Effect of dietary energy supply and fat source on the fatty acid pattern of adipose and lean tissues and lipogenesis in the pig[1]

G. Bee*[2], S. Gebert†, and R. Messikommer†

*Swiss Federal Research Station for Animal Production, Posieux 1725 Switzerland and
†Institute of Animal Sciences ETH-Zurich, Zurich 8052 Switzerland

ABSTRACT: Forty Large White barrows were used to determine whether the effects of dietary fat source (tallow or soy oil at 5% of the diet) on lipogenesis and fatty acid profile of porcine adipose and lean tissue were dependent on dietary digestible energy density (8.8 vs 14.0 MJ DE/kg). Barrows were allocated to one of four groups and offered a fixed amount of feed (170 g × $BW^{0.569}$/d) from 27 to 105 kg BW. The fatty acid composition of the backfat layers (BF), omental fat (OF), and i.m. adipose tissue of longissimus muscle as well as the activity of lipogenic enzymes of the adipose tissues were determined. Growth performance and carcass characteristics were affected by the dietary energy level ($P < 0.01$) but not by fat source. In accordance with the lower carcass fat deposition, the activity of lipogenic enzymes were decreased in the low-energy groups ($P < 0.01$). Within dietary energy level, inclusion of soy oil resulted in increased proportion of PUFA that was compensated by decreased saturated (SFA) and monounsaturated fatty acid (MUFA) proportions ($P < 0.01$). The SFA changes accounted for 23 (BF) and 24% (OF) of the PUFA changes in the high-energy and 31 (BF) and 39% (OF) in the low-energy diets. The differences in the fatty acid proportions between the soy oil and tallow group were more pronounced in the low-energy groups (fat source × energy density interactions: $P < 0.01$). Pigs fed the soy oil, low-energy diet had decreased SFA (BF: 28%; OF: 30%) and MUFA (BF: 13%; OF: 19%) concentration, whereas PUFA concentration was increased (BF: 59%; OF: 88%) compared with pigs fed the soy oil, high-energy diet. However, in the tallow groups, pigs fed the low-energy diets had slightly decreased SFA (BF: 14%; OF: 12%) and relatively constant MUFA (BF: 3%; OF: 1%), whereas PUFA concentration increased (BF: 39%; OF: 62%) relative to pigs fed the tallow high-energy diet. Lipid content of the i.m. adipose tissue was decreased in the low-energy groups ($P < 0.05$). Contrary to what was observed in the adipose tissues, increased PUFA concentration in the neutral and polar lipid fractions of the longissimus muscle was predominantly compensated by reduced MUFA deposition. In the polar lipid fraction, the proportions of both SFA and MUFA were decreased by the low-energy diet. Thus, the extent to which tissue concentration of fatty acids are altered from dietary fats differing in the degree of unsaturation depends on the dietary energy level.

Key Words: Adipose Tissue, Fatty Acids, Longissimus Dorsi, Pigs, Soyabean Oil, Tallow

 J. Anim. Sci. 2002. 80:1564–1574

Introduction

Examinations of adipose tissue fatty acid profile of pigs fed high-energy diets or with added fat are extensive, whereas examination in the alternate situation (i.e., low-energy diets or diets without added fat) are less extensive. Although pigs fed commercial high-energy diets are always in a positive energy balance and do not rely on stored fat to meet energy needs (Enser, 1984), decreased triacylglycerol synthesis is observed in adipose tissue of pigs fed low levels of intake (Mersmann et al., 1981; Mersmann and Koong, 1984). And extreme changes in energy intake combined with altered ratio of linoleic acid to energy in the diet have been reported to produce marked changes in lipid and fatty acid concentration in porcine adipose tissue (Wood et al., 1985, 1986). Raclot et al. (1995) reported that during fasting-induced energy depletion, the mobilization of fatty acids from the adipose tissue is selective and leads to a profound remodeling of the composition of adipose tissue. Food restriction could therefore alter the relationship between intake of fatty acids and both the absolute and relative content of individual fatty acids in adipose and lean tissues.

[1]The authors would like to thank M. D. Lindemann from the University of Kentucky for the review of the manuscript and to M. Barman and H. Bossi for their excellent technical assistance.

[2]Correspondence: La Tioleyre, 4 (phone: +41-26-40-77-222; fax:+41-26-40-77-300; E-mail: giuseppe.bee@rap.admin.ch).

Received June 22, 2001.
Accepted January 8, 2002.

Recently we found that the backfat fatty acids of pigs with free access to diets supplemented with a constant amount of dietary fat rich in either saturated or unsaturated fatty acids were affected differently if diets had a high- or low-dietary energy concentration (Bee et al., 1999). However, under the ad libitum conditions of that study, pigs compensated dietary energy dilution with increased daily feed intake. To extend our previous observations on the deposition of dietary fatty acids originating from soy oil and tallow, pigs in the present study were offered a fixed amount of feed based on BW with the aim to restrict the daily energy intake while avoiding compensatory feed intake mechanisms.

Materials and Methods

Animals and Treatments

Forty castrated male Swiss Large White pigs were randomly assigned to four dietary treatments in a 2 × 2 factorial arrangement, with the individual animal as the experimental unit and the two dietary factors being energy concentration (low or high) and fat source (tallow or soy oil). Pigs entered the trial at an average initial weight of 27.3 kg and were housed during the whole experimental period in individual pens on a concrete floor in environmentally controlled buildings under normal husbandry conditions. Barrows were fed individually twice a day and had free access to water. The total daily feed allowance was adjusted weekly according to the BW by the formula 170 g × $BW^{0.569}$. Two basal diets were formulated (Table 1) differing in their digestible energy content (low: 8.8 MJ DE/kg; high: 14.0 MJ DE/kg). The high-energy diets were based on wheat, potato flakes, and soybean meal. The low-energy diets had lower contents of the main ingredients, which were substituted by oat and NaOH-treated straw. Each of the basal diets was supplemented with 5% soy oil (**HS, LS**) (Unilever Bestfoods Schweiz AG, Thayngen, Switzerland) or tallow (**HT, LT**) (Centravo, Zurich, Switzerland). The added soy oil was mainly composed of linoleic [18:2(n–6)] and oleic acids [18:1(n–9)] and in decreasing order, linolenic [18:3(n–3)] and palmitic acids [16:0]. By contrast, in the tallow the predominant fatty acids were palmitic, stearic [18:0], and oleic acids, whereas the concentrations of linoleic and linolenic acids were low. The fat supplements were well reflected in the fatty acid composition of the diets (Table 2). The diets were pelleted (4.5-mm diameters) at 60°C. During feed processing, feed samples were taken and bulked to determine nutrient content and the fatty acid composition.

