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Effect of available dietary carbohydrate on glycolytic potential and meat quality of swine muscles

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Bee, G. 2002. **Effect of available dietary carbohydrate on glycolytic potential and meat quality of swine muscles.** Can. J. Anim. Sci. **82**: 311–320. The aim of this study was to determine whether glycolytic potential (GP) in pork muscle could be modified by the availability of carbohydrates in the diets and, if so, to what extent meat color and drip loss were affected. Biopsy samples of longissimus muscle (LM) from 48 Swiss Large White pigs (25 gilts, 23 barrows) weighing 70 kg were collected, and the GP was determined to vary from 111 to 187 µmol g^{-1} wet weight. At 90-kg body weight, pigs were moved into individual pens and assigned (blocked by GP and sex) to be fed 2.8 kg of a diet either high (H) or low (L) in available carbohydrate up to 104 kg. Pigs were fasted overnight (15 h) before slaughter. Glycogen, glucose, glucose-6-phosphate and lactic acid content were determined in samples of LM (predominantly glycolytic muscle) collected 30 min and 24 h post-mortem and in samples of the dark part of the semitendinosus (ST, oxidative part of the muscle) 24 h post-mortem. After slaughter, the decline in pH and temperature was recorded in the LM from 30 min to 24 h after bleeding. Regardless of the diet, content of glycolytic intermediates and lactic acid were higher in the LM compared to the ST. Diet did not alter the GP, and did not affect color or drip loss of the LM. However, in gilts fed the H diet muscle pH was lower by 0.2 units from 30 min until 6 h post-mortem than in gilts fed the L diet. These effects were not observed in barrows. ST of gilts fed the H diet had higher levels of glycolytic intermediates and lactic acid and, therefore, higher GP compared to gilts on the L diet, but no dietary effects occurred in barrows. Increased GP resulted in paler color and higher drip loss, whereas ultimate pH was not affected. The GP was positively correlated with L* (0.52), a* (0.49), b* (0.59) and drip loss (0.77) of the ST, whereas poor correlations were observed in the LM. In conclusion, dietary treatment only affected paleness and drip loss of the ST muscle and the effects were more pronounced in gilts than barrows. Increased GP resulted in paler meat with higher drip loss.

Key words: Pig, glycolytic potential, meat quality, carbohydrate supply

Bee, G. 2002. **Incidence de la quantité de glucides disponible dans les aliments sur la glycolyse et la qualité de la viande dans les muscles du porc.** Can. J. Anim. Sci. **82**: 311–320. L'étude devait établir si la quantité d'hydrates de carbone présente dans les aliments modifie le potentiel de glycolyse (PG) dans les muscles du porc et, advenant ce cas, comment la couleur de la viande et la perte de liquide au ressuage en sont affectées. L'auteur a prélevé par biopsie des échantillons du *longissimus dorsi* (LD) de 48 gros porcs blancs suisses (25 truies nullipares; 23 castrats) pesant 70 kg. Il a ensuite déterminé le PG, qui variait de 111 à 187 µmol g^{-1} de poids humide. Parvenus au poids de 90 kg, les animaux ont été placés dans des stalles individuelles et divisés en groupes (selon le PG et le sexe) avant de recevoir une ration riche (R) ou pauvre (P) en glucides assimilables jusqu'au poids de 104 kg. Les porcs ont été privés d'aliments la veille (15 h) de l'abattage. L'auteur a dosé la concentration de glycogène, de glucose, de glucose-6-phosphate et d'acide lactique dans les échantillons du LD (muscle très sensible à la glycolyse) 30 minutes et 24 h après la mort de l'animal et dans les échantillons de la partie sombre du semi-tendineux (ST, partie du muscle très sensible à l'oxydation) 24 h après le sacrifice. La chute du pH et de la température dans le LD a été enregistrée de 30 minutes à 24 h après la saignée. Quel que soit le régime, on trouve plus de composés intermédiaires de la glycolyse et d'acide lactique dans le LD que dans le ST. La ration ne modifie pas le PG ni la couleur de la viande et la perte au ressuage dans le LD. Néanmoins, le pH musculaire était plus faible (de 0,2 point) chez les truies nourries avec la ration R que chez celles recevant la ration P, de 30 minutes à 6 h après l'abattage. Cette variation n'a pas été observée chez les castrats. Le ST des truies du groupe R renfermait plus de composés intermédiaires de la glycolyse et d'acide lactique, donc avait un PG supérieur à celui du même muscle chez les truies du groupe P, mais le régime n'a pas eu cet effet sur les castrats. Un PG plus élevé décolore la viande et entraîne plus de pertes au ressuage, mais le pH final n'est pas touché. Il existe une corrélation positive entre le PG et les valeurs L* (0,52), a* (0,49), b* (0,59) et la perte au ressuage (0,77) du ST, mais très peu avec celles du LD. On en conclut que le régime n'affecte que la couleur et la perte au ressuage du ST, et que ces effets sont plus manifestes chez la truie nullipare que le castrat. Une hausse du PG produit une viande plus pâle qui ressue davantage.

