Chapter 10
Fat degradation and absorption in the gastro-intestinal tract

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This chapter will provide:

- A basic understanding of the nutritional value of the different oils and fat for pigs
- A clear understanding of the digestibility of dietary oils and fats
- An insight into the role of oils and fats for carcass quality, reproduction and immunity of pigs.

1. Introduction

The use of fats and oils in diets for pigs is of great importance due to the high energy value, which is approx. 2.25 times that of carbohydrates. The dietary fats used in pig feed are based on vegetable, animal, and marine sources. The chemical and physical properties, and hence nutritional value, differ widely between different sources of fat. Animal fat has been used largely in pig feed, although its energy value is generally lower than the energy value of vegetable fat sources or fish oil. In spite of this, the higher content of saturated fatty acids (FAs) makes animal fat preferred, since high levels of unsaturated FAs from vegetable oil sources may result in a reduced product quality. In addition, the essential linoleic and linolenic FAs, which are highly present in vegetable oil sources, and the longer chained n-3 FAs present in fish oil, may be of special physiological and immunological importance.

The purpose of this chapter is to introduce the reader to our current knowledge of the intestinal lipid absorption and transport in pigs and the importance of the digested fat and FAs for productivity and the product quality of pork. In addition, the impact of dietary fat on health and reproduction of the pigs will be briefly described.

2. Dietary lipids and chemical characteristics

In simple empirical terms, dietary fat is that part of the diet that can be extracted by organic solvents. Consequently, dietary fat is comprised of an array of compounds, from highly non-polar hydrocarbons to highly polar phospholipids and glycolipids. Whether a lipid is characterised as a polar or non-polar lipid depends on its interaction with water, and this ability plays an important role for the digestion and absorption of the dietary lipid.

Figure 10.1 shows the chemical structure of the most frequent lipid components that will be referred to in this chapter. The predominant dietary lipid is triacylglycerol or triglyceride (TGs), which contributes more than 95% of the lipid fraction in pig feed. This molecule consists of a glycerol backbone that is linked to three FAs via ester bonds. Glycerol is approx. 10% by weight of the TGs, but accounts for only 5% of the energy. Thus, the FAs of the TGs is the contributing energy factor of interest in terms of pig nutrition. The remaining dietary lipid fraction consists of phospholipid (PL), cholesterol and fat-soluble vitamins. The PL source may contribute approx. 2% of the total fat intake, but an additional 12 g PL is secreted into the bile (approx. 12 g every 24 hours). The PL source is, preferably in the form of lecithin, provided from vegetable oil producers, and other oil fractions may be fatty acid distillates, e.g. from palm oil as PFAD (palm oil fatty acid distillates). In addition, some types of "mixed fat" may be available for pig feed. The FA composition of these sources is diverse and influences their properties as feedstuffs and affects the digestion of the fat.
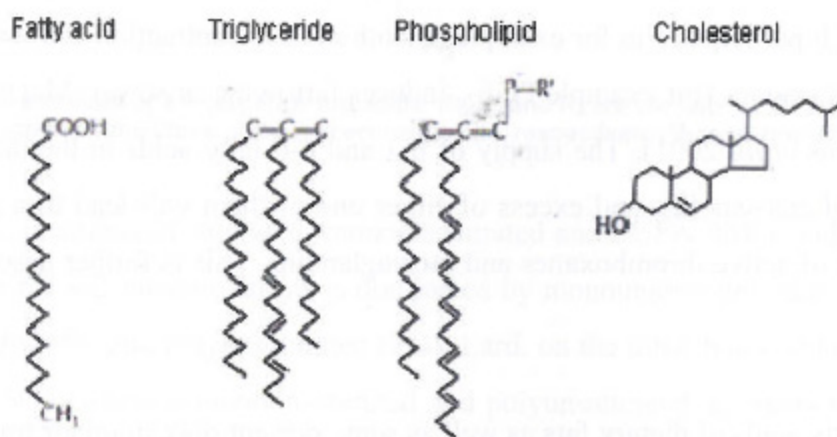

Figure 10.1. Chemical structure of different lipid components.

Table 10.1 provides an overview of the fatty acid composition of dietary fat sources commonly used in pig feed worldwide. Animal fat consists primarily of C16 and C18 FAs with one or more double bonds. Fat sources of vegetable origin are dominated by C18 FAs with one or more double bonds. Marine oils are characterised by the high proportion of long chain polyunsaturated FAs, especially of the n-3 family. Milk fat contains about 20% 4-14 carbon FAs. FAs are divided into different classes based on the chain length, i.e. short chain FAs (SCFA) contain fewer than 8 carbon atoms, medium chain FAs (MCFA) contain 8-12 carbon atoms; long chain FAs (LCFA) contain 14-18 carbon atoms; and very long chain FAs contain more than 20 carbon atoms. Furthermore, dietary FAs differ with respect to their number of double bonds. Both the chain length of the fatty acid and the number of double bonds are known to influence the physical properties of FAs: as the molecular weight increases, the melting point increases, i.e. the melting point increases with increasing chain length, and it is lowered when double bonds are introduced. In other words, the melting point is higher for saturated FAs compared to unsaturated FAs with the same chain length. The melting point may be of interest for the selection of fat source for a diet:

Quiz: At a given room temperature of 25°C, which of the following fatty acids (palmitic and oleic acid) are solid or liquid at room temperature? [Answer: Palmitic still solid, melts at +63°C; oleic still liquid, melts at +16°C].

Table 10.1. Fatty acid composition of selected dietary animal, vegetable and marine fat sources (modified after [13]).

Fatty acids, g/100 DM	Animal		Vegetable						Marine
	Lard[1]	Tallow[2]	Coconut oil[1]	Palm oil[1]	Palm oil mix[3]	Corn oil[2]	Rapeseed oil[l1]	Soy bean oil[4]	Fish oil[1]
C8:0	-	0.13	3.46	0.58	-	0.13	-	0.10	-
C10:0	0.07	0.14	3.51	0.53	-	0.13	-	0.10	-
C12:0	0.09	0.10	34.8	4.42	0.70	-	-	0.49	0.06
C14:0	1.96	4.98	15.9	2.23	1.60	-	-	0.28	4.62
C14:1	0.25	1.24	-	-	-	-	-	-	0.05
C16:0	22.0	25.9	11.2	34.6	37.8	10.3	3.94	10.6	14.6
C16:1	2.48	4.66	-	0.16	0.70	0.07	0.19	0.10	5.13
C18:0	15.3	14.1	3.38	6.79	5.40	1.40	1.31	4.07	1.95
C18:1	37.1	34.6	11.1	35.1	31.0	25.4	55.7	23.2	16.4
C18:2	5.35	4.26	2.73	8.30	8.40	60.3	19.3	52.6	2.19
C18:3n-3	0.68	0.40	0.09	0.67	-	1.06	9.10	7.66	1.48
C18:3n-6	0.09	-	-	-	9.00	-	-	-	0.16
C18:4	-	-	-	-	-	-	-	-	2.40
C20:0	0.25	-	0.11	0.35	-	0.13	0.48	-	0.16
C20:1	0.77	0.08	0.08	0.20	-	0.07	1.11	-	4.66
C20:2	-	?	-	-	-	-	-	-	0.31
C22:1	-	-	-	0.13	-	-	-	-	6.73
C22:0	-	-	-	0.16	-	-	0.31	-	0.31
C24:0	0.15	-	-	0.09	-	-	-	-	0.90
C20:4n-6	-	-	-	-	-	-	-	-	0.42
C20:5n-3	-	-	-	-	-	-	-	-	7.35
C22:5n-3	0.14	-	-	-	-	-	-	-	13.4
SAFA	39.8	45.3	72.4	49.8	45.5	12.0	6.04	15.6	22.6
MUFA	40.6	40.6	11.2	35.6	31.7	25.5	57.0	23.3	33.0
PUFA	6.36	4.66	2.82	8.97	9.30	61.4	28.4	60.3	27.7
UNFA	1.18	1.00	0.19	0.90	0.90	7.22	14.1	5.35	2.68
Total	86.8	90.6	86.4	94.3	86.5	98.9	91.4	99.1	83.3
FFA	ND	ND	ND	ND	79.0	ND	ND	1.75	ND