Carcass Evaluation

Pigs were slaughtered at a BW of 104.7 kg at the abattoir of the MLP-Sempach (Swiss Pig Performance Testing Station, Sempach, Switzerland). Feed was withheld from animals 12 h before the pigs were brought to the abattoir. The slaughter and dissection procedures were carried out according to MLP meat cutting standards (Rebsamen et al., 1995). Briefly, left carcass sides were fabricated 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.

Tissue Preparation

Within 15 min after bleeding, samples of backfat in the region of the 13th and 14th dorsal vertebra and omental fat (**OF**) were collected from each animal. Backfat was immediately separated into outer (**BFO**) and inner layer (**BFI**). Subsequently, all tissue samples were frozen in liquid nitrogen and stored at –80°C until analysis. Prior to lipid extraction, samples of the adipose tissues were thawed over night at 4°C and homogenized in a Moulinette SE homogenizer (Moulinex GmbH, Solingen, Germany).

Samples from longissimus dorsi muscle were obtained at the height of the 10th rib 24 h postmortem. Muscle tissue was carefully freed from adhering fat and connective tissue and homogenized as previously mentioned. The homogenates were sealed under vacuum in plastic bags and stored at –20°C.

Sample Analysis

Dry matter, crude ash, crude fat, and crude fiber analyses of feed were carried out according to the methods of VDLUFA (Naumann et al., 1997). The nitrogen content (CP = N × 6.25) was analyzed using an automated nitrogen elemental analyzer (Leco-Analyzer FP-2000, Leco Corporation, St. Joseph, MI).

Fatty acid profiles of the feed, adipose tissue, and muscle lipids were determined by gas chromatography of the methyl esters (FAME). The dietary lipids were extracted by a modified method of Hara and Radin (1978). Prior to the cold extraction with hexane:isopropanol (3:2), triundecanoin (11:0, T 5534, Sigma-Aldrich Chemie GmbH, Steinheim, Germany) was added as internal standard. The lipids of the adipose and muscle tissues were extracted according to the method of Juaneda and Rocquelin (1985) with some minor modifications. Total lipids were extracted from homogenate with a methylene chloride:methanol mixture (2:1) after adding tritridecanoin (13:0, T 3882, Sigma-Aldrich Chemie GmbH, Steinheim, Germany) and L-α-phosphatidylcholin-di-undecanoyl (11:0, P 8898, Sigma-Aldrich Chemie GmbH, Steinheim, Germany) as internal standards. Extracts were dried under vacuum and redissolved in 2 mL of chloroform. One milli-

Table 1. Percentage composition of the experimental diets (as-fed basis)

Ingredient, %	Diet			
	High DE/soy oil	High DE/tallow	Low DE/soy oil	Low DE/tallow
Wheat	42.0		22.0	
Flaked potatoes	30.0		10.0	
Dextrose	2.0		2.0	
Oat			22.5	
Alkali-treated straw			22.5	
Soybean meal	12.0		9.0	
Potato protein	2.5		2.0	
Dried yeast	2.0		1.5	
Lysine-HCl	2.0		0.25	
DL-Methionine	0.35		0.15	
L-Threonine (98%)	0.18		0.05	
Limestone, ground	0.04		0.50	
Salt	0.35		0.20	
Dicalcium phosphate	1.00		1.00	
Vitamin/mineral mix[a]	0.50		0.50	
Soy oil	5.0		5.0	
Tallow		5.0		5.0
Analyzed nutrients, %				
DM	89.8	89.3	90.8	90.8
CP	16.4	15.9	12.3	12.2
Crude fat	5.3	5.1	5.1	5.4
CF	2.9	3.3	16.6	16.8
Ash	6.2	6.0	6.5	6.6
Calculated nutrients				
NFE, %[b]	59.0	59.0	51.0	49.7
DE, MJ/kg[c]	14.1	13.8	8.8	8.8
CP:DE, g/MJ	11.7	11.5	14.1	13.8

[a]Supplied the following per kilogram of diet: vitamin A, 10,000 IU; vitamin D3, 1,000 IU; vitamin E, 40 IU; vitamin B_2, 4 mg; vitamin B_6, 4 mg; vitamin B_{12}, 0.015 mg; vitamin K_3, 1 mg; pantothenic acid, 15 mg; niacin, 20 mg; folic acid, 0.2 mg; Fe, 60 mg ($FeSO_4$); I, 1 mg ($Ca(IO_3)$); Se, 0.3 mg (Na_2Se); Cu, 15 mg ($CuSO_4$); Zn, 100 mg (ZnO_2); Mn, 40 mg (MnO_2).
[b]Nitrogen-free extracts: DM – ash – CP – crude fat – crude fiber.
[c]Calculated digestible energy content (DE (MJ/kg DM) according to the following formula: 18.974 × CP (g/g DM) + 33.472 × crude fat (g/g DM) – 21.216 × crude fat (g/g DM) + 16.611 × NFE (g/g DM).

liter of the solution obtained from the muscle homogenate was loaded onto a silica gel column (1 g of silica gel mash 60 (Merck KgaA, Darmstadt, Germany) in 5-mL glass columns (International Sorbent Technology Ltd., Mid Glamorgan, U.K.) previously conditioned with hexane. Neutral lipids and phospholipids were eluted with 20 mL of chloroform and 30 mL of methanol, respectively. Solvents were evaporated under vacuum, and the fatty acids were transformed to FAME. The FAME were prepared by transesterification by sodium hydroxide and boron trifluoride both in methanol according to the method of Metcalfe and Smith (1961). FAME were quantified by using a gas chromatograph (HP 5860 A GC, Hewlett-Packard, Urdorf, Switzerland) equipped with a flame ionization detector. The FAME were separated on a 30-m × 0.32-mm Supelcowax TM 10 fused-silica capillary column (Supelco, Bellefonte, PA). The oven temperature was as follows: initial temperature 160°C for 1 min; raised to 190°C with 20°C/min; raised to 230°C with 4°C/min; 230°C held for 16 min, raised to 250°C with 20°C/min; 250°C held for 8 min. The detection temperature was at 270°C and split at 250°C. The quantification was performed with olein as the reference fat to calculate overall response factors for the standards used. Fatty acids were quantified by comparing peak areas with the peak area of the internal standards. Results are expressed as weight percentages of total fatty acids.