Mots clés: Porc, potentiel de glycolyse, qualité de la viande, concentration de glucides

Color and water-holding capacity are essential attributes of fresh pork meat at retail, because they affect its appearance and attractiveness to the consumer. Both quality traits are affected by biochemical processes during the post-slaughter conversion of muscle to meat of which pH and temperature decline post-mortem are important factors. The extent of post-mortem pH fall and ultimate pH vary accord-

Abbreviations: **BW**, body weight; **GP**, glycolytic potential; **H**, diet high in available carbohydrate; **L**, diet low in available carbohydrate; **LM**, longissimus muscle; $\mathbf{pH_i}$, muscle pH 45 min post mortem; $\mathbf{pH_{24}}$, muscle pH 24 h post-mortem; $\mathbf{Temp_i}$, muscle temperature 45 min post-mortem; $\mathbf{Temp_{24}}$, muscle temperature 24 h post-mortem; **ST**, semitendinosus muscle

ing to metabolic and contractile properties of muscles (Laborde et al. 1985) and are mainly determined by the muscle glycogen content at time of slaughter (Bendall and Swatland 1988). An estimate of resting glycogen content and, therefore the potential of lactic acid formation, can be expressed by the glycolytic potential (GP), as proposed by Monin and Sellier (1985), which includes the main intermediates of glycogenolysis and glycolysis in pig muscles (Charpentier 1968). Enfält et al. (1997) reported that GP of longissimus muscle (LM) varied between breeds (Hampshire, GP > 80 to < 300 µmol g^{-1}; Swedish Landrace, GP > 80 to < 260 µmol g^{-1}; Yorkshire, GP > 60 to < 260 µmol g^{-1}) and the distribution pattern within breeds deviated from a normal distribution. Similar variations in the GP of LM were reported by Maribo et al. (1999) for crosses of Landrace-Yorkshire dams and Hampshire-Duroc sires. The reported GP distribution pattern was closely related to the presence of the *RN* gene within the different populations. By contrast, the frequency of the RN^- allele is low in pure European breeds such as Large White, Landrace, and Piétrain (Sellier and Monin 1994; Enfält et al. 1997) and the GP is similar (Sellier et al. 1988; Enfält et al. 1997). Neverthless, the GP in the LM of noncarrieres (rn^+/rn^+) ranges from 110 to 180 µmol g^{-1} wet weight (Lundström et al. 1996). Besides genetic factors, manipulation of glycogen deposition into muscle by dietary means has been discussed. Recently, Rosenvold et al. (2001a) reported that glycogen stores in LM of slaughter pigs can be modulated at the time of slaughter by feeding diets low in available carbohydrates and high in dietary fat. Conversely, data from earlier studies showed that elevating the dietary content of available carbohydrates in the form of sucrose, increased glycogen stores (Briskey et al. 1960) and lowered muscle pH_{24} (Sayre et al. 1963a). However, Fernandez et al. (1992) could not confirm the former results in LM and biceps femoris samples. These studies focused primarily on dietary effects on the level of glycolytic intermediates and meat quality traits of white, predominantly glycolytic, muscles. However, Fernandez et al. (1994) reported that glycogen and lactic acid content vary between muscles exhibiting variable physiological properties and differing in the muscle fiber composition.

The objective of the present work was to evaluate whether muscle glycogen content and quality traits could be influenced by dietary means and if the impact differed in two muscles (LM and the dark part of the semitendinosus muscle), which are known to exhibit different relative composition in types of myofibres. Taking into account that within a breed GP varies between animals, GP analyzed from biopsy samples collected prior to the start of the trial was used to group the animals within dietary treatments.

MATERIALS AND METHODS

Animals and Feeding

The experiment involved 48 pigs (Swiss Large White), 25 gilts and 23 barrows, originating from six rearing pens. The pigs were group-penned from weaning until 25 kg body weight (BW) and fed a conventional starter diet ad libitum. From 25 kg BW until slaughter the pigs were kept in individual pens on solid concrete floors in an environmentally controlled building (temperature: 22°C, humidity: 60–70%). A standard growing-finishing diet was offered ad libitum until the pigs reached 90 kg BW, when the feeding experiment was initiated.

At 70 kg BW, a shot-biopsy was taken from the LM (5 cm caudal to the last rib and also 5 cm off the midline) from all pigs using the device and procedure described by Talmant et al. (1989). The day prior to biopsy, feed was withheld for 15 h and in the morning, approximately 1 h before tissue sampling, pigs were fed 1.4 kg of the standard diet. Biopsies were frozen immediately in liquid nitrogen and stored at −80°C until muscle glycogen, lactic acid, glucose and glucose-6-phosphate content (analytical methods described later) were determined. The GP was calculated and quoted in terms of potential of lactic acid production in postmortem muscle, according to the formula proposed by Monin and Sellier (1985):

$$GP = 2 \times (\text{glycogen} + \text{glucose} + \text{glucose-6-phosphate}) + \text{lactic acid}.$$

Two isoproteic and isoenergetic experimental diets were formulated to meet nutrient requirements for finishing pigs weighing 100 kg (Boltshauser et al. 1993). The selected ingredients varied in the amount of highly available carbohydrates and amount of fat (Table 1). The H diet consisted of barley, wheat, wheat starch, dried sugar beet pulp, corn, sugar beet molasses, dextrose and soybean meal, whereas the main ingredients of the L diet were wheat, barley, alkali-treated straw, apple pulp, animal fat and soybean meal. The diets were pelleted (4.5 mm diameters) at 60°C. During feed processing feed samples were taken and bulked to determine nutrient content.

At 90 kg BW, pigs were blocked (12 blocks) by GP and sex, assigned from within blocks to the two diets (two animals from each sex except in one block: three gilts and one barrow). They were fed for 16 d two daily meals (morning 0700, afternoon 1500) totaling 2.8 kg of the diet with free access to water. The animals were weighed weekly; 8 d after they reached 98 kg BW, they were slaughtered (mean BW 104 kg) at the abattoir of the research station. Feed was withheld from animals 15 h before the pigs were brought to the abattoir. All procedures involving animals were approved by the Swiss Federal Committee for Animal Care and Use.

