 59:39–47.

AOAC. 1995. Official Methods of Analysis. 16th ed. Assoc. Offic. Anal. Chem., Washington, DC.

Bee, G. 2001. Dietary conjugated linoleic acids affect tissue lipid composition but not de novo lipogenesis in finishing pigs. Anim. Res. 50:1–17.

Bee, G. 2002. Effect of available dietary carbohydrate on glycolytic potential and meat quality of swine muscles. Can. J. Anim. Sci. 82:311–320.

Bendall, J. R., and H. J. Swatland. 1988. Review of the relationships of pH with physical aspects of pork quality. Meat Sci. 24:85–126.

Derno, M., W. Jentsch, and L. Hoffmann. 1995. Effect of long time exposure to different environmental temperatures on heat production of growing pigs. Livest. Prod. Sci. 43:149–152.

Dufey, P.-A. 1995. Fleisch- und Fettqualität bei Schweinemast mit Weidegang. Agrarforschung 2:453–456.

Enfält, A. C., K. Lundstrom, I. Hansson, A. Karlsson, B. Essen-Gustavsson, and J. Hakansson. 1993. Moderate indoor exercise: Effect on production and carcass traits, muscle enzyme-activities and meat quality in pigs. Anim. Prod. 57:127–135.

Enfält, A. C., K. Lundström, I. Hansson, N. Lundeheim, and P. E. Nystrom. 1997. Effects of outdoor rearing and sire breed (Duroc or Yorkshire) on carcass composition and sensory and technological meat quality. Meat Sci. 45:1–15.

Essén, B., A. Lindholm, and J. Thornton. 1980. Histochemical properties of muscle fibres types and enzyme activities in skeletal muscles of Standardbred trotters of different ages. Equine Vet. J. 12:175–180.

Essen-Gustavsson, B., and M. Jensen-Waern. 1993. Muscle characteristics and metabolic response at slaughter in domestic pigs reared either outdoors or indoors. Proc. 40th Itn. Cong. Meat Sci. Technol. 40, S2P09. Calgary, Canada.

Gentry, J. G., J. J. McGlone, J. R. Blanton, and M. F. Miller. 2002. Alternative housing systems for pigs: Influences on growth, composition, and pork quality. J. Anim. Sci. 80:1781–1790.

Henckel, P., N. Oksbjerg, E. Erlandsen, and C. Bejerholm. 1997. Histo- and biochemical characteristics of the longissimus dorsi muscle in pigs and their relationships to performance and meat quality. Meat Sci. 47:311–321.

Honikel, K. O. 1998. Reference methods for the assessment of physical characteristics of meat. Meat Sci. 49:447–457.

Larzul, C., L. Lefaucheur, P. Ecolan, J. Gogue, A. Talmant, P. Sellier, P. L. Roy, G. Monin, and R. P. Le. 1997. Phenotypic and genetic parameters for longissimus muscle fiber characteristics in relation to growth, carcass, and meat quality traits in Large White pigs. J. Anim. Sci. 75:3126–3137.

Lebret, B., P. Massabie, R. Granier, H. Juin, J. Mourot, and P. Chevillon. 2002. Influence of outdoor rearing and indoor temperature on growth performance, carcass, adipose tissue and muscle traits in pigs, and on the technological and eating quality of dry-cured hams. Meat Sci. 62:447–455.

Lefaucheur, L., J. Le Dividich, J. Mourot, G. Monin, P. Ecolan, and D. Krauss. 1991. Influence of environmental temperature on growth, muscle and adipose tissue metabolism, and meat quality in swine. J. Anim. Sci. 69:2844–2854.

Lopez, J., G. W. Jesse, B. A. Becker, and M. R. Ellersieck. 1991. Effects of temperature on the performance of finishing swine: II. Effects of a cold, diurnal temperature on average daily gain, feed intake, and feed efficiency. J. Anim. Sci. 69:1850–1855.

Monin, G., and P. Sellier. 1985. Pork of low technological quality with a normal rate of muscle pH fall in the immediate postmortem period: The case of the Hampshire breed. Meat Sci. 13:49–63.

Nilzén, V., J. Babol, P. C. Dutta, N. Lundeheim, A. C. Enfält, and K. Lundström. 2001. Free range rearing of pigs with access to pasture grazing: Effect on fatty acid composition and lipid oxidation products. Meat Sci. 58:267–275.

Nürnberg, K., J. Wegner, and K. Ender. 1998. Factors influencing fat composition in muscle and adipose tissue of farm animals. Livest. Prod. Sci. 56:145–156.

Petersen, J. S. 1997. Muscle structure and meat quality in physically active pigs. Pig News Info. 18:79N–82N.

Petersen, J. S., P. Henckel, H. Maribo, N. Oksbjerg, and M. T. Sorensen. 1997. Muscle metabolic traits, post mortem pH-decline and meat quality in pigs subjected to regular physical training and spontaneous activity. Meat Sci. 46:259–275.

Petersen, J. S., P. Henckel, N. Oksbjerg, and M. T. Sorensen. 1998a. Adaptations in muscle fibre characteristics induced by physical activity in pigs. Anim. Sci. (Pencaitland) 66:733–740.

Petersen, J. S., N. Oksbjerg, B. Jorgensen, and M. T. Sorensen. 1998b. Growth performance, carcass composition and leg weakness in pigs exposed to different levels of physical activity. Anim. Sci. (Pencaitland) 66:725–732.

Rebsamen, A., D. Schwörer, and D. Lorenz. 1995. Die Schlachtkör perzerlegung beim Schwein in der MLP Sempach. Der Kleinviehzüchter 43:223–259.

Rinaldo, D., and J. Le Dividich. 1991. Effects of warm exposure on adipose tissue and muscle metabolism in growing pigs. Comp. Biochem. Physiol. A 100:995–1002.

Roche, H. M. 1999. Unsaturated fatty acids. Proc. Nutr. Soc. 58:397–401.

Sather, A. P., S. D. M. Jones, A. L. Schaefer, J. Colyn, and W. M. Robertson. 1997. Feedlot performance, carcass composition and meat quality of free-range reared pigs. Can. J. Anim. Sci. 77:225–232.

Solomon, M. B., and M. C. Dunn. 1988. Simultaneous histochemical determination of three fiber types in single sections of ovine, bovine and porcine skeletal muscle. J. Anim. Sci. 66:255–264.

Stoll, P. 1995. Schweinemast mit Weidegang hat ihren Preis. Agrarforschung 2:449–452.

van der Wal, P. G., G. Mateman, A. W. de Vries, G. M. A. Vonder, F. J. M. Smulders, G. H. Geesink, and B. Engel. 1993. Scharel (free range) pigs: Carcass composition, meat quality and taste-panel studies. Meat Sci. 34:27–37.

Warnants, N., M. J. Van Oeckel, and C. V. Boucque. 1996. Incorporation of dietary polyunsaturated fatty acids in pork tissues and its implications for the quality of the end products. Meat Sci. 44:125–144.

Warriss, P. D., S. C. Kestin, and J. M. Robinson. 1983. A note on the influence of rearing environment on meat quality in pigs. Meat Sci. 9:271–279.

Williams, C. M. 2000. Dietary fatty acids and human health. Ann. Zootech. 49:165–180.

Wood, J. D., M. Enser, A. V. Fisher, G. R. Nute, R. I. Richardson, and P. R. Sheard. 1999. Manipulating meat quality and composition. Proc. Nutr. Soc. 58:363–370.