1) Analysis of lard, coconut oil, palm oil, rapeseed oil and fish oil were carried out at the Danish Faculty of Agricultural Sciences, Foulum, Denmark.
2) [17]
3) [25]
4) 39]
ND = not determined, but assumed to be very low.

3. Digestion, absorption and transport of dietary fat

A schematic overview of the fat digestion and absorption is given in Figure 10.2, and an excellent review is given by Phan and Tso [44].
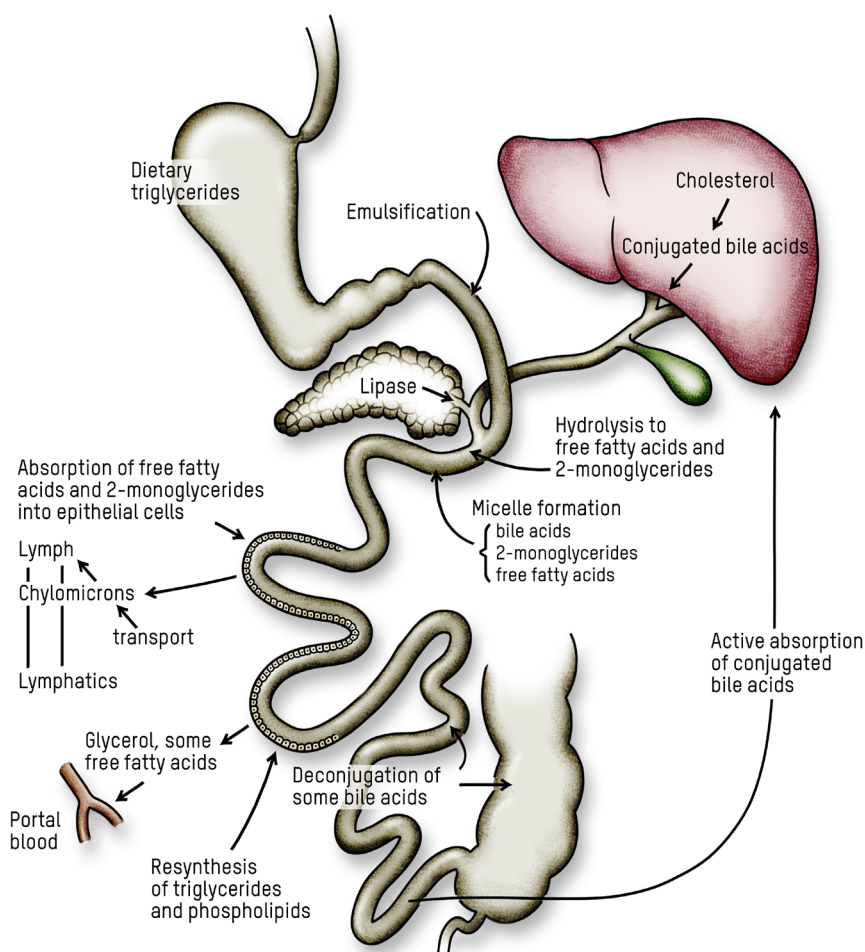

Figure 10.2. Schematic overview of fat digestion and absorption: From [15], illustration by Mads Salicath.

This chapter will mainly concern the absorption of FAs from dietary triglycerides, which are absorbed in the small intestine. In addition, up to 20% of ingested carbohydrates have been estimated to pass to the colon where they are fermented by colonic bacteria to SCFA, mainly acetate, propionate, and butyrate, and their absorption in the hindgut has been reviewed by Cummings [14]. This is described in Chapter 7.

The digestion of dietary lipids begins with emulsification in the stomach in which partial degradation of the TGs is performed. In pigs, this process is primarily undertaken by gastric lipase, which is secreted by the gastric mucosa. The enzyme hydrolyses the FAs in the sn3-position of the triglyceride molecule giving diacylglycerol and FAs (eg. non-ionised long-chain FAs), and does not act on phosphatidylcholine or cholesterol. The gastric lipase, which hydrolyses medium-chain TGs better than long-chain TGs, is responsible for 10 to 30 % of the hydrolysis of the dietary TGs, and therefore plays an important role in lipid digestion, particularly in neonates provided milk fat, which contains a considerable amount of MCFA. Actually, milk fat can be completely digested due to the gastric lipolysis.

The emulsification is an important prerequisite for efficient hydrolysis by pancreatic lipase. The lipid emulsion enters the small intestine as fine lipid droplets, and the combined action of bile and pancreatic juice brings about a marked change in the chemical and physical form of the ingested lipid emulsion. Most of the digestion of TGs is brought about by pancreatic lipase in the upper part of the intestinal lumen. This enzyme (pH optimum of 8) acts mainly on the sn-1 and sn-3 positions of the TG molecule to release 2-monoacylglycerol and free FAs. Pancreatic lipase is abundant in pancreatic juice, and its high concentration in pancreatic secretions and high catalytic efficiency ensure efficient digestion of dietary fat. The lipase is secreted into the duodenum in about 1000-fold excess. Pure pancreatic lipase works extremely inefficiently in a bile-salt-lipid mixture, yet lipase presents in pancreatic juice hydrolyses TGs extremely efficiently. This is due to the present of pancreatic colipase, which binds to the lipid/aqueous interface allowing the lipase molecule to bind to the lipid/aqueous interface.