Slaughtering Procedure and Hot Carcass Sample Collection

Avoiding all unnecessary stress, a maximum of four animals, if possible two of each dietary treatment, were walked to the stunning area (100 m) and were rested for 10 min. Thereafter, every 10 min a pig was electrically stunned using the head-only electric stun tong apparatus (BTR 100 AVS, Freund Maschinenfabrik Gmbh & Co. KG, Paderborn, Germany). After exsanguination, hair was removed by hot water (62°C) scalding and mechanical scrapping, and the warm carcasses were then eviscerated and weighed.

Immediately following evisceration (25 min after stunning), a sample of LM at the height of the 12th rib was obtained from the right carcass side. The sample was immediately wrapped

Table 1. Feed ingredients (%) and chemical composition of experimental diets (as-fed basis)

	Diet[z]	
Item	H	L
Barley	10.0	10.0
Wheat	25.4	52.6
Wheat starch	20.0	0.0
Corn	8.6	0.0
Oats	1.8	0.0
Sugar beet molasses	3.0	0.0
Dextrose	3.0	0.0
Soybean meal	8.3	5.6
Meat and bone meal	3.3	4.0
Potato protein	2.5	0.0
Dried sugar beet pulp	12.4	0.6
Apple pulp	0.0	8.7
Alkali treated straw	0.0	10.1
Animal fat	0.0	7.0
NaCl	0.27	0.02
Dicalcium phosphate	0.59	0.19
Calcium carbonate	0.0	0.15
Lysine-HCl	0.10	0.29
L-Threonine	0.0	0.80
L-Tryptophan	0.0	0.01
Pellan[y]	0.30	0.30
Vitamin-mineral-premix[x]	0.40	0.40
Chemical composition		
Crude ash (g 100 g^{-1})	4.6	4.8
Crude protein (g 100 g^{-1})	14.4	14.3
Crude fat (g 100 g^{-1})	1.6	8.6
NFE[w] (g 100 g^{-1})	68.5	59.5
NDF (g 100 g^{-1})	12.0	18.4
ADF (g 100 g^{-1})	5.6	9.5
Cellulose (g 100 g^{-1})	4.7	7.5
ADL (g 100 g^{-1})	0.9	2.1
Starch (g 100 g^{-1})	45.3	36.6
Sugar (g 100 g^{-1})	6.8	4.2
DE (MJ kg^{-1})[v]	13.2	13.3

[z]Diet H, high amount of highly available carbohydrates; diet L, low amount of highly available carbohydrates.
[y]Pellet aid.
[x]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 cholin, 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, 15 mg Mn as MnO_2.
[w]Nitrogen free extracts: Dry matter – crude ash – crude protein – crude fiber.
[v]Calculated according to the following formulae: crude fat content < 6 g 100 g^{-1} feed: DE = 18.974 × CP (g g DM^{-1}) + 33.472 × XF (g g DM^{-1}) – 21.216 CF (g g DM^{-1}) + 16.611 × NFE (g g DM^{-1}). Crude fat content ≥ 6 and ≤ 9 g 100 g^{-1} feed; DE = 18.615 × CP (g DM^{-1}) + 35.611 × XF (g DM^{-1}) – 20.967 CF (g DM^{-1}) + 16.562 × NFE (g DM^{-1}), where DM = dry matter, CP = crude protein, XF = crude fat, CF = crude fiber.

in aluminum foil and placed in liquid nitrogen and subsequently stored at –80°C until analysis was performed. Thereafter, the carcasses were chilled for 24 h at 2°C.

Longissimus pH and Temperature Measures

The pH and temperature of the LM were monitored 30 (pH_i, $Temp_i$; immediately after muscle collection), 90, 150, 210, 270, 330 min, 6 and 24 h post-mortem (pH_{24}, $Temp_{24}$), using a WTW pH meter (WTW pH196-S, Weilheim, Germany) equipped with a WTW electrode (WTW Eb4, Weilheim, Germany) and a temperature probe. Prior to measurement, the instrument was calibrated with two calibration buffers (solution A: pH 7.080 ± 0.002; solution D: pH 4.667 ± 0.006; Wintion, Weilheim, Germany). Sets of measurements were obtained at different locations at the 13th (pH) and 12th rib (temperature), by insertion of the pH and temperature probe between the ribs from the inside of the left carcass side.

Quantitative Carcass Measures

One day after slaughter, the left side of each carcass was weighed and dissected according to MLP (Swiss Pig Performance Testing Station, Sempach, Switzerland) meat cutting standards (Rebsamen et al. 1995). Briefly, left carcass sides were dissected into the major primal cuts (shoulder, loin, ham and belly). Shoulder, loin and ham were subsequently defatted and the total weight of the three cuts was expressed as a proportion of the cold left carcass side (lean percentage). Accordingly, carcass fat percentage was calculated as the proportion of total weight of the dissected external fat from the loin, shoulder and ham to the cold left carcass side. Omental fat is expressed as the weight percentage of the cold left carcass side. Backfat thickness was measured at the 13th rib level.

Objective Quality Measures

After carcass dissection, two chops (1.5 cm each) of the LM muscle at the 13th rib level were removed. Furthermore, the ST muscle was excised and two slices (approximately 70 g) of the dark part of the ST were obtained. Drip loss and color were determined from the muscle samples. Drip loss was measured as the amount of purge resulting during the storage of the chop for 24 h at 2°C (Honikel 1998). Following a 10-min bloom, light reflectance coordinates (L*: lightness, a*: redness and b*: yellowness) of the muscle surface were measured using a Minolta Chroma Meter CR-300 with the light source D_{65} (Minolta, Dietikon, Switzerland). Three replicate measures were performed on each sample, resulting in six measurements per muscle.

