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Significance for human health of increasing n-3PUFA content in pork

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Abstract

Evidence for the health-promoting effects of food rich in n-3 fatty acids (n-3 PUFA) is reviewed. Pork is an important meat source for humans. According to a report by the USDA (<http://www.ers.usda.gov/topics>), the pork consumption worldwide in 2011 was about 79.3 million tons, much higher than that of beef (48.2 million tons). Pork also contains high levels of unsaturated fatty acids relative to ruminant meats (Enser *et al*, 1996). The available literature indicates that the levels of eicosatetraenoic (EPA) and docosahexaenoic (DHA) in pork may be increased, by fish-derived or linseed products, the extent to which being dependent on the nature of the supplementation. Transgenic pigs and plants show promise with high content of n-3 PUFA

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and low ratio of n-6/n-3 fatty acids in their tissues. The approaches mentioned for decreasing n-6/ n-3 ratios have both advantages and disadvantages. Selected articles are critically reviewed and summarized.

Key words pork, n-3 polyunsaturated fatty acids, human health, enrichment

Introduction

The n-3 polyunsaturated fatty acids (n-3 PUFA) are important constituents of cell membranes playing multiple functions through regulating membrane fluidity, eicosanoid synthesis, cell signaling and gene expression (Jump, 2002). They have effects in protecting the cardiovascular system, and lessening the incidence of atherosclerosis, cancer, hyperlipidemia; they also stimulate structural and functional development of the infant brain. Increasing n-3 PUFA intake and balancing the n-6/n-3 ratio in the body are of significance for human health. Currently, the principal source of n-3 PUFA for human consumption is fish, but global fish stocks are declining and cannot provide a sustainable source of n-3 PUFA. In addition, the presence of chemical contaminants (e.g. mercury) in fish can be harmful to consumers and the odour is unattractive (Mahaffey *et al.*, 2008; Bourdon *et al.*, 2010). Recently, many so-called "functional foods", rich in n-3 PUFA, have been produced including fish oils and spirulina in soft capsules. The n-3 PUFAs are readily oxidized during the processing used to manufacture these human dietary supplements. An alternative approach to increase the intakes of n-3 PUFA without changing the nutritional behavior of consumers would be to fortify traditional food items such as meat and meat products with n-3 PUFA. Pork is an important human food and it is now possible to improve its nutritional value, with regard to human health, by increasing its content of n-3-PUFA and balancing its n-6/n-3 ratio. This review summarizes the sources and functions of n-3 PUFA, their benefits for human health and approaches for increasing the content of n-3 PUFA in pork.

The discovery, classification and sources of n-3 PUFA

The n-3 polyunsaturated fatty acids (n-3 PUFAs), are a series of polyunsaturated fatty acids containing two or more double bonds. The n-3 PUFAs are so called because the first unsaturated bond is on carbon number 3, the methyl carbon being number 1, and they are also called ω -3 PUFAs, with reference to the carboxyl carbon.

The n-3 PUFAs were first discovered in the early 1970s, and shown to play a crucial role in protection against many disorders: cardiovascular, atherosclerosis, heart attack, depression and cancer (Connor, 2000; Kremer *et al.*, 1989; DiGiacomo *et al.*, 1989; Simopoulos, 1991). As important components of the lipid bilayer membrane of cells, n-3 PUFAs affect structure, fluidity and permeability, membrane-protein conformation and membrane protein-mediated responses. The major types of n-3 fatty acids with roles in the body include: α -linolenic acid (C18:3n-3, ALA, the simplest n-3 PUFA), eicosapentaenoic acid (C20:5n-3, EPA), docosapentaenoic acid (C22:5n-3, DPA), and docosahexaenoic acid (C22:6n-3, DHA). Among the n-3 PUFAs, ALA is essential for humans, but as it cannot be synthesized *de novo*, it must be obtained from the diet. Once obtained, ALA can be converted to EPA, DPA and DHA, albeit with inefficiency rate of less than 5% (Bezard *et al.*, 1994; Schmitz and Ecker, 2008). In order to adequately meet human requirements, most of these PUFAs must be obtained from the diet (Thomas, 2002).

The Δ^9 Desaturase exists in animals, and is used to synthesize oleic acid (18:1, OA), but not ALA (only obtained from feed). On the other hand, animals can synthesize n-3 PUFA such as EPA and DHA using ALA as substrate (Figure 1).

Sources of n-3 PUFA for humans are plants and fish that are naturally rich in such fatty acids and from engineered animal products where the content of n-3 PUFA is specifically enhanced by including n-3 PUFA-rich products in the rations fed to animals. Plant sources, such as, flaxseed, walnuts, seeds or oil from *Echium plantagineum*, soybeans, olives and cauliflower, are readily available and are renewable; some are reliably sourced and inexpensive. Animals and human do not possess the Δ^{15} Desaturase needed to synthesize ALA but plants do. However, the main disadvantage is that plants alone are not sufficient for human nutritional requirements. Another possible source is biosynthetic food. Animals can use ALA (from the diet) to synthesize EPA and DHA. Therefore, suitably enriched animal products can be considered as alternative sources of n-3PUFA.