The pancreatic lipase system is not fully developed in the neonate, and in the suckling piglet. Jensen et al. [22] demonstrated a relatively low level of pancreatic lipase which increases with age of the piglet until weaning (Figure 10.3). Due to the high activity of gastric lipase in suckling pigs, the apparent digestibility of fat is high (96%). However, at weaning the digestibility of fat declines to 65-80% [10], and this is partly due to the generally decreased nutrient absorption in the period after weaning, partly due to the composition of the TGs in fat sources than milk fat. After weaning, the piglet is provided with fat sources from other feedstuffs such as vegetable oils, and a prerequisite of a proper fat digestion is largely dependent on pancreatic enzymes rather than gastric lipase. The exocrine pancreatic enzyme secretion is highly dependent on diet composition, age, and feeding regimen [21]. For example, an increase in dietary fat level is closely correlated with a higher secretion of lipase. In addition, the chain length of the dietary fatty acid has a strong impact on the pancreatic secretions as well, ie. the secretion is stimulated post-weaning in piglets fed fish oil compared with piglets fed coconut oil or lard [18].
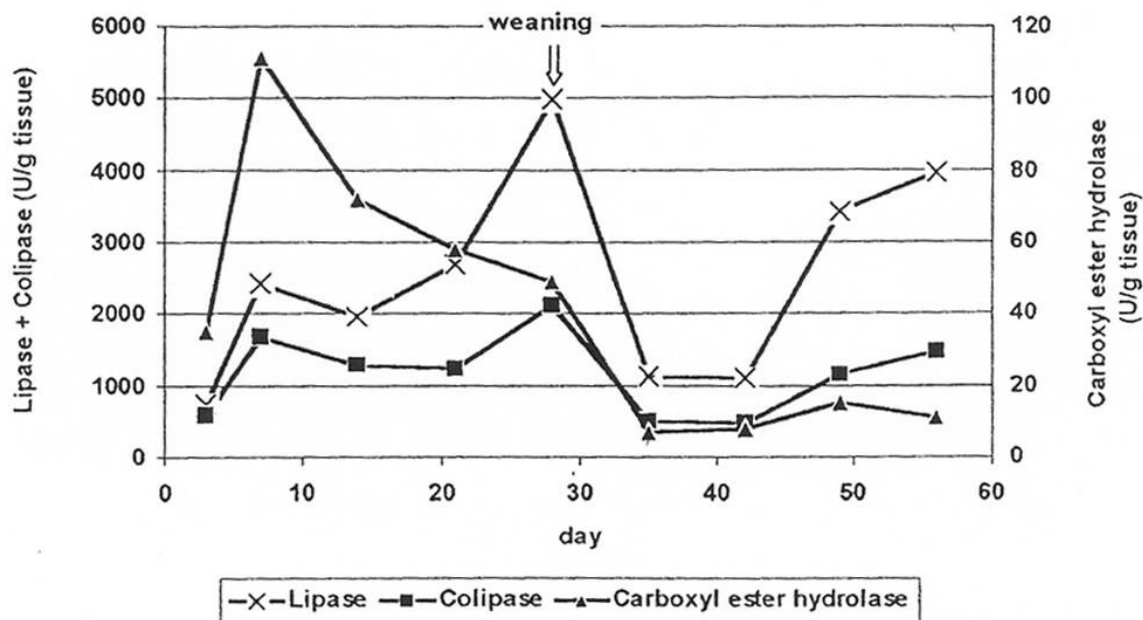

Figure 10.3. Development in activity of lipolytic enzymes in pancreatic tissue in pigs [22].

The digestion of PL occurs in the small intestine. In bile, PL (predominantly phosphatidylcholine (PC)) is found in mixed micelles along with cholesterol and bile salts. Once in the intestinal lumen, the luminal PC will distribute between the mixed micelles and the TG droplets. PC is then acted upon by pancreatic phospholipase A2 (PLA2) to yield an FA and a lysophosphatidylcholine.

The overall scope of the fat digestion is the formation of emulsions, which can be further processed for absorption into the enterocytes. The TGs (mainly of dietary origin) and PCs (mainly secreted from the bile) as well as other lipolytic products (e.g. free fatty acids and monoacyl glycerols (MAG)) form stable emulsions, and the presence of bile forms mixed micelles, which facilitates the transport of the lipids into the enterocytes. From a practical point of view, the formation of mixed micelles may be facilitated by addition of dietary PL in the form of lecithin, whereby the lipid absorption may be increased. The majority of the lipids are absorbed in the proximal part of the small intestine. To be absorbed into the enterocytes, lipids have to cross two barriers: the unstirred water layer and the brush border membrane.

Until very recently, it was generally believed that free fatty acids and MAGs are absorbed by the enterocytes through simple diffusion. However, studies have indicated the existence of a fatty acid binding protein (FABP) associated with the brush border membrane, and that this protein plays a role in the uptake of FAs by enterocytes. Depending on the chain length of the FAs, it may either pass directly from the enterocyte into the portal blood where it is bound to albumin (FAs with fewer than 12 carbon atoms), or re-esterified to triglycerides within the enterocyte and delivered to the lymph (FAs with more than 12 carbon atoms). Thus, with increasing length of FAs, an increasing proportion of the FAs was absorbed into the lymph and less into the portal blood. Dietary fat sources containing medium-chain fatty acids may on the other hand be readily accessible as energy due to the transfer into the portal blood and would therefore be useful in high-energy demanding pigs such as the lactating sow and newborn piglets.

The first step in transport through the intestine is re-esterification, and the second step is the synthesis of transport particles: the so-called lipoprotein (chylomicron) and very low-density lipoproteins (VLDL). The absorbed MAG and FFA are resynthesized to TGs on the membranes of the endoplasmic reticulum and Golgi complex in the intestinal enterocyte. Actually, the re-esterification process can occur in two different ways: either the MAG pathway or the glycerol-3-phosphate pathway. The MAG is the predominant one when monoglycerides (MG) are available in the enterocyte, whereas in absence of MG, the glycerol-phosphate pathway becomes important. Thus, when feeding high amounts of free FAs (i.e. palm oil-mix or byproducts) the glycerol-phosphate pathway becomes important, whereas for diets containing a high amount of triglycerides the MAG is most important. However, the glycerol-phosphate pathway is due when long-chain FAs are absorbed. During resynthesis, rearrangements of the FAs in the triglycerides occur. Most of the FAs placed in the 2-position of the triglyceride are absorbed as 2-monoacylglyceride, and is conserved after resynthesis.

During fasting, VLDL are the only lipoproteins produced by the small intestine, and this lipoprotein is thus the major TG-carrying lipoprotein in the lymph. After a meal, the small intestine produces predominantly CMs, which transport the dietary fat and fat-soluble vitamins into the blood via the thoracic lymphatic duct. The chylomicrons consist primarily of TGs (86-95%) and phospholipids (4-13%). The TG composition of the chylomicron largely reflects the dietary FAs, and the size (but not the number of chylomicrons) is determined by the flux of triglycerides through the intestinal cell.

The TGs enriched CMs are hydrolysed rapidly by lipoprotein lipase (LPL), and the action of this enzyme results in FFA, which are taken up by the peripheral tissue for storage or energy production. Furthermore, the hydrolysis of CM TGs by LPL decreases when about 70-90% of the TGs are removed, resulting in remnant particles, which are taken up by the liver and further hydrolysed by the hepatic lipase [43].