Sample Analysis

Dry matter, crude ash, crude protein, crude fat and crude fiber analyses of feed were carried out according to the methods of the Association of Official Analytical Chemists (1995). Sugar, starch and the fiber fractions (ADF, NDF, ADL) were assessed according to the methods of VDLUFA (Naumann et al. 1997). Biopsies (LM) and meat samples collected at slaughter (LM) and dissection (LM, ST) were essayed for glycogen, glucose, glucose-6-phosphate and lactic acid. Part of the sample was extracted in HCl (37 vol/vol %) for 2 h at 96.2°C. In the neutralized extracts, glycogen was determined as glucose equivalents using hexokinase (Bergmeyer et al. 1974). In the same extracts lactic acid was essayed with lactate dehydrogenase (Noll 1974) using commercially available diagnostic kits (No 139084; Boehringer, Ingelheim, Switzerland). Another part of the sample was deproteinated with Carrez I and Carrez II solutions and subsequently assayed with a

Table 2. Least square means for growth performance and carcass traits in relation to diet (D) and sex (S) daily gain, feed intake and feed conversion ratio during experimental period and carcass meat percentage

	Diet[z]		Sex		P values		
	H (n = 25)	L (n = 23)	Gilt (n = 23)	Barrow (n = 25)	D	S	SEM
Growth performance							
Daily gain (kg d^{-1})	0.94	0.89	0.87	0.97	0.11	< 0.01	0.03
Daily feed intake (kg d^{-1})	2.60	2.51	2.44	2.67	0.24	< 0.01	0.08
Gain:feed (kg/kg)	0.362	0.356	0.356	0.362	0.51	0.52	0.008
Carcass measurements							
Hot carcass weight (kg)	85.5	85.5	85.2	85.8	0.97	0.29	0.6
Lean percentage[y] (%)	57.3	57.8	58.0	57.1	0.41	0.16	0.6
Omental fat[y] (%)	1.8	1.8	1.8	1.8	0.76	0.98	0.1
Subcutaneous fat (%)	13.8	13.5	13.2	14.1	0.50	0.04	0.4
13th rib fat (mm)	20.1	20.2	19.1	21.2	0.98	0.02	0.9

[z]Diet H, high amount of highly available carbohydrates; diet L, low amount of highly available carbohydrates.
[y]Expressed as percentage of cold carcass weight.

diagnostic kit (No 716251; Boehringer, Ingelheim, Switzerland) for glucose and glucose-6-phosphate (Bergmeyer et al. 1974).

Statistical Analysis

Growth performance, carcass evaluation, meat quality traits and muscle metabolites were analyzed with the PROC MIXED procedure (SAS Institute, Inc. 2000). In the model diet, sex and diet × sex interaction were included as fixed factors and block (block = GP estimated from biopsies at 70 kg BW) as a random factor.

The course of the decline in pH and temperature of the LM was analyzed with the PROC MIXED® procedures (SAS Institute, Inc. 2000) with diet and time as fixed effects and block (block = GP estimated from biopsies at 70 kg BW) as a random factor (Littell et al. 1998). The analyses were carried out separately for each sex. The PROC CORR® (SAS Institute, Inc.) option was used to analyze the linear correlation between color, drip, pH (pH_i, pH_{24}) and muscle metabolites. Differences with probability levels of $P \leq 0.05$ were considered significant. When significant diet × sex interactions occurred, least square means of treatment groups for each sex were reported, otherwise only main effect means were stated.

RESULTS

Diet

Diets were formulated to be equal in protein and digestible energy content, while varying in the amount and source of available energy in the small intestine. Hence, the two diets differed primarily in the concentration of crude fat, starch, sugar, and non-starch polysaccharides (Table 1). Compared with the H diet, the L diet contained less highly digestible carbohydrates in the form of starch (–20%) and sugar (–40%). By contrast, the amount of low digestiblility carbohydrates such as cellulose and lignin amounted for 9.5% in the L diet, whereas these carbohydrates were only about half that in the H diet (5.6%). To compensate for the lower amount of available carbohydrates, the L diet was supplemented with 7% animal fat.

Growth Performance and Carcass Characteristics

Growth performance was not affected by the diets (Table 2). However, gilts ingested less feed (9%; $P < 0.01$) and grew more slowly (11%; $P < 0.01$) than barrows, but gain-to-feed ratio was not altered. Although in the experimental period a fixed amount of feed (2.8 kg d^{-1}) was offered, daily intake was on average 0.25 kg lower regardless of the treatment groups. As expected, carcass measurements were not influenced by the short feeding period (Table 2). The percentage of subcutaneous fat and 13th rib fat thickness was lower in gilts than in barrows ($P < 0.05$ for each). The differences in the fat content between gilts and barrows were numerically reflected in the higher lean percentage ($P = 0.16$).

Meat Quality Traits

There were no significant effects of the diet and sex on LM color and drip loss (Table 3). In the H treatment pH_i and $Temp_i$ did not differ between gilts and barrows, but was 0.2 units higher and 1°C lower in gilts compared to barrows of the L group (diet × sex interaction: $P \leq 0.02$ for each). The pH_{24} was 0.1 units higher in gilts compared to barrows ($P = 0.02$), but did not differ between treatments. The $Temp_{24}$ was not affected by the diet and sex.

The pH and temperature in the LM of gilts and barrows are shown in Fig. 1. Gilts fed the L diet had higher LM pH ($P < 0.02$), by 0.2 to 0.3 units, respectively, from 30 min to 6 h post-mortem, but were equal at 12 and 24 h post-mortem. Muscle temperature declined to the same extent in both treatments. By contrast, in barrows, neither pH ($P = 0.34$) nor temperature ($P = 0.47$) was affected by the diet.

In contrast to the LM, values for lightness (L*; diet effect: $P = 0.04$) were higher in the ST of pigs fed the H diet (Table 3). Values for redness (a*) and yellowness (b*) as well as drip loss were significantly higher in gilts fed the H diet, compared to gilts on the L diet and to barrows on either treatments (diet × sex interactions; $P \leq 0.03$ for each). The pH_{24} and $Temp_{24}$ were not affected by diet or sex.