The function of n-3 PUFA for human health

n-3 PUFA and disease

The precursor fatty acid, ALA (18:3n-3) is used for the synthesis of EPA and DHA, both of which play a major role in the function of cardiovascular system (Von Schacky and Harris, 2007), and in neural and retinal development (Alessandri *et al.*, 1998). Numerous recent studies have reported that consumption of diets rich in n-3 PUFAs decrease the incidence of cardiovascular disease, possibly through decreasing the incidence of arrhythmias, thrombi and concentrations of triglycerides in serum, along with improvement of the function of vascular endothelial cells, and decreasing blood pressure and inflammation (Holman, 1978; Burr *et al.*, 1989; Dolecek and Grandits, 1991; Katan, 1995; Sargent, 1997; Kris-Etherton *et al.*, 2003). Intake of n-3 PUFA also has been shown to be associated with a lower risk of Alzheimer's

disease. Vseby (2003) reported that the level of plasma saturated fatty acids and n-6 PUFA were much higher in patients with obesity and diabetes mellitus than in healthy people. Indeed, n-3 PUFA can be used for adjuvant treatment of obesity and diabetes mellitus. Increasing the content of PUFA in the cell membrane can modify the population of insulin receptors producing more high-affinity sites with a concomitant reduction in low-affinity sites (Bruneau *et al.*, 1987; Ginsberg *et al.*, 1991), such a change can ameliorate insulin resistance. Increased membrane content of n-3 PUFA reduces the incidence of some diseases such as essential hypertension, hyperlipidemia, ischemic (coronary) heart disease, atherosclerosis, polycystic ovarian disease and the metabolic syndrome. Liu *et al.* (1994) reported that dietary n-3 PUFA stimulated insulin receptor binding and action by changing the fatty acid composition of phospholipids surrounding the receptors. Hainault *et al.* (1993) and Mori *et al.* (1997) also support this view. Because insulin enhances the activities of Δ^6 and Δ^5 desaturases (Rimoldi *et al.*, 2001) and thereby potentially augments formation of PUFAs that, in turn, enhance the action of insulin, there is opportunity for positive feedback.

n-3 PUFA and brain development

A major constituent of neuronal membrane phospholipids is DHA. Because the fatty acid composition of membrane phospholipids is important for the configuration and function of neurotransmitter receptors, DHA has been postulated to be the most important n-3 fatty acid for brain function (Lauritzen *et al.*, 2001; Innis, 2004, 2007; Anderson and Heird, 2005). Breastfeeding is thought to influence brain development through nutritional processes involving fatty acids (Institute of Medicine 2004). The predominant long-chain polyunsaturated fatty acids

(LC-PUFAs) such as DHA, arachidonic acid (AA or ARA; 20:4n-6), and EPA are present in human milk, but not in cow's milk or most infant formulas (Sauerwald *et al.*, 2001). Caspi *et al.* (2007) reported that breastfed children attain higher IQ scores than children who are not breastfed, presumably because of higher concentrations of DHA and AA in breast milk than in un-supplemented formulas (Farquharson *et al.*, 1992; Makrides *et al.*, 1994). Anderson *et al.* (2005) and Mortensen *et al.* (2002) also found children who were breastfed have higher IQs than children not breastfed, and this advantage persists into adulthood. Substantial accumulation of DHA and AA in the human brain occurs during the earliest postnatal months (Heird and Lapillonne, 2005), a critical period for brain development. Children, whose mothers consumed DHA during pregnancy, are more intelligent than others when tested at 4 years of age (Helland *et al.*, 2003). Supplementation with DHA in rodents and nonhuman primates also increased brain DHA concentrations and enhanced performance on a wide variety of learning, memory, and problem-solving tasks (Carrie *et al.*, 2000; Champoux *et al.*, 2002; Takeuchi *et al.*, 2002). It was also found that DHA significantly enhanced brain NOS activity (Li *et al.*, 2009), which is very important for cognitive ability (Holscher *et al.*, 1996; Kanit *et al.*, 2003). Also crucial in brain development and function is AA. Sakayori *et al.* (2011) found that it promoted the maintenance of neural stem/progenitor cells and might induce the glial cell differentiation of neural stem/progenitor cells. When AA was supplemented to maternal rat diets, their offspring performed better and showed higher exploratory behavior, such as improved wire hanging endurance and water maze latency, than did control-diet offspring (Zhao *et al.*, 2009; 2011). Eicosatetraenoic acid is the precursor of eicosanoids which have important functions as

secondary messengers and neuromodulators (Lin and Su, 2007), such as affecting the activities of phospholipase A2 and cyclooxygenase-2 and their gene expression (Serhan *et al.*, 2000).

n-3 PUFA and intestinal development

The n-3 PUFA content and n-6/n-3 ratio of the maternal diet during pregnancy and lactation affects the development of brain (Lauridsen and Jensen, 2007) and small intestine of the offspring (Jarocka-Cyrta *et al.*, 1998). Increasing the n-3 PUFA content and decreasing the n-6/n-3 ratio in the diet enhanced the recovery of the intestinal microvilli from starvation-induced damage in piglets (Lopez-Pedrosa *et al.*, 1999). Bomba *et al.* (2003) reported that n-3 PUFA administration increased the adhesion of *Lactobacillus paracasei* to the jejunal mucosa of gnotobiotic piglets by 12%. Such supplementation also almost doubled the phagocytic activity of neutrophils at 28 d of age and increased the CD8 subpopulation of lymphocytes in the peripheral blood of germ-free piglets on day 21. Dietary n-3 PUFA can modulate the action of probiotics and stimulate growth of piglets. Gabler *et al.* (2007) indicated that n-3 PUFAs, particularly DHA, improve intestinal glucose absorption and muscle glycogen concentrations in newly weaned pigs. Thomson *et al.* (1986) also found that feeding rats with n-3 PUFA increased the active transport rates of glucose into the jejunum and gut motility; there was a tendency for increases in the glucose transporters in whole jejunal tissue. Thomson *et al.* (1986) reported that the intestinal uptake of glucose by the sodium-glucose co-transporter (SGLT1) was increased by dietary fatty acids. From these studies, it was deduced that n-3 PUFAs in the diet influenced the intestinal uptake of molecules transported both actively and passively. Mechanistically, n-3 PUFAs regulate glucose transporter 2 (GLUT2) (Gabler *et al.*, 2007) through its influence on

AMP-activated protein kinase (AMPK) (Suchankova *et al.*, 2005). Supporting this view, Walker *et al.* (2005) reported that the activation of AMPK in murine jejunal tissue resulted in an increase in net glucose flux.