3.1. Essential fatty acids

Mammals lack the $\Delta 12$ and $\Delta 15$-desaturases to insertion of double bonds at carbon atoms beyond C9 in the fatty acid carbon chain. FAs with double bonds lower than carbon atom 9 therefore have to be supplied to mammals through the diet. The essential FAs are linoleic (C18:2n-6) and

α-linolenic acid (C18:3n-3), which are building blocks of FAs of longer chain length in the n-3 and n-6 family through elongation and desaturation (Figure 10.4).
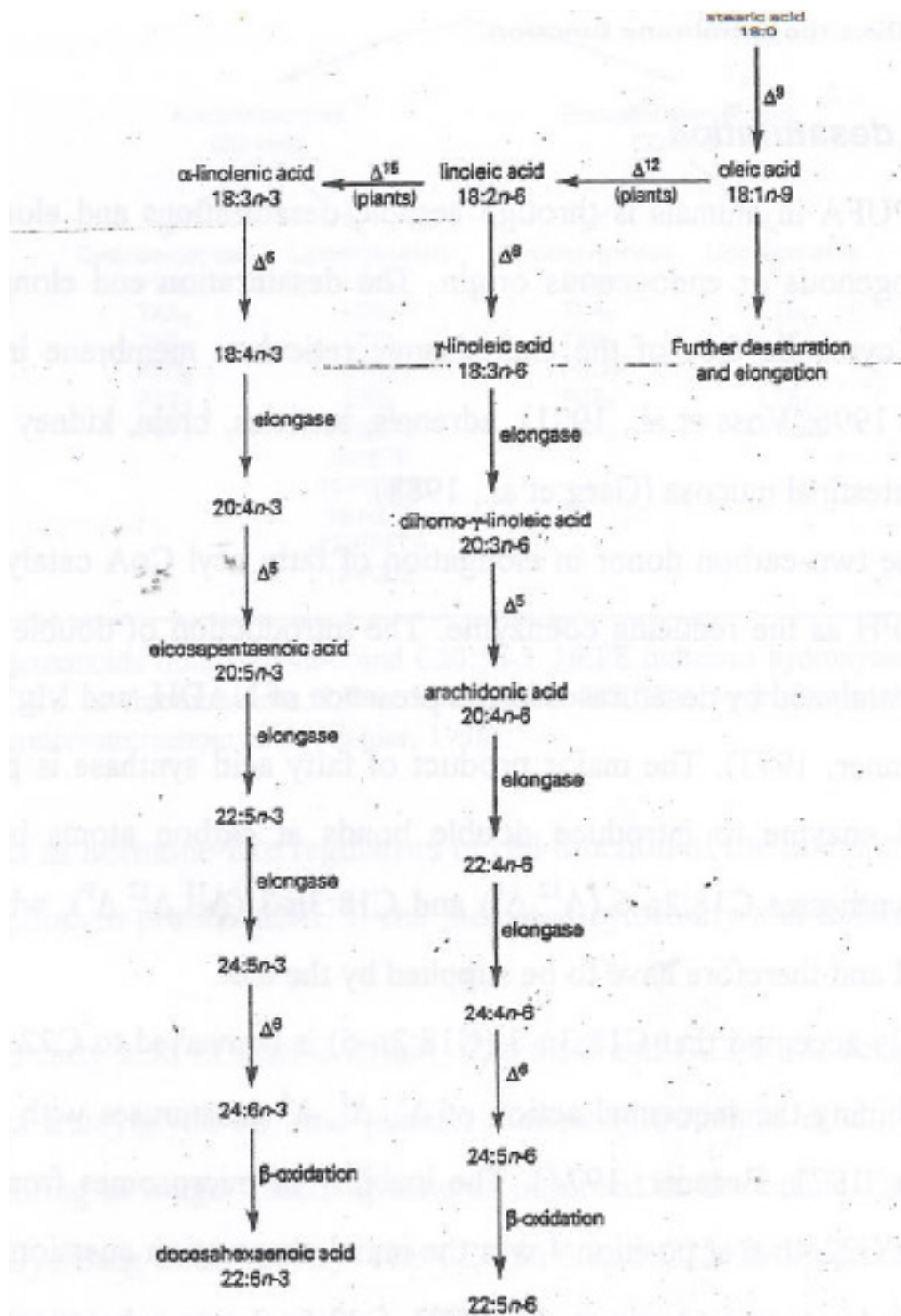

Figure 10.4.Metabolism of PUFA. Δ^5, Δ^6, Δ^9, Δ^{12}, and Δ^{15} indicate desaturase enzymes [8].

These essential FAs are precursors for prostaglandins, leukotrienes, and thromboxans. By desaturation and elongation processes, linoleic acid (C18:2n-6) is formed to arachidonic acid (C20:4n-6). By the action of cyclooxygenase, C20:4n-6 is converted to prostaglandins, whereas the action of lipoxygenase converts the n-6 FAs into leukotrienes and other oxidative products. These eicosanoid products of the n-6 series have been found to exert clinical efficacy in diseases, including inflammation. The eicosanoids formed through desaturation and elongation of linolenic acid (C18:3n-3) have a very similar molecular structure, but with different biological activity. The

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eicosanoids act as hormone-like regulators of cell function of the immune system, and thus influence e.g. lymphocyte proliferation, T-cell mediated cytotoxicity and inflammatory response.

3.2. Modification of muscle fatty acid composition and biological importance

Dietary fat modifies cellular membrane lipid properties resulting in an increase or decrease in some membrane functional activities, which may overall be of importance for animal health and product quality. The fatty acid profile is responsible for the fluidity of the membrane, i.e., incorporation of more saturated FAs increases the rigidity of the membrane, and this may influence the membranal function through altering the protein-mediated activities in the membrane.

Long-chain n-3 and n-6 PUFA are mainly found in phospholipids, but are also detected in pig neutral lipid and adipose tissue. Lauridsen et al. [30] compared a basal diet (without inclusion of rapeseed oil) with a diet containing 6% rapeseed oil for growing pigs with regard to, for instance, incorporation of FAs into muscles cellular membranes. Inclusion of rapeseed oil increased the proportion of C18:1 in PL and TGs of longissimus dorsi (white muscle) compared to psoas major (red muscle). The proportion of C18:3n-3 increased and the proportion of C16:1 decreased in the TG2 and PL with inclusion of dietary rapeseed oil. Overall, the ratio of unsaturated FAs to saturated FAs of the TGs increased with rapeseed oil, whereas in PL, this ratio was not influenced. However, the concentration of monounsaturated FAs was increased, and the concentration PUFA decreased in PL with the addition of rapeseed oil. The dietary treatments had no influence on the membrane function in terms of accumulation of calcium by the sarcoplasmic reticulum. In agreement with previous studies, this experiment [30] demonstrated that the proportion of PUFA was higher and the proportion of MUFA was lower in the PL than in the TGs, and that the FA composition of the TGs and PL was affected by the fibre composition of the muscles.

3.3. De novo synthesis and storage of fatty acids in adipose tissue

The presence of high amounts of dietary fat irrespective of source will increase the incorporation of dietary FAs in triglycerides synthesized by adipocytes and decrease the amount of glucose converted to FAs and subsequently stored in adipocytes.