Muscle Metabolites

The distributions of the GP in the LM biopsy collected from all pigs at 70 kg BW are illustrated in Fig. 2. The values var-

Table 3. Least square means for Meat meat quality attributes in relation to diet (D) and sex (S)

	Diet[z]							
	H		L		*P* values			
	Barrow (n = 12)	Gilt (n = 13)	Barrow (n = 11)	Gilt (n = 12)	D	S	D × S	SEM
Longissimus								
L*	50.6	49.7	50.2	50.2	0.99	0.29	0.28	0.39
a*	6.7	6.7	7.0	6.6	0.73	0.39	0.36	0.25
b*	6.3	3.3	3.7	3.6	0.29	0.11	0.56	0.16
Drip loss (%)	4.6	4.2	4.3	3.8	0.63	0.50	0.92	0.62
pHi	6.3	6.2	6.2	6.4	0.77	0.22	0.02	0.08
Tempi	39.0	39.3	39.6	38.6	0.68	0.14	< 0.01	0.20
pH 24	5.5	5.6	5.5	5.6	0.91	0.02	0.68	0.03
Temp 24	1.8	1.6	1.6	1.9	0.92	0.82	0.20	0.17
Semitendinosus								
L*	43.1	44.3	42.7	42.4	0.04	0.39	0.15	0.52
a*	14.6	15.9	14.9	15.0	0.27	0.02	0.03	0.28
b*	5.9	6.8	5.8	5.6	0.01	0.15	0.03	0.24
Drip loss (%)	3.3	4.9	3.5	3.1	0.06	0.11	0.01	0.38
pH 24	5.6	5.7	5.7	5.7	0.08	0.33	0.63	0.02
Temp 24	3.7	3.4	3.4	3.8	0.74	0.76	0.11	0.21

[z]Diet H, high amount of highly available carbohydrates; diet L, low amount of highly available carbohydrates.

ied from 110.6 to 187.9 μmol g^{-1} wet weight and were on average 143.8 ± 15.3 μmol g^{-1}. Overall distribution and distribution within sex (gilts: 143.4 ± 16.2 μmol g^{-1}; barrows: 144.3 ± 14.5 μmol g^{-1}) did not differ from a normal distribution (Shapiro Wilk W Test; overall: P = 0.10; gilts: P = 0.11; barrows: P = 0.51) and 60% of the values ranged between > 130 and < 150 μmol g^{-1} wet weight.

Glucose, lactic acid content and the GP of the LM 30 min and 24 h post-mortem were influenced neither by diet nor sex (Table 4). At slaughter, but not 24 h post-mortem, the content of glucose-6-phosphate in the LM of pigs fed the H diet was higher than in pigs fed the L diet. Glycogen levels 24 h post-mortem in gilts fed the H diet tended to be higher compared to gilts fed the L diet or barrows of both treatment groups (diet × sex interaction; P = 0.09), whereas 30 min post-mortem no differences were observed.

ST muscle of gilts on the H diet had higher levels of glucose and lactic acid and consequently higher GP compared to gilts fed the L diet, whereas metabolite content and GP were similar in barrows fed either the H or L diet (diet × sex interaction; $P \leq 0.05$). There was a tendency for the same effects to be observed for the glycogen content (P = 0.09). Glycogen, lactic acid and GP were lower in the ST than in the LM ($P < 0.05$), independently of diet and sex.

Results from Correlation Analysis

Pearson correlation coefficients between the investigated traits are presented in Table 5. In general, higher correlations were observed in the ST than in the LM. In both muscles, b* values were positively correlated with L* (LM: r = 0.65; ST: r = 0.61) and a* (LM: r = 0.66; ST: r = 0.77). Drip loss in the ST was positively correlated with L* (r = 0.68), a* (r = 0.63) and b* (r = 0.78), whereas in the LM drip loss was only significantly correlated to the a* value (r = 0.63). The correlations between LM quality traits and the GP or the concentration of glycolytic intermediates were not significant, except for lactic acid, which was positively related to the drip loss (r = 0.45). By contrast, color measurements and drip loss of the ST were positively correlated with the GP and the concentration of glycolytic intermediates and lactic acid. The highest values were found between drip loss, glycolytic intermediates, lactic acid and the GP. Low negative correlations occurred between pH_i, a*, drip loss and pH_{24}, L*, b* in the LM. In accordance, poor or weak correlations were found in the ST for pH_{24} and the measured parameters, being significant for b*, drip loss and lactic acid.

DISCUSSION

In the present experiment the overall mean of the GP determined in the LM biopsy is similar to values found in Swedish Landrace, Yorkshire (Enfält et al. 1997) and Large White pigs (Talmant et al. 1989), but substantially below values observed in Hampshire breeds (Fernandez et al. 1992). This is consistent with the known observation that Hampshire, Hampshire crossbred pigs and pigs within certain breeds carrying the dominant *RN*⁻ gene have higher levels of muscle glycogen than pigs from other breeds or noncarriers (rn^+/rn^+). In contrast to Swedish Landrace and Yorkshire pigs (Enfält et al. 1997), in this study, overall and within-sex distribution of the GP followed a normal distribution. The lack of a bimodial GP distribution further indicates the absence of the dominant *RN*⁻ allele in the pigs used in this study.