The n-6/n-3 PUFA ratio and human health

Both n-6 and n-3 PUFA are important structural components of the phospholipid cell membranes of tissues; they participate in cell regulation, affect gene expression and contribute to signal transduction. There is, however, competition between n-3 and n-6 PUFA for at least three metabolic enzymes in the animal body, phospholipase A2, cyclooxygenase and lipoxygenase. There is a greater inhibitory effect of n-3 PUFA than n-6 PUFA on fatty acid synthase (Hilakivi-Clarke *et al.*, 2005), so the n-6/n-3 ratio significantly influences the ratio of the ensuing eicosanoids such as prostaglandins, leukotrienes, and thromboxanes, thereby altering the body's metabolic function (Tribble *et al.*, 2006). Several reports (Vancassel *et al.*, 2008; Williams *et al.*, 2011) showed that unbalanced fatty acid intake was a major factor influencing the incidence of cancer of the breast, colon and prostate. Excessive intake of n-6 PUFA in humans, especially linoleic acid (18:2n-6), has been associated with many disorders including cardiovascular disease, cancer, and inflammatory and autoimmune disease (Czernichow *et al.*, 2010). Typical Western diets have n-6/n-3 ratios of 10-30:1, with dramatically higher levels of n-6 (Hibbeln *et al.*, 2006). There is a consensus that a lower n-6/n-3 ratio in food plays a positive role in human health (Kitz *et al.*, 2010).

The currently high n-6 PUFA level in the human food supply is a concern due to the fact that these fatty acids can interfere with the conversion of ALA to EPA and DHA. Furthermore, diets

rich in n-6 PUFA lead to increased AA content in membrane phospholipids, which then results in overproduction of eicosanoids, hence intensifying arterial and other chronic conditions (Simopoulos, 2002). In contrast, consuming less n-6 and more n-3 PUFA may help in decreasing the risk of heart disease and cancer (Simopoulos, 2002). An appropriate balance of dietary n-6/n-3 is therefore very important.

For optimal human health, the recommendation for dietary n-3 PUFA is between 1.8 and 1.9 g/d, and n-6/n-3 PUFA ratio is less than 4:1 (Simopoulos, 1991; BNF, 1992; Sim, 1997; Molendi-Coste *et al*, 2011). Furthermore, the WHO (2003) has recommended consumption of 5-8 % of the total lipid in the form of n-6 PUFA, 1-2 % as n-3 PUFA and with no more than 1 % *trans* fatty acids. Some of the international nutritional organizations, such as The Joint Food and Agriculture Organization/World Health Organization committee, advised nutritional recommendations concerning the n-6/n-3 PUFA ratio, suggesting a value between 5:1 and 10:1, as reported in the International Society for the Study of Fatty Acids and Lipids (ISSFAL, 2004). The recommendations of different international organizations or national healthy committee are provided in Table 1.

It is now widely recommended that long-chain n-3 PUFA consumption should be increased and the n-6/n-3 ratio should be decreased in the human diet. This could be accomplished by increasing the consumption of fish or fish products such as fish oil rich in long-chain n-3 PUFA, or by enriching more traditionally consumed foods such as meat with long-chain n-3 PUFA.

Three common sources of n-3 PUFA in human life

Fish is well known to be a major source of n-3 PUFA, but the availability of sea products often is limited and may be incapable of meeting increasing demands, if the public health recommendations are followed. Fish is relatively expensive compared to pork and the smell and taste of fish or fish oil may be deterrents to increased consumption, so opportunities of using fish or fish oil as the principal n-3 source are limited. Another constraint is the possibility of heavy metal toxicity (in particular mercury, lead, nickel, arsenic, and cadmium) from excessive consumption of fish or fish oil supplements. Vegetable oils including soybean oil can also supply n-3 PUFAs, they are produced in larger volumes and are much cheaper than marine sources of n-3 PUFA for enrichment, with possibly less likelihood of tainting (Romans *et al.*, 1995). As they mainly contain LA and ALA, however, they are unable to satisfy the nutritional requirements for humans. The UK population has been advised to change their diet by modifying the n-3 PUFA content in the major components (meat and milk) of the current UK diet. Pork represents more than 50% of all meat consumed by humans. The proportion of PUFA in intramuscular fat is generally higher than in beef and is more easily modulated by dietary factors (Wood and Enser, 1997). Modifying n-3 PUFA content in meat can be accomplished through feeding domestic animals such as pig feedstuffs rich in n-3 PUFAs. Therefore, researchers have particularly focused on different ways to correct the imbalance between n-6 and n-3 PUFA in pork and pork products.

In summary, people intake n-3 PUFA directly from pork is more efficient and economic than from fish or soybean oil and something like that.