Weighted quantities of BFO, BFI, and OF were homogenized in an ice-cooled 0.25 mol/L sucrose buffer (in 0.1 mol/L phosphate buffer, pH 7.4) using a Potter-Elvehjem homogenizer. The samples were centrifuged at 15,000 × *g* for 10 min and supernatant recentrifuged at 30,000 × *g* for 40 min in the same buffer. The supernatants were assessed for lipogenic enzyme activities using standard photometric methods. Samples were analyzed in duplicates for glucose-6-phosphate dehydrogenase (**G6PDH**, EC 1.1.1.49), malic enzyme (**ME**, EC 1.1.1.40), and fatty acid synthase (**FAS**, EC 2.3.1.85) activities, using the methods of Löhr and Waller (1974), Hsu and Lardy (1969), and Roncari (1981), respectively. Formation of NADPH (G6PDH, ME) or oxidation (FAS) was measured at 37°C by absorbance at 340 nm. A commercial protein dye-binding assay kit, using bovine γ-globulin as a standard, was used to measure the soluble protein concentration in

Table 2. Fatty acid composition of the experimental diets[a]

Fatty acid[b]	Diet			
	High DE/soy oil	High DE/tallow	Low DE/soy oil	Low DE/tallow
	wt %			
14:0 (myristic)	0.21	3.25	0.21	3.55
16:0 (palmitic)	11.92	24.41	11.77	24.85
17:0 (heptadecanoic)	0.14	0.96	0.12	1.00
18:0 (stearic)	4.07	17.46	3.97	18.01
20:0 (eicosanoic)	0.39	0.28	0.46	0.32
24:0 (tetracosanoic)	0.19	n.d.[c]	0.23	n.d.
14:1n-5 (myristoleic)	n.d.	0.42	n.d.	0.45
16:1n-7 (palmitoleic)	0.29	2.06	0.25	2.17
17:1n-7 (heptadecenoic)	0.10	0.50	0.10	0.52
18:1n-7 (vaccenic)	1.39	1.29	1.44	2.74
18:1n-9 (oleic)	22.41	32.77	24.14	32.66
20:1n-9 (eicosenoic)	0.34	0.35	0.37	0.35
18:2n-6 (linoleic)	51.83	14.20	50.56	11.63
18:3n-3 (α-linolenic)	6.61	1.96	6.23	1.65
20:2n-6 (eicosadienoic)	0.10	0.10	0.13	0.11
SFA[d]	16.93	46.35	16.77	47.73
MUFA[e]	24.53	37.39	26.30	38.89
PUFA[f]	58.54	16.26	56.93	13.39
16:1(n-7)/16:0	0.02	0.08	0.02	0.09
18:1(n-9)/18:0	5.50	1.88	6.08	1.81

[a]Only fatty acids that accounted for > 0.1 g/100 g of total are presented.
[b]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 indicated. The sums of the main fatty acid series are represented as SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids.
[c]n.d. = not detectable
[d]SFA = sum of saturated fatty acids.
[e]MUFA = sum of monounsaturated fatty acids.
[f]PUFA = sum of polyunsaturated fatty acids.

the supernatant fraction (Bio-Rad Protein Assay, Bio-Rad, Glattbrugg, Switzerland). The enzyme activities were expressed as μmol NADPH produced or oxidized · min^{-1} · mg $protein^{-1}$.

Statistical Analysis

Data were analyzed with the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). Least square means were obtained assuming fixed models that included the effects of dietary fat source, dietary energy concentration, and fat source × energy concentration interaction. In addition, for the carcass evaluation data, hot carcass weight was included as a covariate in the model. Differences with probability levels of $P < 0.05$ were considered significant. Two pigs of treatment HS and one of treatment HT were excluded due to leg-related problems. One animal in treatment LS did not reach the 105 kg BW for slaughter due to extremely low growth rate, and, therefore, it was decided to exclude it from data evaluation.

Results and Discussion

Growth Performance

Growth performance and carcass measurements were mainly affected by the energy concentration of the diets, whereas dietary fat sources had no effect (Table 3). Compared with the HS and HT diets, the 38% lower DE content of the respective low-energy diets resulted in higher total feed intake (+90%), lower ADG (−46%), and lower feed utilization (−48%) ($P < 0.01$ for all). Although BW at slaughter was not different between treatments, hot carcass weights were higher in the high-energy groups compared with the low-energy groups ($P < 0.01$). The percentages of valuable cuts were increased (loin: +5.3%; shoulder: +8.4%; ham: +9.5%), whereas the percentage of subcutaneous fat (−27.5%), percentage of OF (−33%), and backfat thickness were decreased in the low-energy groups ($P < 0.01$ for all).

Effects of the Fat Source

Dietary fat supplementation was well reflected in both backfat layers (BFO: Table 4; BFI: Table 5) and in the OF (Table 6) especially for linoleic and linolenic acids and the higher unsaturated fatty acids of the n-6 (eicosadienoic, 20:2[n-6]; arachidonic acids, 20:4[n-6]) and n-3 family (eicosatrienoic, 20:3[n-3]; docosapentaenoic acids, 22:5[n-3]), which is in agreement with our earlier results (Bee et al., 1999). The inclusion of soy oil resulted in a markedly increased PUFA concentration in the three adipose tissues that was compensated by a decreased saturated (SFA) and monounsa-

Table 3. Growth performance and carcass measurements[a]

Item	Diet: High DE/soy oil (n = 8)	High DE/tallow (n = 9)	Low DE/soy oil (n = 9)	Low DE/tallow (n = 10)	SEM	*P*-value[b]: F	E	F × E
Growth performance								
Weight gain, g/d	849	842	460	461	16	0.90	<0.01	0.80
Total feed intake, kg	191.2	195.1	368.4	365.3	11.3	0.97	<0.01	0.76
Gain:feed, kg/kg[c]	0.41	0.40	0.21	0.21	0.01	0.51	<0.01	0.49
Carcass measurements								
Hot carcass weight, kg	84.1	83.2	81.4	81.4	0.5	0.40	<0.01	0.40
Lean percentage, %[d]	55.5	55.4	59.5	60.0	0.5	0.67	<0.01	0.60
Loin, %	25.1	25.0	26.4	26.7	0.3	0.93	<0.01	0.51
Shoulder, %	12.0	12.1	13.0	13.1	0.1	0.79	<0.01	0.86
Ham, %	18.3	18.4	20.1	20.2	0.3	0.58	<0.01	0.89
Belly, %	17.1	17.2	17.1	16.7	0.3	0.65	0.27	0.41
Omental fat, %[e]	2.1	1.9	1.4	1.3	0.2	0.13	<0.01	0.71
Subcutaneous fat, %[f]	14.4	14.3	10.2	10.1	0.3	0.31	<0.01	0.96
13th-rib fat, mm	21	19	14	15	0.8	0.37	<0.01	0.06

[a]Results are presented as least square means and SEM.
[b]Effects of fat source (F), dietary energy level (E), and fat source × dietary energy level interaction (F × E).
[c]Feed utilization is expressed as kilograms of weight gain per kilogram of feed intake.
[d]Percentage of total amount of shoulder, loin, and ham without fat layers relative to cold carcass weight.
[e]Percentage of total amount of omental fat relative to cold carcass weight.
[f]Percentage of total amount of dissected fat from shoulder, loin, and ham relative to cold carcass weight.