Growth performance and carcass measurements were not affected by the diets. The lack of difference between the H and L diets was expected, because both diets were formulated to be isoproteic and isoenergetic. Although the experiment was not designed to offer feed ad libitum, animals had free access to feed, because total amount of feed offered daily (2.8 kg) was on average higher than daily feed intake (H: 2.59 kg; L: 2.52 kg). Due to lower feed intake, gilts grew more slowly and deposited less fat than barrows. However, because no interaction between diet and sex existed for

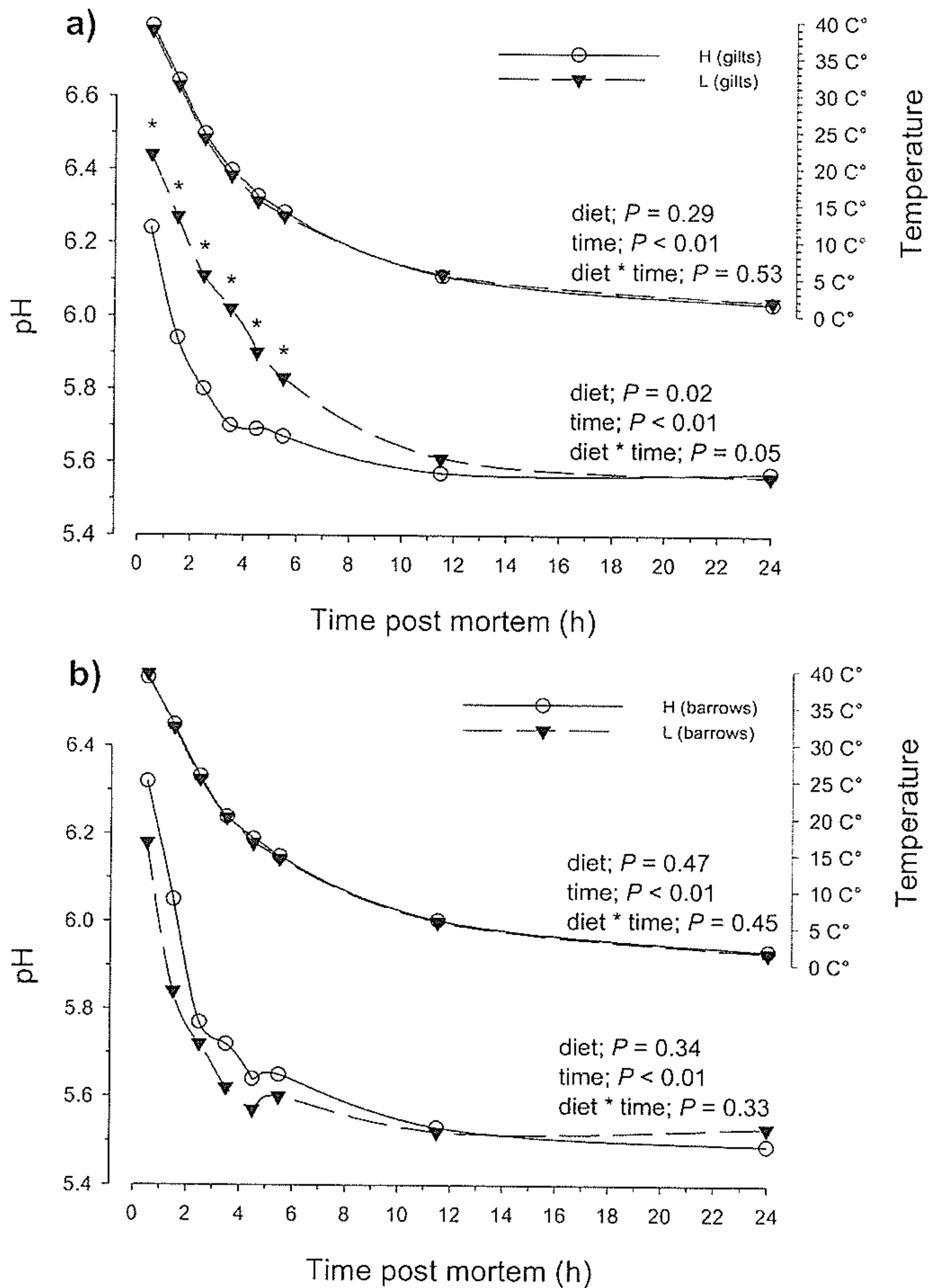

Fig. 1. The pH and temperature in longissimus muscle from 30 min to 24 h post-mortem in gilts (a) and barrows (b) of treatment H and L (*; $P < 0.05$).

growth and carcass data, these effects can be attributed solely to the known sex effect.

Experimental data reported by Briskey et al. (1960) and Sayre et al. (1963b) suggested that feeding high-carbohydrate or high-sugar diets to pigs can elevate the muscle glycogen content. In a similar approach using pigs exhibiting a high GP (258 to 309 μmol g^{-1}), Fernandez et al. (1992) could not confirm the former results. Because Sayre et al.