The adipose tissue plays a very important role in the storage and release of energy substrates. Lipogenesis is one of the processes that take place in fat cells. The substrates for the synthesis of TGs in the fat cell originate from TGs in the blood stream, mainly in the CM or VLDL, or by de novo synthesis. In comparison with other mammals, pigs are special in the sense that the formation of FAs and glycerol from glucose takes place in the adipose tissue and not in the liver. From a virtually fat-free diet with inclusion of 1% sunflower oil to avoid deficiency of essential FAs, the pig synthesized mainly oleic acid (62% of FAs) from dietary carbohydrates [40]. Increasing the fat level of a diet distinctly inhibits the de novo synthesis of FAs in fat cells obtained from growing pigs. Allee et al. [1] found a linear reduction in the de novo capacity with feeding of up to 13% fat, and Berschauer et al. [5] obtained a reduction of up to 30% by feeding of 18.5% fat, but at higher dietary fat levels no linear response was obtained. At feeding levels of 35% fat the de novo capacity was only reduced to 15% [53]. The reduction in synthesis capacity seems to result from the fact that a high dietary fat content markedly restricts the uptake of glucose by fat cells.

In addition to lipogenesis, a second important process occurring in the adipose tissue cells is lipolysis or degradation/mobilisation of the deposited TGs. The oxidation of FAs as an energy source, referred to as β-oxidation, occurs in either mitochondrial matrix or in peroxisomes depending on the length of the FAs.

The intensity of the breakdown of TGs in adipocytes is to a large extent dependent on the formation of cyclic adenosine monophosphate (cAMP). Factors such as dietary copper have been demonstrated to influence the biosynthetic pathway of the deposited TGs, but it is unclear in what manner copper affects lipid metabolism.

In addition, conjugated linoleic acid may affect fat deposition, i.e. by reducing the activity of lipoprotein lipase, fewer FAs whereby TGs are incorporated into the adipocytes and fat storage will be reduced.

In order to be stored in the adipocyte, the FAs must be broken down into glycerol and FFA before entering the cell, and this reaction is catalysed by LPL synthesized and excreted by fat cells.

The provision of energy from oxidation of FAs is especially of consideration for piglets, weaners and lactating sows. Certain FAs, such as 18:1, have a faster oxidation rate than 18:0 and 18:2 and thus release more energy from the tissue whereby glucose is spared [6].

3.4. Digestibility of dietary fat

The small intestine has a remarkable capacity to absorb dietary fat, and several mechanisms are involved in the adaptation of the fat absorption to the lipid content of the diet. The lipid-mediated adaptability appears to be sufficient to prevent excessive lipid elimination in faeces when fat supply is enhanced. Evaluation of the nutritional value of different dietary fat sources can be assessed in digestibility experiments, in which apparent digestibility of fat is determined as the difference between ingested fat in feed and excreted fat in faeces. Collection can be performed by either collection of all faeces, or by using a marker (for instance Cr_2O_3) whereby only a fraction of faeces needs to be collected. However, the apparent digestibility of fat represents an underestimation of the true digestibility, because of the occurrence of endogenous or metabolic losses. Hence, the true digestibility of dietary fat is the difference between ingested fat and the sum of excreted fat and endogenous fat loss relative to the feed intake. The endogenous loss occurs due to loss of bile acids, desquamated cells, structural lipids from mucosa and cholesterol, and may vary not only with dry matter intake, but also with source and level of dietary fat.

Fats of animal origin are normally considered as having lower digestibility and hence lower energy value than fats of vegetable origin owing to a higher content of saturated fatty acid (C16:0 and C18:0), which have lower ileal digestibility than unsaturated FAs (C18:1, C18:2 and C18:3) [27],[28]. Dietary minerals have no influence on ileal fatty acid digestibility, while dietary protein level has a slight positive influence on the digestibility of some saturated FAs [27]. Another factor of influence for fat digestibility, which has not been investigated in pigs, is the melting point of dietary fat. From other animal species it is known that apparent digestibility of fat decreased as melting point increased from -3 C° to 41 C°, irrespective of fat source.

Most digestibility trials regarding different fat sources for pigs have addressed post-weaning digestibility rather than digestibility during the growing period, and, in general, the apparent fat digestibility increased with age in most experiments. The main outcome of the trials is that vegetable fat sources are generally better digested than animal fat, although high-quality fat sources of animal origin may also be utilised efficiently.

Although several experiments with varying levels of dietary fats have been published, information concerning different fat sources for growing pigs is scarce, and most of the experiments on growing pigs in relation to fat digestion have actually been carried out in Denmark as reviewed by Christensen [13]. In growing pigs, apparent fat digestibility does not differ markedly between vegetable and animal fat sources, and actually only a few studies have revealed effects of dietary fat source on apparent fat digestibility, i.e. that the ratio of unsaturated to saturated FAs has a major

influence on apparent and hence true digestibility of fats [47]. Table 10.2 shows the digestibility of fat of different fat sources [25].

Table 10.2. Digestibility and energy value of different fat sources [25].					
	Animal fat	**Soy bean oil**	**Palm oil**	**Palm oil mix**	**Vegetable oil by-product**
Gross energy, MJ/kg	35.5	39.5	40.8	38.7	38.9
Fat, %	99.6	99.9	99.9	99.9	98.1
Fatty acids, %	89.0	92.3	92.6	85.4	52.9
Free fatty acids, %	10	-	2	79	55
Fat digestibility, %	89.9	91.2	85.3	71.5	62.3
Digestible energy, %	90	91	80	66	62
FUp/kg dry matter[1]	3.19	3.37	2.89	2.23	2.03

1) FUp = feed unit for pigs.

The digestibility of fat from soy oil is higher compared with animal fat, and this is in accordance with the higher content of monounsaturated and especially polyunsaturated FAs in soy oil. Palm oil has been found to have lower digestibility than soy oil, but also lower digestibility than animal fat. This is in agreement with the high content (44.3%) of the saturated FAs palmitic (16:0) and stearic acid (18:0). Both C16:0 and C18:0 have relatively low ileal digestibility compared with the unsaturated FAs [27]. Sewell & Miller [44] studied the uptake of different types of FAs and concluded that the uptake of saturated FAs (C16:0 and C18:0) is lower than that of unsaturated FAs (C18:1 and C18:2) in pigs. Although most dietary fat sources of potential use in swine feed would be as TGs, there are other lipids of interest from an economic point of view. Palm oil mix has a high content of free FAs (79%), which may lead to lower fat digestibility (71.5%) when compared with palm oil (85.3%) [25] because of reduced capability of pigs to form mixed micelles. The fat digestibility in the vegetable oil by-product is also lowest (62.3%) of the fat sources tested, and this has partly been ascribed to the low content of FAs relative to HCL-fat extracted (52.9%) in this product [25].