Table 4. Fatty acid composition of carcass backfat outer layer (BFO)[ab]

Fatty acid[d]	Diet: High DE/soy oil (n = 8)	High DE/tallow (n = 9)	Low DE/soy oil (n = 9)	Low DE/tallow (n = 10)	SEM	*P*-value[c]: F	E	F × E
	wt %							
14:0	1.15	1.42	0.81	1.58	0.03	<0.01	<0.01	<0.01
16:0	21.09	22.79	15.53	19.78	0.31	<0.01	<0.01	<0.01
17:0	0.19	0.45	0.27	0.64	0.02	<0.01	<0.01	<0.01
18:0	12.58	13.79	8.44	11.07	0.35	<0.01	<0.01	0.07
20:0	0.23	0.20	0.17	0.17	0.01	0.12	<0.01	0.12
16:1n–7	1.42	2.18	1.05	2.37	0.06	<0.01	0.08	<0.01
17:1n–7	0.17	0.49	0.22	0.68	0.01	<0.01	<0.01	<0.01
18:1n–7	2.16	3.10	2.07	3.57	0.05	<0.01	<0.01	<0.01
18:1n–9	34.77	43.99	30.23	44.26	0.29	<0.01	<0.01	<0.01
20:1n–9	0.84	0.96	0.74	1.12	0.14	<0.01	0.56	<0.01
18:2n–6	21.40	8.82	34.30	12.17	0.48	<0.01	<0.01	<0.01
18:3n–3	2.29	0.96	3.66	1.37	0.07	<0.01	<0.01	<0.01
20:2n–6	1.02	0.41	1.49	0.57	0.03	<0.01	<0.01	<0.01
20:3n–3	0.35	0.15	0.50	0.23	0.01	<0.01	<0.01	<0.01
20:4n–6	0.20	0.18	0.33	0.24	0.01	<0.01	<0.01	<0.01
22:5n–3	0.13	0.11	0.21	0.18	0.01	<0.01	<0.01	0.43
SFA	35.24	38.65	25.22	33.25	0.60	<0.01	<0.01	<0.01
MUFA	39.36	50.73	34.30	52.00	0.47	<0.01	<0.01	<0.01
PUFA	25.40	10.63	40.49	14.75	0.56	<0.01	<0.01	<0.01
16:1(n–7)/16:0	0.07	0.10	0.07	0.12	0.01	<0.01	<0.01	<0.01
18:1(n–9)/18:0	2.76	3.19	3.58	4.00	0.12	<0.01	<0.01	0.87

[a]Results are presented as least square means and SEM.
[b]Only fatty acids that accounted for > 0.1 g/100 g of total are presented.
[c]Effects of fat source (F), dietary energy level (E), and fat source × dietary energy level interaction (F × E).
[d]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 indicated. The sums of the main fatty acid series are represented as SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids.

Table 5. Fatty acid composition of carcass backfat inner layer (BFI)[ab]

Fatty acid[d]	Diet				SEM	P-value[c]		
	High DE/soy oil (n = 8)	High DE/tallow (n = 9)	Low DE/soy oil (n = 9)	Low DE/tallow (n = 10)		F	E	F × E
	wt %							
14:0	1.06	1.28	0.76	1.51	0.03	<0.01	0.13	<0.01
16:0	21.55	23.38	16.00	20.49	0.38	<0.01	<0.01	<0.01
17:0	0.18	0.42	0.26	0.65	0.02	<0.01	<0.01	<0.01
18:0	14.83	16.06	10.12	13.00	0.36	<0.01	<0.01	0.05
20:0	0.26	0.26	0.22	0.21	0.01	0.64	<0.01	0.68
16:1n–7	1.13	1.82	0.75	2.07	0.03	<0.01	0.05	<0.01
17:1n–7	0.14	0.40	0.16	0.62	0.02	<0.01	<0.01	<0.01
18:1n–7	1.86	2.69	1.77	3.39	0.05	<0.01	<0.01	<0.01
18:1n–9	33.88	43.28	28.50	43.17	0.49	<0.01	<0.01	<0.01
20:1n–9	0.89	1.21	0.81	1.25	0.06	<0.01	0.72	0.58
18:2n–6	20.48	7.67	34.53	11.29	0.62	<0.01	<0.01	<0.01
18:3n–3	2.12	0.80	3.57	1.26	0.09	<0.01	<0.01	<0.01
20:2n–6	1.01	0.39	1.61	0.54	0.04	<0.01	<0.01	<0.01
20:3n–3	0.33	0.13	0.49	0.20	0.01	<0.01	<0.01	<0.01
20:4n–6	0.16	0.12	0.27	0.19	0.01	<0.01	<0.01	0.06
22:5n–3	0.11	0.08	0.18	0.15	0.01	<0.01	<0.01	0.47
SFA	37.88	41.41	27.36	35.87	0.69	<0.01	<0.01	<0.01
MUFA	37.90	49.40	31.99	50.50	0.55	<0.01	<0.01	<0.01
PUFA	24.22	9.19	40.65	13.63	0.75	<0.01	<0.01	<0.01
16:1(n–7)/16:0	0.05	0.08	0.05	0.10	0.01	<0.01	<0.01	<0.01
18:1(n–9)/18:0	2.29	2.69	2.82	3.32	0.10	<0.01	<0.01	0.51

[a]Results are presented as least square means and SEM.
[b]Only fatty acids that accounted for > 0.1 g/100 g of total are presented.
[c]Effects of fat source (F), dietary energy level (E), and fat source × dietary energy level interaction (F × E).
[d]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 indicated. The sums of the main fatty acid series are represented as SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids.

turated (MUFA) proportions. The SFA changes accounted for 23 (BFO and BFI) and 24% (OF) of the PUFA changes in the high-energy diets, and 31 (BFO and BFI) and 39% (OF) in the low-energy diets.