Increasing the n-3 content and decreasing the n-6/n-3 ratio in pork

Pork is one of the most important meat sources for human. The proportion of PUFA in intramuscular fat is generally higher than in beef and is more easily modulated by dietary factors (Wood and Enser, 1997), thereby facilitating opportunity for qualitatively modifying human intake of dietary fat. Coates *et al.* (2009) found that the modest increases in long chain n-3 PUFA intake, resulting from regular consumption of enriched pork, can reduce cardiovascular risk. Changing the diet of pig provides an effective method of increasing n-3 PUFA content and reducing the n-6/n-3 ratio. The main advantages of producing pork rich in n-3 PUFA are described below. (1) Pork represents more than 50% of all meat consumed by humans, it is more traditional and relatively cheap compared with fish or fish products (Ian Givens and Gibbs, 2008); (2) The fatty acid composition in pig lipids can be greatly modified by changing the appropriate oil source in their feed, because dietary fatty acids can be absorbed without hydrogenation changes and incorporated unchanged into tissue lipids. In ruminants, PUFAs are reduced to monounsaturated and saturated fatty acids in the rumen by microbial bio-hydrogenation and only a small proportion escapes to be available for incorporation into tissue lipids (Nurnberg *et al.*, 1998; Wood *et al.*, 1999); (3) Although n-3 PUFA are rich in porcine liver, muscle and lipid, pigs are not recognized as having a nutritional requirement for n-3 fatty acids, so pigs are possibly ideal vehicles for supplying them to humans; (4) Dietary fatty acid are readily incorporated into pig muscle and fat tissues so n-3 PUFA enrichment by adding fish oil, fishmeal or linseed to rations, is much more effective than in ruminants unless the latter are fed using protective coatings (Ashes *et al.*, 1992; Mandell *et al.*, 1997). Feeding n-3 PUFA sources to livestock may lead to tainting of the meat, however, thereby reducing consumer acceptability (Hertzman *et al.*, 1988; Valaja *et al.*, 1992; Wood and Enser, 1997; Buckley *et al.*, 1995); (5) Pig

raising can include outdoor access to green feed, which results in a higher level of n-3 PUFA in intramuscular fat (Nilzén *et al.*, 2001).

In summary, it is quite feasible and practical to increase n-3 PUFA content and decrease the n-6/n-3 ratio in pork as a means of satisfying the public health guidelines for improving human nutrition and health.

Increasing the content of n-3 PUFA and decreasing the ratio of n-6/n-3 by dietary supplementation

Supplementation of the feed with fish oil or fish meal

Previous studies have shown that feeding pigs on a diet containing fish oil leads to significant enrichment of n-3PUFA without detrimentally affecting meat quality (Irie and Sakimoto, 1992; Leskanich *et al.*, 1997) and Otten *et al.* (1993) supplemented with fish oil (5% fish oil) over 13 weeks and significantly enhanced (40%-165% higher) the relative amounts of n-3 fatty acid (EPA and DHA) in skeletal muscles and adipose tissues compared to the control (fed 5% coconut oil). Fish oil can be expensive and its use for supplementation-increases the risk of producing flavor taints and rancidity in meat (Wood *et al.*, 1999). Fishmeal offers a cheaper and more plentiful source of n-3 PUFA than does fish oil, for direct n-3 enrichment of pork (Fontanillas *et al.*, 1998), however, its potential for adverse effects on sensory qualities also limits its use (Emken *et al.*, 1994). Appropriate strategies for avoiding sensory deficits are important and meaningful. Howe *et al.* (2002) used a stabilized tuna fishmeal product (PorcOmega[®] (POM), as a source of DHA for enrichment of pork products and showed that a 5%-10% POM diet can achieve palatable meat with increased content of n-3 PUFA. That study

demonstrated the potential for using suitably processed fishmeal as an alternative source of n-3 PUFA for enrichment of meat. The variable extent of n-3 PUFA incorporation in different tissues, perhaps due to tissue-specific metabolic pathways, indicates the need for additional study. It can be concluded that, with further refinement of fish by-product processing and perhaps the feeding strategy used, there may be promise in meeting the needs of pig industry in providing designer food for humans.

Supplementation with linseed or rapeseed and their oil products

As described for use of fish oil/meal, linseed oil markedly increased the content of n-3 PUFA in pork (Leskanich *et al.*, 1997). Linseed and its by-products contain about one-third oil, of which more than 50% is 18:3n-3 (Enser *et al.*, 2000; Matthews *et al.*, 2000). Many studies have shown that linseed oil, compared to linseed meal, is more efficient in increasing the n-3 PUFA content in muscles of pigs (Cherian and Sim, 1995). Rey *et al.* (2001) found that 0.5% linseed oil could markedly increase intramuscular n-3 PUFA content. Nuernberg *et al.* (2005) reported that pig diets containing 5% linseed oil increased n-3 PUFA content in muscle, heart, and back-fat tissues, without affecting carcass composition and meat quality; dietary linseed oil also significantly reduced the n-6/n-3 ratio (Hoz *et al.*, 2003). Kralik *et al.* (2006) found that 3 and 6% rapeseed oil in pig diets increased the DHA content in muscle tissue, consistent with pigs being able to synthesize DHA. Feeding linseed has advantages over use of the oil because of practicality and its natural content of antioxidants (Cunnane *et al.*, 1990). Kouba *et al.* (2003) found that total n-3 PUFA and the n-3/n-6 ratio increased in muscles of pigs fed a diet containing 6% crushed linseed for up to 100 days; a similar result was obtained by Shepard *et al.* (2000).

Long term (65-day) fed with 3% linseed to pigs increased the content of DHA in pork (Drackley, 2000). Enser *et al.* (2000) reported that dietary linseed increased the liver content, relative to muscle, of both EPA (10-fold) and DHA (20-fold). More recently, Juarez *et al.* (2010) compared three levels of co-extruded flaxseed (5%, 10% and 15%) and three durations of feeding (4, 8 and 12 weeks) on the contents of n-3 fatty acids in pig tissues, and found that feeding higher levels of flax for shorter period (vs. lower levels) for longer periods appeared to be more efficient in increasing n-3 PUFA content in backfat. Key articles using linseed or linseed oil as pig supplementation are listed in Table 2.