Thus, based on previous research studies, the major conclusion is that growing pigs are more capable than weaners of digesting fat sources as the secretion of lipases and bile is sufficient in growing pigs, but could be limited in weaners, and the higher dietary fat level added to a diet, the higher apparent digestibility will be obtained. In addition, it is generally accepted that the apparent digestibility of fat is less affected by dietary fat source in growing pigs than in weaned pigs. However, a Danish study on fat digestibility of weaners and growers actually revealed the opposite. The background of the experiment was that no recent studies had considered the digestibility of different fat sources in pigs using the same individuals throughout the weaning and growing periods. Therefore, a digestibility trial was conducted, in which diets included 5% of either animal fat, palm oil mix, palm oil vegetable oil mix, coconut oil, or rapeseed oil were tested in weaned and growing pigs [34],[35]. The digestibility of the different fat sources is shown in Figure 10.5, and the results showed that in weaned pigs, rapeseed oil and coconut oil lead to a higher apparent digestibility than animal fat, palm oil and vegetable oil mix diets, and the palm mix diet was intermediate. In growing pigs, the apparent fat digestibility was lower than in weaned pigs, and the rapeseed oil diet had a higher apparent fat digestibility than the other diets, whereas animal fat, palm oil mix, fat blend diets were intermediate and that of vegetable oil mix diet was significantly lower than all other diets.

The higher apparent fat digestibility obtained by using coconut oil rather than animal fat can probably be attributed to the content of MCFA in coconut oil, which are more water-soluble, facilitating the absorption through the unstirred water layer in comparison to LCFA. In case of insufficient lipase or bile secretion, this would have been even more compromised. Phospholipids like lecithin, a by-product from the vegetable oil industry, have in experiments with weaned pigs been shown to increase absorption of tocopherols, and to increase the digestibility of starch in the upper part of the small intestine [24].
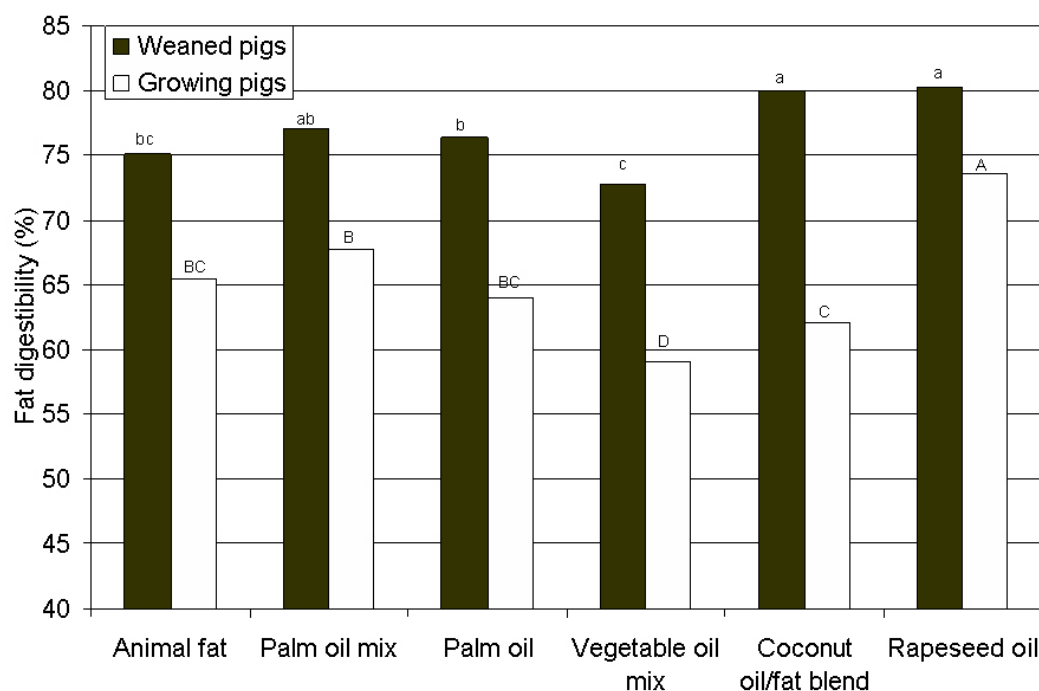
Figure 10.5. Effect of dietary fat sourcs in apparent fat digestibility of weaned and growing pigs (SE=1.1 and 1.5% for weaners and growers, respectively). Means with different letters within each group of pigs are significantly different (P<0.05) [35].

The difference found between results obtained by weaners and by growers in capability of dige-sting fat may be attributed to the chemical methods used for analysing lipid content and not real. In order to evaluate the digestibility of fat, extraction of fat in feed and faeces is required. A broad range of extraction methods exist, and the evaluation and discussion of the specific extraction methods is complex. In connection with the study mentioned above [35], a method (modified Bligh and Dyer method) for quantitative measurement of fat extraction from feed and faeces was develo-ped [23]. In general, the fat digestibility observed in the digestibility trial on the different fat sources was low in comparison with results of previously published studies. However, this may be due to the fact that the modified Bligh and Dyer method was more efficient in fat extraction than the Stoldt method [48], which will lead to a lower apparent fat digestibiliy. Chloroform (in the modified Bligh and Dyer method) is a better solvent for polar lipids than petroleum ether (as used in the Stoldt-method). Due to a rather constant secretion of endogenous fat, the apparent digestibility of fat normally increases with increasing dietary fat content. In addition, the amount of fat used in digesti-bility trials (which was 5% in the study by [35]) was lower than for other experiments investigating effects of dietary fat sources on fat digestibility. It is well-known that the apparent fat digestibility increases when the level of added dietary fat is increased. Since most of the previous experiments have investigated the effect of dietary fat sources on fat digestibility of either weaners or growers, and have used a higher dietary level of fat, using less efficient fat extraction methods, these factors may explain the differing results observed in our experiment in comparison to the literature.

4. Impact on carcass quality

In many countries, fat is an unpopular constituent of meat for consumers, being considered unhealthy. Yet fat and FAs, whether in adipose tissue or muscle, contribute importantly to various aspects of meat quality such as palatability and storage stability, and are central to the nutritional value of meat. Of major concern for humans according to WHO [47] is the total fat intake, the cholesterol intake, and the ratio of PUFA to SAFA. In addition, ratio of n-6 PUFA to total n-3 PUFA has been taken into consideration with regard to the nutritional value of dietary fat for humans [20].

The pig is amenable to changes in the FA composition of adipose tissue and muscle using diets containing different oils. Thus, the past 50 years of agricultural research has worked on changing the FA profile and fat content of the carcass through manipulating genetics, feeding regimes, housing, and management systems taking into account the health and welfare of the animals and the quality, storage stability and technological value of the animal products into consideration. Early work on meat fatty acid composition concentrated on adipose tissue, since that is where the bulk of the body's FAs is located. Madsen et al. [40] reviewed the Danish experiments with growing pigs with regard to the impact of dietary fat on carcass fat quality. The effects of a variety of feeds have been studied, supplying varying amounts of fat differing greatly in fatty acid composition (Table 10.3). The FA composition is dominated by C18:1 and C16:0 under de novo synthesis, while the content of C18:0 is increased, and the content of C18:1 is decreased irrespective of the type of dietary fat. Thus, it was concluded that de novo fatty acid synthesis will result in the predominance of saturated and monounsaturated FAs and firm backfat, while the deposition of polyunsaturated FAs will produce soft backfat [40].

Table 10.3. The influence of dietary fat source on fatty acid composition of backfat[1] (modified after [12],[40]).