The proportions of myristic (14:0), heptadecanoic (17:0), palmitic, and stearic acids in the adipose tissues of pigs fed the soy oil-fortified diets were decreased compared to those of the tallow groups ($P < 0.01$ for all). To assess the effect of dietary fat source on lipogenesis, we determined the activity of G6PDH and ME, the main enzymes supplying NADPH for the reductive biosynthesis of fatty acids (Mourot et al., 1995) as well as of FAS, which catalyses the synthesis of palmitate. Except for G6PDH in the OF, source of dietary fat did not affect the activity of the enzymes (Table 7). The lack of difference in lipogenesis between the soil oil and tallow treatments within energy concentration was not surprising because the diets had equal calculated digestible energy contents (Table 1). Likewise, we previously reported that feeding diets varying in the fatty acid composition but with a moderated fat concentration did not affect production and carcass traits (Bee and Wenk, 1994). Hence, it seems unlikely that overall de novo fat synthesis was affected by the dietary fat source. However, our results disagree with those of certain authors (Waterman et al., 1975; Kouba and Mourot, 1999), who demonstrated a significant effect of PUFA intake on lipogenic enzyme activities in adipose tissues. Kouba and Mourot (1999) reported a 9% decrease in the adipose tissue lipid content of pigs fed a maize oil-fortified diet compared with a diet supplemented with tallow.

The proportion of oleic acid, the main MUFA in swine adipose tissue, is determined by the dietary supply as well as by the elongation and desaturation of the saturated homologs. Furthermore, dietary PUFA of the n–6 family are known to impair the activity of the stearoyl-CoA desaturase (**SCD**), the key enzyme in the desaturation process of stearic acid (Kouba and Mourot, 1998). In the present study, we did not actually measure the SCD activity, but the desaturation indexes (palmitoleic to palmitic acid; [16:1(n–7) to 16:0]; oleic to stearic acid; [18:1(n–9) to 18:0]) have been reported to relate well with the activity of the enzyme (Klingenberg et al., 1995; Kouba et al., 1997). Compared with the tallow groups, conversion of palmitic and stearic acids into their desaturated homologs was decreased in the adipose tissues of pigs fed the soy oil-supplemented diets, indicating a regulatory effect of PUFA on SCD activity. In accordance with an earlier study of Buller and Enser (1986), the ratio of oleic to stearic acid suggests that the activity of the SCD is tissue-specific, being higher in the BFO (4.00 to 2.76) and lower in the OF (2.36 to 1.56). The reason for these tissue-specific differences could be the lower linoleic acid concentration in the OF

Table 6. Fatty acid composition of omental fat (OF)[ab]

Fatty acid[d]	Diet: High DE/soy oil (n = 8)	High DE/tallow (n = 9)	Low DE/soy oil (n = 9)	Low DE/tallow (n = 10)	SEM	P-value[c]: F	E	F × E
	wt %							
14:0	1.24	1.47	0.96	1.90	0.04	<0.01	0.23	<0.01
16:0	24.72	26.69	18.43	23.85	0.40	<0.01	<0.01	<0.01
17:0	0.19	0.42	0.29	0.81	0.02	<0.01	<0.01	<0.01
18:0	18.67	19.60	11.61	15.84	0.45	<0.01	<0.01	<0.01
20:0	0.28	0.27	0.22	0.23	0.01	0.36	<0.01	0.60
16:1n–7	1.08	1.84	0.62	2.00	0.03	<0.01	0.01	<0.01
17:1n–7	0.12	0.36	0.14	0.56	0.01	<0.01	<0.01	<0.01
18:1n–7	1.42	2.22	1.47	2.79	0.05	<0.01	<0.01	<0.01
18:1n–9	29.21	37.82	23.54	37.40	0.35	<0.01	<0.01	<0.01
20:1n–9	0.66	0.82	0.53	0.88	0.04	<0.01	0.17	0.02
18:2n–6	19.10	7.09	36.45	11.56	0.68	<0.01	<0.01	<0.01
18:3n–3	2.06	0.80	3.87	1.37	0.08	<0.01	<0.01	<0.01
20:2n–6	0.71	0.27	1.04	0.34	0.03	<0.01	<0.01	<0.01
20:3n–3	0.23	0.09	0.30	0.12	0.01	<0.01	<0.01	0.02
20:4n–6	0.18	0.15	0.33	0.21	0.01	<0.01	<0.01	<0.01
22:5n–3	0.11	0.09	0.20	0.16	0.01	<0.01	<0.01	0.20
SFA	45.10	48.46	31.52	42.62	0.80	<0.01	<0.01	<0.01
MUFA	32.49	43.06	26.30	43.63	0.52	<0.01	<0.01	<0.01
PUFA	22.41	8.48	42.19	13.76	0.78	<0.01	<0.01	<0.01
16:1(n–7)/16:0	0.04	0.07	0.03	0.08	0.01	<0.01	0.31	<0.01
18:1(n–9)/18:0	1.56	1.93	2.03	2.36	0.07	<0.01	<0.01	0.98

[a]Results are presented as least square means and SEM.
[b]Only fatty acids that accounted for > 0.1 g/100 g of total are presented.
[c]Effects of fat source (F), dietary energy level (E), and fat source × dietary energy level interaction (F × E).
[d]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 indicated. The sums of the main fatty acid series are represented as SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids.

compared with the BFO and making linoleic acid less available to block the enzyme activity.

Effects of the Dietary Energy Concentration and Interaction with Dietary Fat Source

Dietary energy concentration significantly determined fatty acid composition of the adipose tissues except for myristic acid in the BFI and OF, palmitoleic acid in the BFO, and eicosenoic acid (20:1[n–9]) in the three tissues. Regardless of dietary fat source, PUFA concentration was increased whereas SFA and MUFA were decreased in the low-energy groups. Except for the proportion of eicosenoic acid in the BFI, of eicosanoic (20:0), and docosapentaenoic acids in all three tissues,

Table 7. Lipogenic enzyme activities of backfat outer (BFO) and inner layer (BFI) and omental fat (OF)[a]

Item[c]	Diet: High DE/soy oil (n = 8)	High DE/tallow (n = 9)	Low DE/soy oil (n = 9)	Low DE/tallow (n = 10)	SEM	P-value[b]: F	E	F × E
G6PDH[d]								
BFO	84.9	95.1	55.1	61.7	9.6	0.39	<0.01	0.85
BFI	100.1	94.6	60.7	62.6	6.5	0.78	<0.01	0.58
OF	88.2	102.3	55.2	58.4	4.1	0.04	<0.01	0.19
ME[d]								
BFO	127.6	152.2	79.7	99.0	16.1	0.18	<0.01	0.87
BFI	117.9	135.8	123.3	130.1	23.5	0.60	<0.99	0.82
OF	87.4	103.7	8.5	9.6	9.6	0.38	<0.01	0.44
FAS[e]								
BFO	6.3	6.9	2.6	1.8	0.63	0.85	<0.01	0.27
BFI	9.3	9.1	5.4	5.2	0.69	0.99	<0.01	0.81
OF	9.2	9.4	6.2	7.2	0.59	0.31	<0.01	0.49