From the foregoing studies, it can be concluded that suitable linseed or linseed oil supplementation increase n-3 PUFA content and decrease the n-6/n-3 ratio in muscle and fat without detrimental effects on pork quality. However, the conversion rate of ALA consumed from linseed or linseed oil to EPA and DPA and DHA is different. In addition, the PUFAs were incorporated into tissues through different modes. Nguyen *et al* (2003) reported that in pigs fed diets supplemented with 1%-3% linseed, ALA is stored preferentially in adipose tissue rather in muscles, while EPA, DPA and DHA are preferentially stored in the muscle or organs rather than in the adipose tissue. Musela *et al* (2009) reported that slightly more EPA, DPA and DHA were deposited in the muscle than in subcutaneous adipose tissue. These differences may be due to the different amounts of n-3 PUFA in the diets, different sources of n-3 PUFA , length of feeding and difference in pig genotypes (Cunnane *et al.*,2000; Enser *et al.*, 2000; Kloareg *et al.*, 2007; Musella *et al.*, 2009). In summarary, these feeding practices may provide foods with more desirable lipid composition (decreased n-6/n-3 PUFA ratio), consistent with recommendations for diets for improved human health. As linseed or linseed oil is readily oxidized, the content of

these additives should not exceed a threshold, which depends on the duration of supplementation, dietary antioxidant levels, feed storage and processing conditions of the meat. Additional anti-oxidative compounds such as vitamin E reduce oxidation of n-3 PUFA and are beneficial (Romans *et al.*, 1995). Further research is needed to optimize level and duration of feed supplementation.

Supplementation with genetically-modified plants

The n-3 PUFAs mainly found in plants are linoleic acid (ω -6 18:2, LA) and ALA, respectively, which are essential fatty acids for mammalian diets due to the lack of the biosynthetic enzymes, Δ^{12} and Δ^{15} desaturases, required for their production. LA and ALA serve as precursors for the synthesis of long-chain PUFAs in mammals (Fig. 2). It is interesting to transfer these enzymes into commodity crops as a means of producing higher content of n-3 PUFA. Eckert *et al.* (2006) also reported that co-expression of the borage Δ^6 desaturase and the *Arabidopsis* Δ^{15} desaturase created a soybean crop with omega-3 fatty acids representing over 60% of the fatty acid profile in soybean. Kinney *et al.* (2004) also reported increasing EPA by 20% in soybean seeds after co-expression of five desaturase/elongation enzymes from lower organisms, but this was not obtained in the seeds of transgenic linseed (Fraser *et al.*, 2004). As soybean is one of the most important protein sources of pig feed, using soybeans rich in n-3 PUFA have promise in the pig feed Industry. Corn also is an important pig feed component, and it is promising to use corn rich in n-3 PUFA as a pig feed source if the transgenic corn is produced.

The leaves of *Arabidopsis thaliana* over-expressing Δ^9 , Δ^8 and Δ^5 genes from the alga *Isochrysis galbana*, *Euglena gracilis*, and *Mortierella alpine*, respectively, have higher levels of

long chain PUFA, including EPA as compared to controls (Qi *et al.*, 2004). Feeding pigs with *Arabidopsis* also is beneficial for accumulating n-3 PUFA in pork.

These reports demonstrate that these technologies potentially offer a sustainable and plentiful supply of n-3 PUFA for pigs. However, mass production of these transgenic plants specifically has yet to be established. Plants with balanced n-6 and n-3 ratio and high content of n-3 PUFA have potential market niches in areas of the feed industry.

Rearing method

Apart from supplementation of pig diets with linseed or fish oil, changing the rearing conditions is also an effective method for increasing n-3 PUFA content and decreasing the n-6/n-3 ratio (Kim *et al.*, 2009). The fatty acid composition of porcine intramuscular fat is affected by feed composition (Bosi, 1999; Wood and Enser, 1997). Hansen *et al.* (2006) found that organic diets resulted in a lower proportion of saturated fatty acid (SFA) and monounsaturated fatty acid (MUFA) in muscle; n-3 PUFA was much higher and the n-6/n-3 ratio was much lower than those of the conventional pigs. Similar results were obtained by Hogberg *et al.* (2003). The intramuscular fat content in organic pork was higher than in conventional pork (Sundrum *et al.*, 2000), and the n-6/n-3 ratio is lower than in traditionally reared pigs (Hansen *et al.*, 2006). Lipid oxidation might occur in organic meat indicating the possible benefit of supplementation with vitamin E in feed.

Limiting feed intake also can increase the content of n-3 PUFA in pork. Wi cek *et al.* (2011) reported that restricted feed intake caused slight but favorable changes in the fatty acid profile in pork, namely decreased contents of SFA and increased PUFA. The level of nutrients influences

both the amount of deposited fat and its fatty acid composition. Daza *et al.* (2007) demonstrated that inadequate supply of dietary energy lowers the activity of lipogenic enzymes, resulting in limited synthesis of saturated and monounsaturated fatty acids, which increases the relative proportion of unsaturated fatty acids. The period of limited feed intake was often introduced once during the initial stage of fattening (Kristensen *et al.*, 2004; Heyer and Lebret, 2007; Skiba, 2010; Wi cek *et al.*, 2010). Several studies (Mason *et al.*, 2005; Daza *et al.*, 2007; Wi cek *et al.*, 2010) showed inconsistent results regarding the effect of limiting feeding on the fatty acid profile in muscle and adipose tissue. These differences may be due to the level of restricted feeding and the type of tissues. Given that such an approach seems to be counter-intuitive in an animal production system, the practical feasibility of restricted feeding (extent and duration) remains to be established, and needs to be evaluated economically.

As mentioned earlier, another potential strategy is to use outdoor rearing with access to green feed. Outdoor rearing with access to green feed can improve the meat quality (Nilzén *et al.*, 2001) and significantly increase the content of n-3 PUFA in muscles of the pigs (Rey *et al.*, 2006).

Conventional breeding methods

Like most pig production traits, fatty acid composition is influenced by both genetic and dietary factors. Piasentier *et al.* (2009) and Cameron and Enser (1991) reported that different breeds have different contents of n-3 PUFA and n-6/n-3 ratio, but the dietary effects were larger than the genetic effects, especially on the n-6/n-3 ratio (Cameron and Enser, 1991). Although large changes in fatty acids composition can be achieved more effectively by altering feeding

strategies than selective breeding, it still is feasible to select pigs with high content of n-3 PUFA and lower n-6/n-3 ratio in muscle or adipose tissue without affecting the carcass traits and meat quality (Smet *et al.*, 2004) and to breed them for producing healthier pork rich in n-3 PUFA.