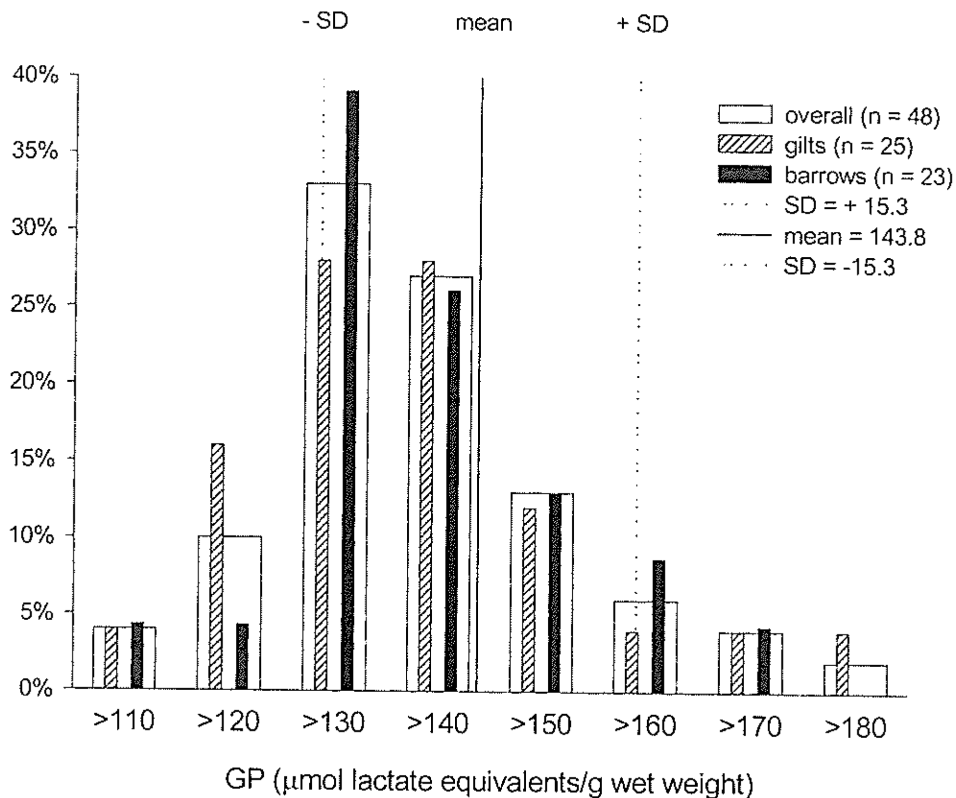

Fig. 2. Distribution of the glycolytic potential (GP) determined in biopsy samples of longissimus muscle of pigs weighing 70 kg. The sum of glycolytic intermediates (glycogen, glucose, glucose-6-phosphate) was on average 24.3 and 24.5 μmol g^{-1} for barrows and gilts, respectively. SD, standard deviation.

(1963b) did not include an overnight fasting period before slaughter, Fernandez et al. (1992) questioned whether the dietary sugar load was a long-term effect rather than a time-limited increase in the amount of glycogen immediately after the sugar load. Apart from the lack of a fasting period prior to slaughter and regardless of the dietary treatment, pigs in the earlier studies had markedly lower glycogen levels compared to pigs in the study of Fernandez et al. (1992). Thus one could question if the basal glycogen level of the muscle is determinant to the ability to alter muscle level by dietary means. The difference in the dietary effects could therefore also be attributed to differences in the basal glycogen concentration of the muscle. In the present study, overall level of glycolytic intermediates in the biopsies (Fig. 2) and samples collected 30 min post-mortem (Table 4) were markedly lower compared to those reported by Fernandez et al. (1992), but somewhat higher than those in the study of Briskey et al. (1960). Nevertheless, our results indicate that compared to the high-fat/low-available carbohydrate diet (L), the starch-/sugar-based diet (H) affected neither glycogen storage nor the GP in the LM. In accordance, no dietary effects on meat quality traits were observed. The weak Pearson correlation coefficients between the various traits further confirm that the LM reacted to the diets with a low variability.

The question arises whether the carbohydrate load supplied by the H diet was sufficient to boost glycogen deposition in the LM, or if the 15-h fasting was responsible for the lack of effect. Lemme et al. (2000) using similar diets reported that following a 24-h period of fasting a high glycemic index diet (comparable to the H diet) reduced the insulin level and the insulin:glucagon ratio significantly compared to a low glycemic index diet. They concluded that high and rapid availability of dietary carbohydrates during digestion caused a down-regulation of insulin during fasting and concomitantly turned on gluconeogenesis with the purpose of maintainting glucose homeostasis. Furthermore, they observed a reduction of gluconeogenesis 3 h post-feeding induced by a high glucose and insulin concentration. These observations support the conclusion that the effects on glycogen deposition reported by Briskey et al. (1960) and Sayre et al. (1963b) were probably the result of a post-prandial increase in muscle glycogen.

Somewhat unexpectedly, pH_i and values assessed within the first 6 h post-mortem were lower in gilts fed the H diet compared with gilts of the L diet. No treatment effects occurred in the barrows. These differences were related to small but nonsignificant ($P = 0.61$) differences in the concentration of glycolytic intermediates 30 min post-mortem.

Table 4. Least square means for the Glycolytic glycolytic potential, glycogen, glucose, glucose-6-phosphate and lactic acid concentrations (µmol g^{-1} wet tissue) in the longissimus dorsi and semitendinosus muscles 30 min and 24 h post mortem in relation to diet (D) and sex (S)

	Diet[z]							
	H		L		*P* values			
	Barrow (*n* = 12)	Gilt (*n* = 13)	Barrow (*n* = 11)	Gilt (*n* = 12)	D	S	D × S	SEM
Longissimus								
30 min post mortem								
GP[y]	152.7	153.2	153.3	152.6	0.99	0.98	0.88	4.06
GI[x]	30.0	32.1	29.5	29.4	0.44	0.61	0.58	2.02
Glycogen	13.3	14.5	14.5	13.7	0.91	0.91	0.58	1.71
Glucose	10.1	10.3	10.0	10.5	0.92	0.64	0.86	0.76
G-6-P[w]	6.5	7.3	5.0	5.2	0.02	0.56	0.69	0.73
Lactic acid	92.8	90.5	94.2	93.7	0.18	0.41	0.59	1.71
24 h post mortem								
GP	154.1	166.5	159.8	161.7	0.91	0.06	0.17	3.68
GI	29.7	35.2	32.3	33.0	0.91	0.10	0.19	1.81
Glycogen	4.8	9.4	7.7	7.5	0.72	0.11	0.09	1.34
Glucose	11.8	12.9	12.2	11.8	0.46	0.55	0.18	0.27
G-6-P	13.1	12.9	12.5	13.7	0.83	0.41	0.28	0.64
Lactic acid	94.6	96.1	95.0	95.6	0.96	0.25	0.65	0.92
Semitendinosus								
24 h post mortem								
GP	102.7	119.9	106.9	99.4	0.06	0.25	< 0.01	4.15
GI	13.8	20.5	16.2	13.5	0.20	0.24	< 0.01	1.69
Glycogen	0.7	3.4	2.1	0.5	0.54	0.65	0.09	1.26
Glucose	8.8	12.0	9.8	8.7	0.07	0.11	< 0.01	0.63
G-6-P	4.2	5.1	4.4	4.4	0.46	0.29	0.23	0.36
Lactic acid	75.2	78.7	74.5	72.4	0.01	0.60	0.05	1.38