[a]Results are presented as least square means and SEM.
[b]Effects of fat source (F), dietary energy level (E), and fat source × dietary energy level interaction (F × E).
[c]G6PDH: glucose-6-phosphate dehydrogenase; ME: malic enzyme; FAS: fatty acid synthase.
[d]Activity expressed as μmol NADPH formed·min^{-1}·mg protein^{-1}.
[e]Activity expressed as μmol NADPH oxidized·min^{-1}·mg protein^{-1}.

the differences in the fatty acid pattern between the soy oil and tallow group were more pronounced in the low-energy group (fat source × energy concentration interactions: $P \leq 0.05$). Pigs fed the LS diet had 28 to 30% decreased SFA and 13 to 19% decreased MUFA concentration, whereas PUFA concentration was increased by 59 to 88% compared with pigs fed the HS diet. The respective differences in the low-energy groups amounted to −12 to −14% for SFA and +39 to +62% for PUFA, whereas MUFA concentration was almost similar (+1 to +3%). The differences were more distinct in the OF than in the backfat layers and were larger among the two soy oil groups than the two tallow groups.

Except for ME in the BFI (Table 7), the activities of key lipogenic enzymes were distinctly reduced ($P < 0.01$) by the restricted daily energy supply, and this finding is consistent with the lower fat deposition rate in pigs fed the L diets. Similar effects of limiting energy intake were found in adipose tissue of gestating sows (Parmley et al., 1996), and this is in accordance with the concept that lipogenesis is the first-limiting pathway in storage of body fat and is the most tightly regulated by alterations in energy intake (Vernon et al., 1999).

The desaturation index (18:1[n–9] to 18:0; Tables 4 through 6) was increased in the low-energy treatments, regardless of the dietary fat source (fat source × energy concentration interaction; $P > 0.05$), suggesting an elevated SCD activity. Saturated fatty acids either in the diet or synthesized de novo constitute the main substrate for SCD (Enser and Roberts, 1982). Because lipogenesis was decreased in both low-energy treatments, the higher activity might be mainly the result of the increased provision of substrate SFA.

The increased PUFA concentration in the low compared with the respective high-energy treatments could be attributed on the one hand to the significantly higher total feed intake (90%; Table 3) and on the other hand to the lower total amount of deposited backfat (27%; Table 3) and OF (33%; Table 3). However, the increased intake did not account for the tissue changes. Assuming a similar incorporation rate of linoleic and linolenic acids into the OF of animals fed the low-energy compared with the high-energy diets, one would expect 2.8-fold (compared with the high-energy treatments: 190% intake/67% amount of OF) higher tissue proportions. However, in the soy oil and tallow groups, the increase in the proportions of the two essential fatty acids amounted to 1.9 and 1.6, respectively, and therefore was markedly below the expected concentration based on intake of those fatty acids. As recently reported (Warnants et al., 1999), the linoleic, linolenic, eicosatrienoic, and arachidonic acids in the backfat could not be further increased, when pigs were fed a PUFA-enriched diet for more than 6 wk. Apparently, in the present study, a plateau in the PUFA tissue content was reached that limited a further deposition of PUFA.

Lean Tissue Fatty Acid Pattern

Table 8 shows the fatty acid composition of the neutral (**NL**) and polar lipid (**PL**) fractions in the i.m. fat. Concentrations of palmitic, stearic, arachidonic, docosatetraenoic (22:4[n–6]), eicosatrienoic, docosapentaenoic, and docosahexaenoic (22:4[n–3]) acids, and total lipid extract of the NL fraction was primarily affected by the dietary energy concentration, whereas both dietary factors had an impact on the heptadecanoic, palmitoleic, heptadecenoic (17:1[n–7]), oleic, linoleic, eicosadienoic, and linolenic acid contents. The differences in the heptadecanoic, heptadecenoic, linoleic, eicosadienoic, and linolenic acid concentrations due to the dietary fat source were more pronounced in the low-energy groups (fat source × energy concentration interactions: $P < 0.05$).

The NL fraction is composed of triacylglycerols originating from adipocytes in the muscles, and, therefore, one would expect that total lipid extract of NL is decreased by the low-energy supply. Contrary to the fatty acid pattern of the adipose tissues, increased PUFA deposition was predominantly compensated by a reduced MUFA deposition. The MUFA changes in the high- and low-energy groups accounted for 92 and 83% of the PUFA changes, respectively. In accordance with the present data, Pfalzgraf et al. (1995) reported significant effects of dietary fat source (soy oil/tallow) on the oleic, linoleic, linolenic, and eicosadienoic acid contents of the triacylglycerols. The distinct effect of the dietary energy concentration on the lipid content and fatty acid composition of the NL fraction contradicts earlier results of Bee and Wenk (1993) and Kuhn (1997), who did not report any implication of dietary energy or feed restriction on the i.m. lipid composition. Compared with the aforementioned studies, dietary energy restriction in the present experiment was more severe and might have been responsible for the reported effects.

Surprisingly, the amount of lipid extract of the PL fraction was decreased in the low-energy treatments ($P = 0.04$) and tended to be lower in the tallow groups ($P = 0.07$). Compared with the related triacyglycerols, the PL fraction contained higher proportions of PUFA regardless of the treatments. Both dietary factors had significant effects on the myristic, stearic, palmitoleic, oleic, vaccenic (18:1[n–7]), linoleic, arachidonic, linolenic, and docosahexaenoic acid concentration, whereas eicosatrienoic acid proportions were influenced only by the dietary energy concentration. However, stearic and arachidonic acid concentration were similar in the high-energy diets, but, in the low-energy group proportions were decreased by the tallow supplementation (fat source × energy concentration interaction; $P < 0.05$). Compared with the NL fraction, the fat × energy interaction was not significant for the sum of SFA, MUFA, and PUFA.