Transgenic pigs

Advances in gene technology have enabled more complete identification of the genes responsible for synthesizing n-3 and n-6 fatty acids in plants and lower organisms. Some of them are responsible for the conversion of n-6 fatty acids to n-3 fatty acids and have been identified in plants, microorganisms and *C. elegans* (Spychalla *et al.*, 1997). One such gene, *fat-1*, identified in *C. elegans*, has been successfully transferred into pigs and mice (Lai *et al.*, 2006; Kang, 2007). The n-6/ n-3 PUFA ratio was dramatically reduced in various tissues compared to controls. Pan *et al.* (2010) also successfully transferred *synthesized fatty acid desaturase-1* gene (*sFat-1*) into pigs from *C. briggsae*. Saeki *et al.* (2004) used microinjection technology to transfer the *fatty acid desaturation II* gene for a Δ^{12} fatty acid desaturase from spinach to pigs which can then express the plant gene for the production of ALA. The expression of those genes in the transgenic pigs can result in more n-3 PUFA and a decreased n-6/n-3 ratio. The white adipose tissues of these transgenic pigs had approximately 20% more ALA than that in wild-type pigs. At the same time, the fat tissue of transgenic pigs also had more LA as compared to that of wild-type pigs. This technology provides opportunities to have adequate amount food products rich in n-3 fatty acids to feed the world population. However, it is still too early to determine consumer acceptability of food products from such transgenic pigs.

Conclusion

The n-6/n-3 PUFA ratio in common Western diets is presently about (10-25):1, which fails to reach well-based recommended level. Enser *et al.* (1996) have extensively studied the fatty acid composition of pork and found that the n-6/n-3 ratio was 7.22, which was also sub-optimal given the recommendations for human diets. There is a need to use a variety of effective methods to increase the content of n-3 PUFA and especially that of EPA and DHA in pork. In order to ensure a more balanced and desirable fatty acid composition of dietary lipids for humans, with attendant health benefits, continued emphasis must be placed on increasing the content of n-3 PUFA and reducing the ratio of n-6/n-3 in pork. So far, the most feasible and acceptable way to enrich the pork with n-3 PUFA has been dietary provision of n-3 fatty acids and selective breeding, with the acceptability of food products from transgenic pigs increased, transgenic method also have useful application in the future.

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Table 1 Recommendations concerning the n-6/n-3 ratio of different international organizations or national health committees

Organization	Recommendation date	The n-6/n-3 ratio
Organization/World Health Organization committee	2004	4:1
WHO	2003	4:1
The sixth revised lipid requirement of Japanese	2000	4:1
Canadian health committee	1998	4-10:1
FAO/WHO human nutritional oil committee	1994	5-10:1
European Community food Scientific Committee	1993	4-4.5:1
Canadian scientific statement committee	1990	5-6:1
English nutrition foundation	1992	6:1

Table 2. Effect of linseed or linseed oil on fatty acid composition in pork

Authors	year	Additives	dosage	Main findings
Beckova and Vaclakova	2010	Ground linseed	13.4%	α -linolenic acid and linolenic acid increased in muscle, n-3 PUFA increased from 1.11 to 3.79g/100g total fat, The n-6/n-3 PUFA ratio in muscle was reduced from 12.36 in control group to 3.83 in linseed group. The n-6/n-3 PUFA ratio in backfat was reduced from 8.76 in control group to 1.97 in linseed group. The SFA/ PUFA ratio was reduced from 3.92 in control group to 2.34 in linseed group. drip loss increased, pH value also increased.
Cai et al	2009	Linseed oil	1.5%, 3.0%	The 1.5% and 3.0% linseed oil diet significantly increased the ALA, EPA and DPA levels, and total n-3 PUFA concentration, and significantly reduced the ratio of n-6/n-3 PUFA. The 1.5% linseed oil diet produced the ratio of n-6/n-3 PUFA in the subcutaneous fat of 4.1:1, and the ratio of 2.5:1 for the 3.0% linseed oil diet.
Corino et al	2008	Whole extruded Linseed	5%	Dietary extruded linseed had no effect on growth, carcass characteristics, meat quality, or the activity of malic enzyme in LM and backfat. Inclusion of linseed increased n-3 PUFA content in both LM and backfat and decreased the n-6/n-3 PUFA ratio from 12 to 4.5 in LM, and from 11 to 3 in backfat.
Cunnane et al	1990	linseed	5%	Increase the content of ALA and EPA, but not of DHA in subcutaneous adipose tissue.
Dannenberger et al	2012	Linseed oil	4.5%	Diets supplemented with linseed oil allow the production of pork meat with a high n-3 fatty acid content (up to 113mg/100g muscle) and low n-6/n-3 PUFA ratio (up to 1.8:1), which is