Fatty acid	Fat-free[2]	Barley+soybean meal	Coconut fat[3]	Soy oil	Linseed oil
C12:0	0.1	0.1	5.3	-	Trace
C14:0	1.4	1.1	15.8	2.0	1.0
C16:0	15.9	21.1	30.5	16.2	14.1
C16:1	6.5	3.1	ND[4]	ND	1.5
C18:0	5.6	15.0	11.5	11.3	10.9
C18:1	63.4	46.9	32.6	29.3	33.2
C18:2	8.1	9.3	4.2	38.6	13.2
C18:3	-	3.4	ND	2.8	26.1

1) The pigs were fed from 20 kg to 90 kg LW on barley-soybean meal, vitamins and minerals according to scale.
2) Basal diet consisted of 85% sucrose, 10% tapioka meal, 5% potato starch. Casein was used as protein source. 1% sunflower oil was added as a source of linoleic acid.
3) 30% of dietary energy substituting barley.
4) Not detected.

Changes in adipose tissue FA composition can be expected with age and fatness of pigs. At the same fat thickness as females, subcutaneous adipose tissue from boars contained a higher proportion of water and a lower proportion of lipid, signifying a less mature tissue [52]. In addition, a higher proportion of PUFA in subcutaneous adipose tissue of entire male is observed than in female pigs and castrates. Another way of assessing the fat quality of the carcass is to calculate the iodine value (IV), which is a measure of the unsaturation of the fat and is defined as the amount of iodine (in g) bound by 100 g of fat. Barton-Gade [3] examined the fat quality in boars, castrates and gilts, and found that IV of more than 70 is unacceptable owing to the soft backfat and reduced storage stability. The IV of backfat has been shown to be related to the iodine value product (IVP) of the dietary fat through the following equation [40]: IV = 47.1 + 0.14 x IVP/day. Østerballe et al. [53] supplemented a barley-soybean meal diet with 6% fat of varying FA composition, and, as shown in Table 10.4, increasing amounts of dietary C18:2 and C18:3 increased the concentrations of C18:2 and C18:3 in the backfat. Consequently, the ratio of PUFA to SAFA increased from 0.2 to 0.6, and IV increased from 55 to 78.

Table 10.4. Fatty acid composition and iodine value (IV) of backfat in relation to dietary intake of C18:2, C18:3, and iodine value product (IVP) [53].

Dietary fat (% fatty acids)						
C18:2	15	15	15	31	31	31
C18:3	1.4	3.7	5.9	1.6	3.8	6.0
IVP[1]	52	58	64	81	87	93
Backfat (% fatty acids)						
C16:0	25.6	24.9	24.9	23.4	23.0	22.3
C18:0	12.2	12.3	12.6	12.0	11.7	11.9
C18:1	39.1	38.2	38.0	36.0	35.1	35.3
C18:2	7.4	8.0	8.3	16.8	17.7	17.7
C18:3	0.6	1.6	2.7	0.8	1.8	3.0
IV[2]	54.9	59.0	62.6	70.0	74.4	78.2

1) IVP = hectogram crude fat x iodine.
2) IV = iodine value (defined as the amount of iodine (in g) bound by 100 g of fat).

Recent research on this aspect has focused on the inclusion of conjugated linoleic acid (CLA) in pig feed, which has been reported to reduce body fat in pigs [2], and increase in the proportion of SAFA to PUFA in backfat of pigs by inclusion of CLA in diet for pigs, leading to an improved storage stability of the carcass backfat. However, it should be mentioned that the pronounced reduction in backfat by CLA inclusion for growing pigs in experiments performed in other countries was not seen in Danish experiments [32], probably owing to breeding towards leaner meat. However, in this study as well as shown recently in a Danish study [41], CLA inclusion increased the proportion of SAFA in the carcass, which may be of interest when optimising meat product quality through dietary means.

In recent years, emphasis has increased on muscle FA composition because of an increasing aversion to visible fat at retail. Muscle also contains higher concentrations of the long-chain n-6 and n-3 FAs, and the importance of which in human nutrition has been recognized relatively recently. Detection procedures for low levels of unsaturated FAs in muscle have also greatly improved in recent years.

In contrast to backfat quality, the amount of intramuscular fat (IMF) is strongly influenced by genetics. Cores from the centre of the longissimus typically contain 1% total lipid in pigs. Lean meat with a high content of IMF has better sensory properties and higher palatability than meat with a low fat content. The structural lipids cannot be removed as they form the integral part of all biological membranes. If the deposited fat is removed, the intramuscular fat (the marbling) is removed. The major lipid class in adipose tissue (>90%) is TGs. In muscle, a significant proportion is PL and its amount remains fairly constant. PL has a much higher PUFA content in order to perform its function as a constituent of cellular membranes. As body fat increases, TGs predominate in overall FA composition. Results from a study of Kouba et al. [29] of pigs fed a control diet from 40 kg live weight for 20, 60 or 100 days showed that the PL declined from 46% of total lipid at 20 days to 28% at 100 days. As previously mentioned, the FA composition of TGs is more prone to dietary manipulation than that of PL. Hence, the it is important to be aware of the dietary FA composition especially during the late growing period when the contribution of TGs is relatively higher than PL in order to optimise the carcass quality.

Several studies have investigated the possibility of enriching pork with n-3 FAs. The motivation for this research is the high n-6:n-3 fatty acid ratio in pork (probably due to a high dietary content of wheat and barley), and the need to reduce this ratio for human nutritional reasons. The aim has been to favour deposition of C18:3n-3 and its long-chain products in TGs and PL. An example is the work of Enser et al. [16], who showed that a linseed oil diet (with a C18:2n-6:C18:3n-3 of 2 versus a control diet of 11) increased the deposition of C18:3n-3 in adipose tissue and muscle, particularly muscle PL. Conversion of C18:3n-3 into long-chain n-3 FAs (DPA and DHA) occurred and these were deposited in muscle PL, but not in muscle neutral lipid. However, the conversion