Although in the adipose tissues increased PUFA intake and daily energy restriction were responsible for the distinct decrease in the SFA and MUFA concentra-

Table 8. Fatty acid composition of longissimus dorsi intramuscular neutral and polar lipid fractions[ab]

Fatty acid[d]	Diet: High DE/soy oil (n = 8)	Diet: High DE/tallow (n = 9)	Diet: Low DE/soy oil (n = 9)	Diet: Low DE/tallow (n = 10)	SEM	*P*-value[c]: F	*P*-value[c]: E	*P*-value[c]: F × E
	wt %							
Neutral lipid								
Lipid extract[e]	2.60	2.95	1.69	1.26	0.22	0.88	<0.01	0.09
14:0	1.46	1.50	1.34	1.44	0.09	0.48	0.25	0.86
16:0	23.90	24.20	19.67	20.48	0.30	0.14	<0.01	0.77
17:0	0.18	0.23	0.43	0.87	0.06	<0.01	<0.01	<0.01
18:0	12.62	12.83	11.16	11.80	0.38	0.34	<0.01	0.75
20:0	0.21	0.16	0.20	0.19	0.01	<0.01	0.67	<0.04
16:1n–7	2.96	3.49	1.93	2.93	0.11	<0.01	<0.01	0.06
17:1n–7	0.23	0.31	0.32	0.65	0.02	<0.01	<0.01	<0.01
18:1n–7	3.34	3.85	2.98	3.96	0.09	<0.01	0.08	0.02
18:1n–9	38.36	43.75	31.50	38.89	0.77	<0.01	<0.01	0.27
20:1n–9	0.60	0.59	0.55	0.61	0.03	0.29	0.30	0.14
18:2n–6	12.45	6.42	23.51	12.19	0.66	<0.01	<0.01	<0.01
20:2n–6	0.46	0.20	0.76	0.31	0.02	<0.01	<0.01	<0.01
20:4n–6	1.18	1.05	2.23	2.98	0.25	0.39	<0.01	0.13
22:4n–3	0.14	0.10	0.20	0.24	0.02	0.84	<0.01	0.10
18:3n–3	1.04	0.51	2.03	0.84	0.05	<0.01	<0.01	<0.01
20:3n–3	0.21	0.21	0.28	0.39	0.03	0.14	<0.01	0.08
22:5n–3	0.40	0.34	0.64	0.75	0.04	0.95	<0.01	0.19
22:6n–3	0.25	0.28	0.30	0.47	0.03	0.02	<0.02	0.07
SFA	38.37	38.92	32.79	34.78	0.69	0.07	<0.01	0.30
MUFA	45.50	51.99	37.27	47.05	0.86	<0.01	<0.01	0.07
PUFA	16.13	9.10	29.94	18.17	0.97	<0.01	<0.01	<0.02
16:1(n–7)/16:0	0.12	0.14	0.10	0.14	0.01	<0.01	<0.01	0.01
18:1(n–9)/18:0	3.04	3.41	2.82	3.30	0.14	<0.01	<0.16	0.58
Polar lipid								
Lipid extract[f]	0.44	0.40	0.39	0.35	0.02	0.07	0.04	0.86
14:0	0.47	0.47	0.29	0.46	0.03	0.04	0.02	0.07
16:0	17.20	16.65	16.65	17.73	0.49	0.75	0.85	0.66
18:0	16.11	15.78	14.31	12.49	0.41	0.02	<0.01	<0.01
20:0	0.50	n.d.[g]	n.d.	n.d.				
16:1n–7	0.87	1.29	0.67	1.28	0.07	<0.01	0.05	0.14
17:1n–7	1.43	1.05	1.52	1.65	0.09	0.54	<0.01	<0.01
18:1n–7	2.87	3.62	2.73	3.23	0.08	<0.01	<0.01	0.55
18:1n–9	12.11	20.14	9.38	17.52	0.39	<0.01	<0.01	0.60
20:1n–9	0.24	n.d.	n.d.	n.d.				
18:2n–6	31.13	23.23	34.39	27.10	0.40	<0.01	<0.01	0.66
20:2n–6	0.98	1.31	1.77	0.58	0.16	0.01	0.84	<0.01
20:4n–6	10.16	10.25	13.16	11.17	0.40	0.02	<0.01	0.01
22:4n–6	0.96	0.85	0.74	0.91	0.07	0.63	0.32	0.09
18:3n–3	0.74	0.64	1.09	0.92	0.04	<0.01	<0.01	0.30
20:3n–3	1.20	1.52	0.90	1.29	0.07	0.14	<0.01	0.64
20:5n–3	0.54	0.85	0.50	1.04	0.05	<0.01	0.14	0.03
22:5n–3	1.63	1.36	1.60	1.81	0.13	0.87	0.10	0.07
22:6n–3	0.86	0.97	0.31	0.82	0.07	<0.01	<0.01	<0.01
SFA	34.28	32.90	31.25	30.68	0.47	0.04	<0.01	0.31
MUFA	17.53	26.09	14.30	23.67	0.45	<0.01	<0.01	0.32
PUFA	48.19	41.01	54.45	45.64	0.60	<0.01	<0.01	0.25
16:1(n–7)/16:0	0.05	0.08	0.04	0.07	0.01	<0.01	0.06	0.24
18:1(n–9)/18:0	0.75	1.28	0.66	1.40	0.05	<0.01	0.99	<0.01

[a]Results are presented as least square means and SEM.
[b]Only fatty acids that accounted for > 0.1 g/100 g of total are presented.
[c]Effects of fat source (F), dietary energy level (E), and fat source × dietary energy level interaction (F × E).
[d]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 indicated. The sums of the main fatty acid series are represented as SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids.
[e]Lipid extract of the neutral lipid fraction expressed in g/100 g wet muscle weight.
[f]Lipid extract of the polar lipid fraction expressed in g/100 g wet muscle weight.
[g]n.d.= not detectable.

tions, in the PL fraction the differences in the SFA concentration were small among treatments. Several studies have shown that the saturated-to-unsaturated ratio is constant in membrane polar lipids and that the effects of dietary fatty acids (Scheeder et al., 2000) and energy supply (Kuhn, 1997) are limited to an exchange between MUFA and PUFA. Comparing the results of those experiments and the present study, SFA concentration was similar (29 to 33 wt%) despite the differing amounts and source of dietary fats. In view of the considerable differences in the amount of ingested SFA, endogenous desaturation of saturated fatty acids by SCD has to play a key role to ensure nearly constant proportions of SFA in the polar lipids. Because experimental diets did not contain detectable amounts of arachidonic acid, the concentration of this fatty acid depended on the conversion from its precursors. In accordance with other studies (Pfalzgraf et al., 1995; Warnants et al., 1996; Scheeder et al., 2000), we report no dietary effect on the deposition of arachidonic acid in the high-energy treatments, regardless of the differing supply and incorporation of its precursors. By contrast, in the low-energy groups, overall arachidonic acid proportions were markedly increased and were further elevated if the supply of linoleic acid was higher (LS). Apparently, in the PL compared with the NL fraction, the increased linoleic acid supply resulted in a higher conversion to arachidonic acid rather than higher deposition of linoleic acid.

Implications

Linoleic acid in swine adipose and lean tissues derives exclusively from dietary source, and the concentration in tissues depends on the intake and overall fat deposition. Our investigation provided evidence that linoleic acid was incorporated less efficiently into adipose tissues when the feed was low in energy and when the dietary fat was rich in saturated fatty acids like tallow compared with a fat rich in unsaturated fatty acids like soy oil. Consequently, the synthesis of saturated, monounsaturated, and higher polyunsaturated fatty acids of linoleic acid are also profoundly affected. Attempts made to alter fat quality or fatty acid profile must, therefore, consider both dietary energy content and dietary fat source to accomplish the desired effect.