				beneficial for human nutrition.
Enser <i>et al</i>	200 0	Crushed whole linseed, rapeseed et al.	3.3%	Diet containing linseed significant increases in all n-3 PUFA in muscle. Specifically, the increases were: EPA 100%, ALA 55%, DHA 35%, and DPA 29%. n-6/n-3 ratio decreased to 5(Control: 15.5 g/kg linoleic acid and 1.9 g/kg a-linolenic acid; test: 10 g/kg linoleic acid and 4 g/kg a-linolenic acid)
Eastwood <i>et al</i>	200 9	Flaxseed meal	15%	Significantly increase the n-3 PUFA content in backfat and muscles.
Kralik <i>et al</i>	201 0	sunflower oil, rapeseed oil, linseed oil	2%	Linseed oil increased the n-3 PUFA content and n-3/n-6 ratio in meat. Sunflower oil increased the n-6 PUFA content in meat and increase the n-6/n-3 PUFA ratio. The effect of rapeseed oil is between them.
Haak <i>et al</i>	200 8	Linseed oil Fish oil	1.2% 1.2%	Linseed oil or fish oil added to the diet of pigs had no effect on the meat ultimate pH, drip loss and lipid or color oxidation, fish oil increase the EPA and DHA content in muscle. It seems that the incorporation efficiency of EPA and DHA from fish oil into muscle was much greater than the one of -ALA from linseed.
Hoz <i>et al</i>	200 4	linseed	3%	The content of ALA, EPA and DPA increased, the meat quality is not affected. The n-6/n-3 ratio decreased from 12 to 3 because of an increase in the total content of n-3 PUFA and a decrease in n-6 PUFA.
Huang <i>et al</i>	200 8	linseed	10%	Duration of feeding linseed diet linearly increased the concentration of C18:3n-3, C20:5n-3 and C22:5n-3 and linearly decreased the ratio of n-6/n-3 in the longissimus muscle and backfat.
Juárez <i>et al</i>	201	Co-	5%,	The duration and level of co-extruded flaxseed

<i>al</i>	0	extruded flaxseed	10%, 15%	feeding affected most fatty acids except for 22:6n-3. Increasing the duration of flax feeding led to significant quadratic effects in total n-3 fatty acids, when feeding 5% co-extruded flaxseed. Those increases were linear when feeding 10% and 15% co-extruded flaxseed..
Kouba <i>et al</i>	200 3	whole crushed linseed	6%	The n-3 PUFA content in plasma, muscle, and adipose tissue of pigs increased, but DHA was not altered by diet. The n-6/n-3 ratios in muscle decreased (3.00 vs. 7.34 and 3.11 vs. 8.71, respectively, for pigs fed 60 and 100 d) and adipose tissue (2.05 vs. 6.30 and 2.07 vs. 6.39, respectively, for pigs fed 60 and 100 d). Organoleptic characteristics, oxidant and color stability of pork were not affected.
Liu <i>et al</i>	200 6	linseed	10%	The n-3 PUFA content and n-3/n-6 ratio increased as the adding time extended, at last, n-3 PUFA content arrived 7.13 g/100 g (control 1.11 g/100 g), n-3/n-6 ratio arrived 1:2.63 (control 1:13.92).
Lu <i>et al</i>	200 8	Linseed oil	3%	Dietary linseed oil significantly increased the contents of C18:3 and C18:2 in the neutral lipids and phospholipids in both longissimus muscle and biceps brachii muscle, respectively. Feeding 3% linseed oil did not deleteriously affect the flavour of cooked longissimus muscle.
Luo <i>et al</i>	200 9	linseed	10%	Dietary linseed significantly increased the content of n-3 PUFA in muscle, which lead to increase the content of IMF.
Matthews <i>et al</i>	200 0	linseed	5%	Dietary linseed (5%) decreased the n-6:n-3 ratio from 7.2 to 3.5 without affecting carcass or meat quality.

Morel <i>et al</i>	200 6	Soybean oil linseed oil Vitamin E	4% 2% 0.01%	Dietary soybean oil and linseed oil significantly increased the PUFA in muscle and back fat, but bring a slight oxidation, Vitamin E reduce the extent of lipid oxidation in meat.
Musella <i>et al</i>	200 9	Whole extruded linseed	5%	The content of n-3 in muscle and fat increased significantly, the n-6/n-3 ratio decreased from 12 in control to 3 in test group without affecting the meat quality.
Nolan <i>et al</i>	199 5	Linseed	10%	The content of ALA in muscle arrived 23.16%.
Nuernberg <i>et al</i>	200 5	Linseed oil	5%	The content of n-3 fatty acids and the n-3/n-6 ratio increased significantly in muscle, heart, and back fat tissues, without affecting carcass composition and meat quality.
Riley <i>et al</i>	200 0	Linseed	3%	The n-6/n-3 ratios decreased (3.9 with a 3% linseed diet vs. 8.5 with a control diet) in muscle and (3.2 with a 3% linseed diet vs. 8.4 with a control diet) adipose tissue.
Roman <i>et al</i>	199 5	linseed	15%	Increase in the quantities of DHA (approximately +200%) in the inner and outer layers of subcutaneous adipose tissue in light pigs fed diets with linseed at 15% (3.5% ALA) for different lengths of time(7, 14, 21, or 28d).
Santos <i>et al</i>	200 8	linseed	3%	The contents of EPA and DHA and the ratio of n-3/n-6 in muscle of light pigs increased.
Sheard <i>et al</i>	200 0	Linseed	10%	Total n-3 PUFA increased and n-6: n-3 ratio decreased without adversely affecting normal eating quality parameters.