[z]Diet H, high amount of highly available carbohydrates; diet L, low amount of highly available carbohydrates.
[y]Glycolytic potential (GP) calculated as 2 × [(glycogen + glucose + glucose-6-phosphate)] + lactic acid).
[x]Glycolytic intermediates represent the sum of glycogen, glucose and glucose-6-phosphate.
[w]G-6-P, glucose-6-phosphate.

Table 5. Correlation between L*, a*, b* values, drip loss, glycolytic potential (GP), content of glycolytic intermediates (GI)[z] and lactic acid, pH post mortem (30 min: pHi; 24 h: pHu24) in the longissimus (LM) and semitendinosus muscles (ST)[y]

	a*		b*		Drip loss		GP		GI		Lactic acid		pHi	pHu24	
	LM	ST	LM	ST	LM	ST	LM	ST	LM	ST	LM	ST	LM	LM	ST
L*	0.19	0.26	**0.65****	**0.61****	0.14	**0.68****	−0.02	**0.52****	−0.04	**0.43***	0.12	**0.52***	−0.03	**−0.32***	−0.25
a*			**0.66****	**0.77****	**0.63****	**0.63****	0.02	**0.49****	−0.02	**0.40***	0.17	**0.49****	**−0.36***	−0.18	−0.26
b*					0.20	**0.78****	−0.08	**0.59****	−0.08	**0.50****	0.02	**0.54****	−0.07	**−0.35***	**−0.46****
Drip loss							0.11	**0.77****	0.01	**0.67****	**0.45****	**0.67****	**−0.47****	−0.16	**−0.42****
GP									**0.98****	**0.94****	**0.35****	**0.71****	0.07	−0.04	−0.25
GI											0.14	**0.44****	0.10	−0.04	−0.15
Lactic acid													−0.10	0.02	**−0.34***
PHi														**0.29***	

[z]The term "glycolytic" intermediates (GI) represent the sum of glycogen, glucose and glucose–6–phosphate.
[y]Correlation coefficients in bold fonts are significant (* $P < 0.05$, ** $P < 0.01$).

Recently, Rosenvold et al. (2001b) reported that a small reduction in muscle glycogen stores induced by a diet with a high-fat/low-digestible starch content resulted in a significant increase in the pH_i in three different muscles. They concluded that the diet, rather than muscle glycogen stores, directly affected glycogen metabolism and/or composition of the muscle. The latter is supported by results from Lemme et al. (2000), reporting lower protein and higher lipid content in the LM from pigs fed the low glycemic index diet. In addition, it has been reported that a diet with a low content of digestible starch and a high fat content decreased protein turnover, supporting the fact that metabolic changes occurred in the muscle tissues. However, the reason why the dietary effects on pH within the first 6 h post-mortem could only be found in gilts and not in barrows is not clear. Differences between barrows and gilts were also reported by D'Souza and Mullan (2002) for pH_{24} and surface exudate of longissimus thoracis, but no information was given about the pH_i.

In the above-mentioned, studies effects of diets on glycogen deposition were studied in glycolytic white muscles like the LM (Fernandez et al. 1992; Sayre et al. 1963b), biceps femoris (Briskey et al. 1960; Fernandez et al. 1992) or gluteus medius (Briskey et al. 1960). In contrast to white muscles, the dark part of the ST is regarded primarily as the oxidative part of this muscle (Laborde et al. 1985), express-

ing mainly slow-twitch βR and fast-twitch βR fibers. Regardless of the treatment, GP was lower in the ST than the LM (Table 4). One can hypothesize that the ST was more susceptible to dietary effects, because of the lower glycogen content and the higher sensitivity to food deprivation of oxidative, compared to glycolytic, muscles (Wittmann et al. 1994). The reason for the difference in the response is primarily due to differences in the muscle fiber composition; slow-twitch βR fibers are depleted more rapidly followed by the fast-twitch αR and αW fibers. The present data revealed that, at 24 h post-mortem, gilts fed the H diet had significantly higher levels of glycolytic intermediates as well as a higher GP compared with gilts fed the L diet. These findings suggest either that glycogen depletion occurred to a lesser extent in these animals or that glycogen deposition was higher at the time of slaughter. However, there is inconsistency in the observed dietary effect, because no differences were found in the ST of barrows. We do not have any explanation for these differences between sexes. The differences in the GP between the gilts of the two treatments was consistent with the observed effects on meat quality traits. Increased GP resulted in paler color and higher drip loss. Accordingly, these observations were reflected in significant positive correlations between GP and meat quality traits in the ST.

CONCLUSIONS

The results of the present work show that the GP of muscles at slaughter can be manipulated by applying appropriate feeding strategies in the finishing period. Under our experimental conditions, where attention was paid to minimize possible ante-mortem stress, dietary impact was observed in an oxidative muscle, but not in a glycolytic muscle. Increasing the GP by supplying highly available carbohydrates negatively affected meat color and drip loss of the ST.

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