Literature Cited

Bee, G., R. Messikommer, and S. Gebert. 1999. Dietary fats and energy levels differently affect tissue lipogenic enzyme activity in finishing pigs. Fett. Lipid 101:336–342.

Bee, G., and C. Wenk. 1993. Der Nährstoffgehalt und das Fettsäurenmuster von Mastscheinen unter Berücksichtigung der Wachstumsgeschwindigkeit. Proc. Soc. Nutr. Physiol. 1:80 (Abstr.).

Bee, G., and C. Wenk. 1994. Effect of soybean oil and beef tallow supplementation to pig diets on the fatty acid profile of body lipids. J. Anim. Physiol. Anim. Nutr. 71:277–288.

Buller, K. J., and M. Enser. 1986. The effect of food intake and dietary fatty acids on the activity of stearoyl-CoA Δ^9 desaturase in pig adipose tissue. J. Agric. Sci. 106:601–609.

Enser, M., and J. L. Roberts. 1982. The regulation of hepatic stearoyl-coenzyme A desaturase in obese-hyperglycaemic (ob/ob) mice by food intake and the fatty acid composition of the diet. Biochem. J. 206:561–570.

Enser, M. 1984. The chemistry, biochemistry and nutritional importance of animal fats. In: J. Wiseman (ed.) Fats in Animal Nutrition. pp 23–51. Butterworths, London, UK.

Hara, A., and N. S. Radin. 1978. Lipid extraction of tissues with a low-toxicity solvent. Anal. Biochem. 90:420–426.

Hsu, R. Y., and H. A. Lardy. 1969. Malic enzyme. Methods Enzymol. 13:230–235.

Juaneda, P., and G. Rocquelin. 1985. Rapid and convenient separation of phospholipids and non-phosphorus lipids from rat heart using silica cartridges. Lipids 20:40–41.

Klingenberg, I. L., D. A. Knabe, and S. B. Smith. 1995. Lipid metabolism in pigs fed beef tallow or high-oleic acid sunflower oil. Comp. Biochem. Physiol. 110:183–192.

Kouba, M., and J. Mourot. 1998. Effect of a high linoleic acid diet on Δ9-desaturase activity, lipogenesis and lipid composition of pig subcutaneous adipose tissue. Reprod. Nutr. Dev. 38:31–37.

Kouba, M., and J. Mourot. 1999. Effect of a high linoleic acid diet on lipogenic enzyme activities and on the composition of the lipid fraction of fat and lean tissues in the pig. Meat Sci. 52:39–45.

Kouba, M., J. Mourot, and P. Peiniau. 1997. Stearoyl-CoA desaturase activity in adipose tissues and liver of growing Large White and Meishan pigs. Comp. Biochem. Physiol. 118B:509–514.

Kuhn, M. 1997. Zum Einfluss der Fütterungsintensität und des Mastendgewichtes auf die Mast- und Schlachtleistung von Schweinen sowie das Fettsäurenmuster der Gesamt- und Phospholipide des M. long. dorsi. 3. Mitteilung: Intramuskulärer Fettgehalt und Fettsäurenmuster der Gesamt- und Phospholipide des M. long. dorsi. Züchtungskunde 69:396–404.

Löhr, G. W., and H. D. Waller. 1974. Glucose-6-phophat dehydrogenase. In: H. U. Bergmeyer (ed.) Methoden der Enzymatischen Analyse. pp 673–681. Verlag Chemie, Weinheim, Germany.

Mersmann, H. J., C. D. Allen, E. Y. Chai, L. J. Brown, and T. J. Fogg. 1981. Factors influencing the lipogenic rate in swine adipose tissue. J. Anim. Sci. 52:1298–1305.

Mersmann, H. J., and L. J. Koong. 1984. Effect of plane of nutrition on adipose tissue lipid metabolism in genetically obese and lean pigs. J. Nutr. 114:862–868.

Metcalfe, L. D., and J. F. Smith. 1961. The rapid preparation of fatty acid esters for gas chromatographic analyses. Anal. Chem. 33:363–364.

Mourot, J., M. Kouba, and P. Peiniau. 1995. Comparative study of in vitro lipogenesis in various adipose tissues in the growing domestic pig (Sus domesticus). Comp. Biochem. Physiol. 111B:379–384.

Naumann, C., R. Bassler, R. Seibold, and C. Barth. 1997. Methodenbuch Band III, VDLUFA, Darmstadt.

Parmley, K. L., C. R. Machado, and J. P. McNamara. 1996. Rates of lipid metabolism in adipose tissue of pigs adapt to lactational state and dietary energy restriction. J. Nutr. 126:1644–1656.

Pfalzgraf, A., M. Frigg, H. Steinhart, M. Kirchgessner, and F. X. Roth. 1995. Influence of dietary fat and vitamin E on the lipids in pork meat. Fat Sci. Technol. 97:13–20.

Raclot, T., and R. Groscolas. 1995. Selective mobilization of adipose tissue fatty acids during energy depletion in the rat. J. Lipid Res. 36:2164–2173.

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

Roncari, D. A. 1981. Fatty acid synthase from human liver. Methods Enzymol. 71:73–79.

Scheeder, M. R. L., K. R. Gläser, B. Eichenberger, and C. Wenk. 2000. Influence of different fats in pig feed on fatty acid composition of phospholipids and physical meat quality characteristics. Eur. J. Lipid Sci. Technol. 102:391–401.

Vernon, R. G., M. C. Barber, and M. T. Travers. 1999. Present and future studies on lipogenesis in animals and human subjects. Proc. Nutr Soc. 58:541–549.

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.

Warnants, N., M. J. Van Oeckel, and C. V. Boucqué. 1999. Incorporation of dietary polyunsaturated fatty acids into pork fatty tissues. J. Anim. Sci. 77:2478–2490.

Waterman, R. A., D. R. Romsos, A. C. Tsai, E. R. Miller, and G. A. Leveille. 1975. Influence of dietary safflower oil and tallow on growth, plasma lipids and lipogenesis in rats, pigs and chicks. Proc. Soc. Exp. Biol. Med. 150:347–351.

Wood, J. D., P. J. Buxton, F. M. Whittington, and M. Enser. 1986. The chemical composition of fat tissues in the pig: effects of castration and feeding treatment. Livest. Prod. Sci. 15: 73–82.

Wood, J. D., C. D. Jones, J. A. Bayntun, and E. Dransfield. 1985. Backfat quality in boars and barrows at 90 kg live weight. Anim. Prod. 40:481–487.