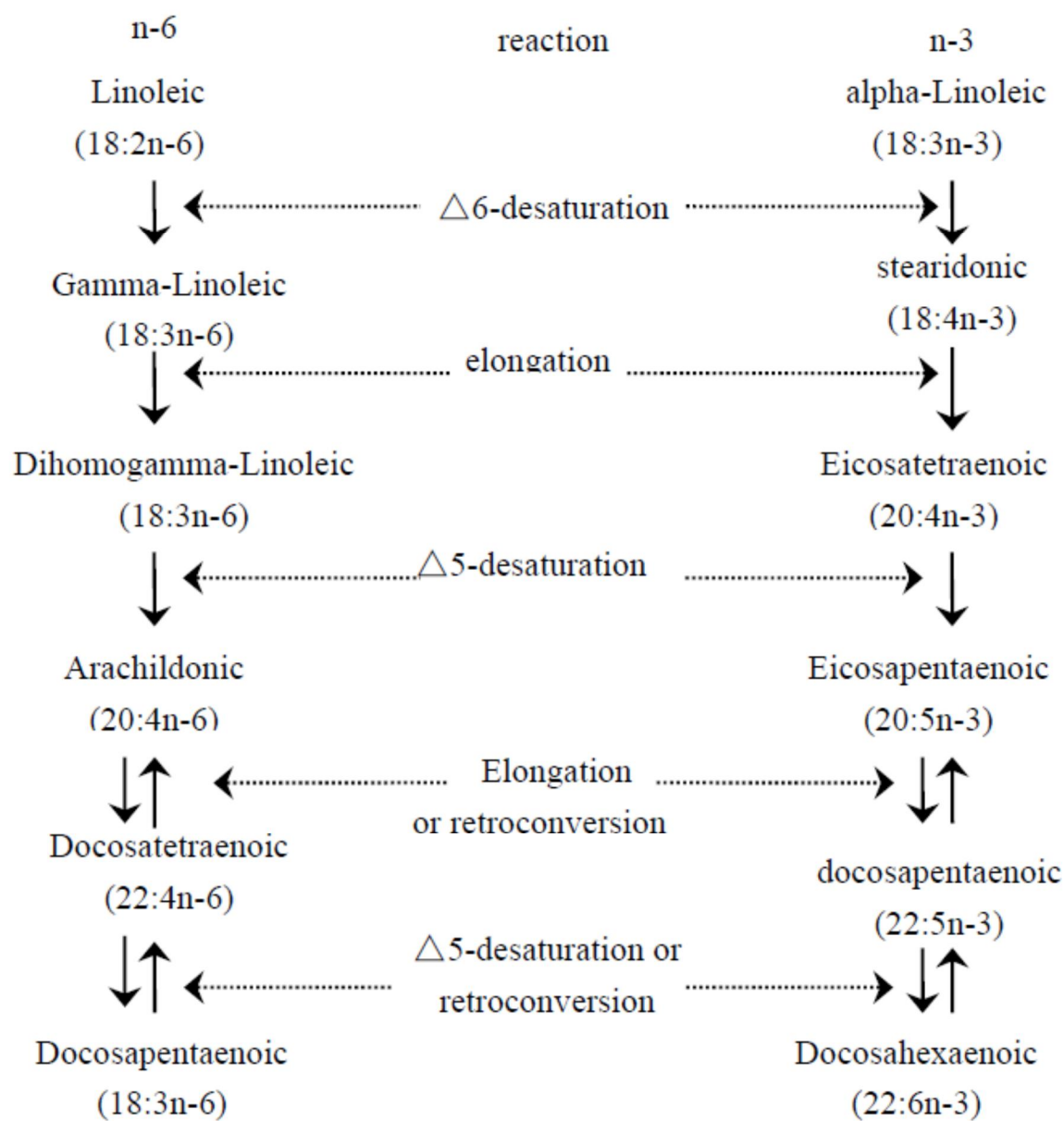


Figure 1. n-3 PUFA synthesis and transformation pathways in animal tissue from Bezard *et al.*, 1994; Wall *et al.*, 2010)

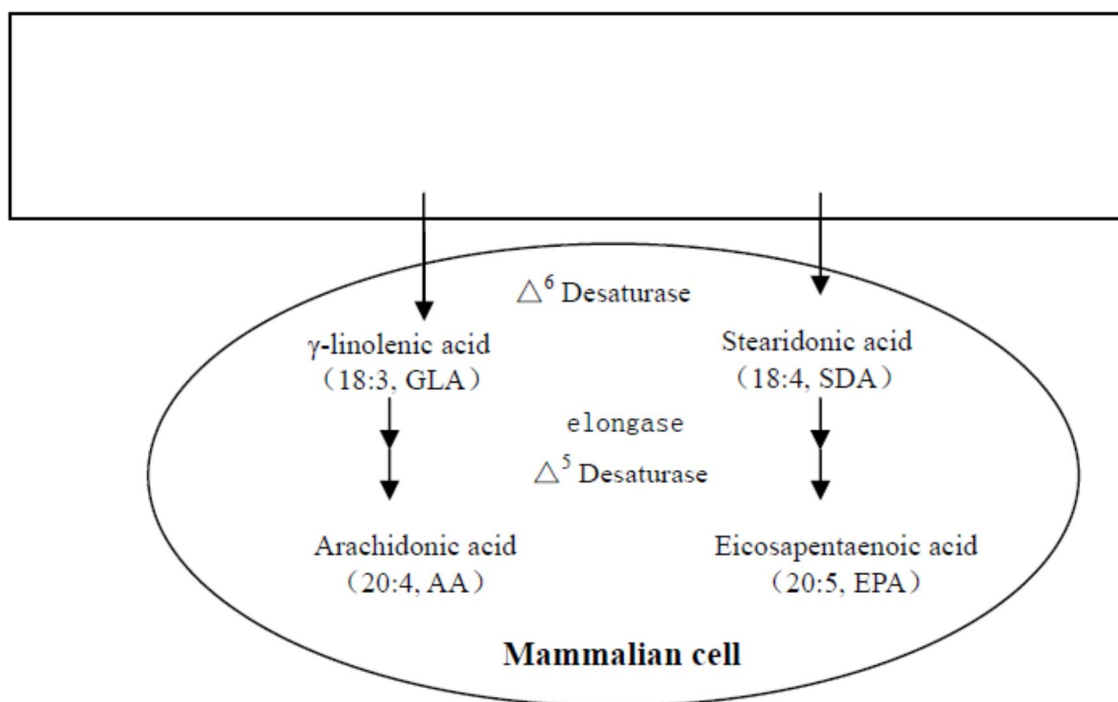


Figure 2 Desaturation and elongation steps for n-6 and n-3 PUFA (Adapted from ursin 2003; Eckert *et al.*, 2006)