of C18:2n-6 and C18:3n-3 to longer chain PUFA is limited in farm animals, and the latter FAs will therefore not accumulate to any great extent in the edible parts of the body [20]. In order to enrich pork with the nutritional beneficial DPA and DHA, Lauridsen et al. [30] investigated the effect of increasing dietary dose of fish oil to growing pigs from weaning until 60 kg live weight. From 60 kg live weight and until slaughter, pigs were fed a control diet containing 2% tallow. As shown in Figure 10.6, there was a linear response of incorporation of C22:6n-3 (DHA) in muscle and fat tissue with increasing dietary C22:6n-3 in the form of fish oil supplementation, and the concentration of C20:5n-3 (EPA) and C22:5n-3 (DPA) was also increased in the muscle and fat tissue. However, feeding of 3-6% unrefined fish oil until approximately 60 kg live weight caused off-flavour of the pork, which was therefore unsuitable for human consumption [28]. Thus, the study confirmed the strategy for Danish pig producers, i.e., that it is not allowed to add fish oil to feed for pigs after 30 kg live weight. More research is needed to develop strategies on how to increase the ratio of n-3 to n-6 fatty acids in order to obtain a high-quality product for human nutrition.
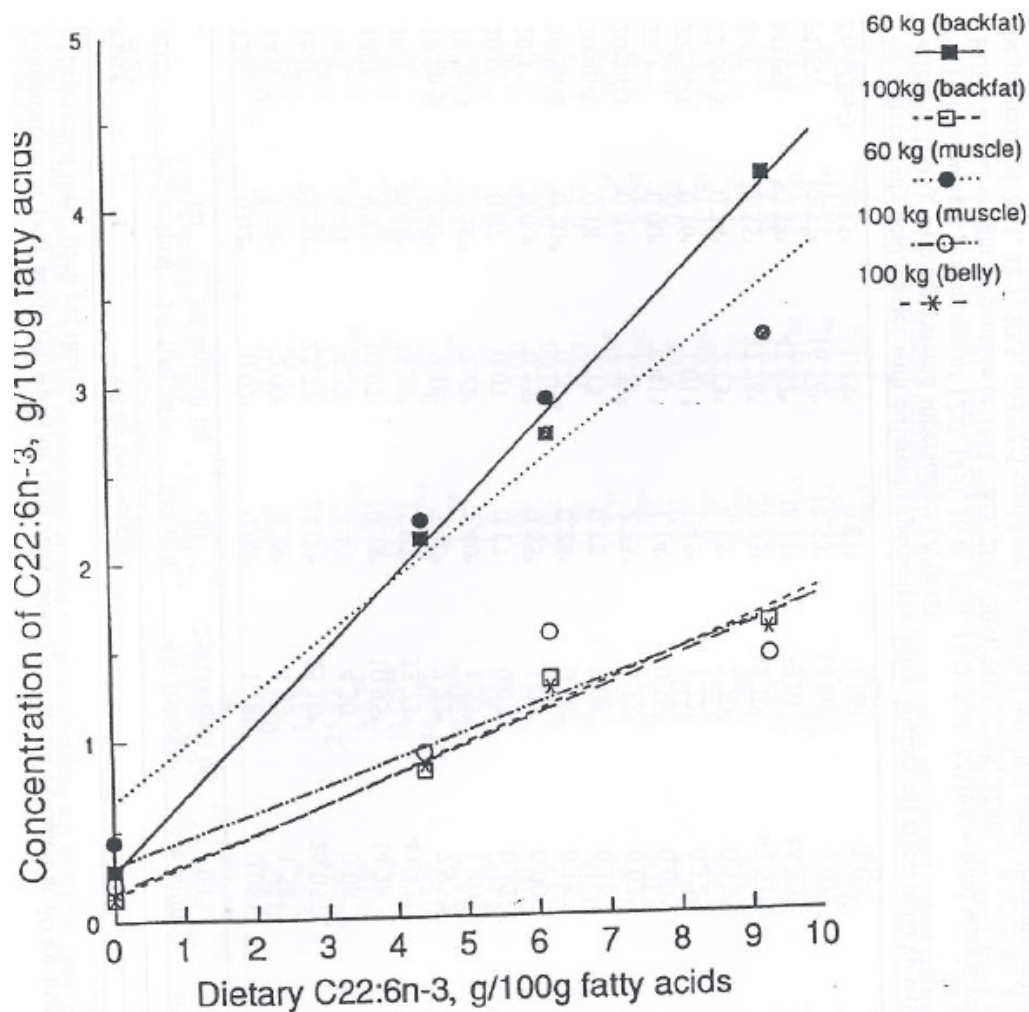

Figure 10.6. Plots of the concentration of C22:6n-3 in the belly, backfat and muscle tissue at 60 and 100 kg LW against dietary concentration of C22:6n-3 provided from weaning to 60 kg LW [37].

5. Other biological effects of n-3 fatty acids

In recent years, it has become clear that the diet plays a substantial role in the regulation of the immune system. The PUFA are important regulators of numerous cellular functions including those related to inflammation and immunity [8]. The main physiologic roles of PUFA are as components of cell membranes and as precursors of eicosanoid production. Only little information is available regarding the impact of dietary FAs on the immune function of pigs. The addition of 8% of animal fat, fish oil or sunflower oil to a diet for lactating sows changed the FA composition of the milk [31] and influenced the eicosanoid production of immune cells obtained from the progeny pre- and post weaning [33]. In addition, supplementation of fish oil to weaner diets increased the immune cell n-3 content of n-3 fatty acids and reduced n-6 compared with sunflower oil and animal fat and fish oil reduced the inflammatory responses of the immune cells relative to the other dietary fat sources [42]. Thus, some beneficial effects could be obtained by using dietary fish oil for weaned pigs, but the practical relevance of feeding n-3 FAs instead of n-6 FAs in terms of improved immune function and optimal growth of pigs needs to be further investigated.

Little is known regarding the effect of dietary fat sources on reproduction of pigs. However, supplementing the maternal diet for pigs with n-3 FAs has improved pre- and postnatal survival [46] and n-3 FA supplementation affected endometrial, conceptus, and foetal FA composition in early gestation [7]. In addition, n-3 PUFA supplementation is known to benefit male fertility. However, according to the authors' knowledge, no information is available on the effect of dietary fat sources on reproduction performance of sows during subsequent reproduction cycles.

6. Summary

Triglycerides are the major lipid components in pig feed, and they are carriers of energy as well as important FAs. Fat sources commonly used in pig feed originate from animal, vegetable and marine sources, which differ widely in fatty acid composition. Many factors affect the digestion and absorption of triglycerides. Nursing piglets digest dietary fat efficiently, but post-weaning insufficient secretion of lipases may cause a drop in apparent digestibility. In general, dietary fats of vegetable origin are more digestible than animal fat sources, and especially fat sources with polyunsaturated or medium chain FA are efficiently digested. The de novo synthesis of FAs decreases as dietary fat content increases, and the essential FA, the dietary n-6 and n-3 FAs are absorbed practically intact in pigs, and are incorporated into adipose tissue and cellular membranes, where desaturation and chain elongation may occur. From a human nutritional point of view, enrichment of pork with the long-chain PUFA may be beneficial, but the product quality may be reduced due to the production of soft backfat. There are several possibilities in practical pig feeding to meet the human nutritional requirements for "healthy pork products", and to pay attention to special fatty acid requirement for pigs in terms of immunity and reproduction. However, practical pig nutrition has traditionally focused primarily on quality of different fat sources in terms of optimal digestibility of the feed without negative impact on carcass quality.

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List of abbreviations:

cAMP = cyclic adenosine

CLA = conjugated linoleic acid

CM = chylomicrones

DHA = docosahexanoic acid

DPA = docosaoentanoic acid

EPA = eicosapentaenoic acid

FA = fatty acids

FABP = fatty acid binding protein

FFA = free fatty acids

IMF = intramuscular fat

IV = iodine value

IVP = iodine value product

LCFA = long chained fatty acids

LPL = lipoprotein lipase

MG = monoglycerides

MAG = monoacyl glyceride

MCFA = medium chained fatty acids

MJ = mega joule

PC = phosphatidylcholine

PFAD = palm oil fatty acid destillate

PL = phospholipid

PLA2 = phospholipase A2

PUFA = polyunsaturated fatty acids

SAFA= saturated fatty acids

SCFA = short chain fatty acids

TG = triglyceride

VLDL = very low density lipoprotein