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Review

Recent advances in the use of fatty acids as supplements in pig diets: A review

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ABSTRACT

The lipids in feed commonly fed to pigs consist mainly of neutral fats (specifically triglycerides), esters of fatty acids and glycerol. The degree of unsaturation, the length of the carbon chains and the isomeric form of the fatty acids greatly influence both the physical and the chemical characteristics of fat. In swine nutrition, fats are traditionally introduced in diets as a high-energy constituent; moreover, they also supply liposoluble vitamins and essential fatty acids. In addition, the efficiency of using metabolisable energy from lipids is very high, with a minimum heat increment compared to the other nutrients. Recently, nutritionists have become interested in specific fatty acids for their potentially beneficial physiological effects on metabolism in the intestinal mucosa, and anti-microbial, anti-inflammatory and immunomodulatory activity and functional food design. The following are examples of fatty acids that show these favourable effects: short- and medium-chain fatty acids, omega-3 fatty acids conjugated linoleic acid, and they will form the basis of this review.

Contents

Abbreviations: AA, arachidonic acid; ALA, α-linolenic acid; CLA, conjugated linoleic acid; DHA, docosahexaenoic acid; EFA, essential fatty acids; EPA, eicosapentaenoic acid; Ig, immunoglobulin; SFA, saturated fatty acids; MCFA, medium-chain fatty acids; LA, linoleic acid; LPL, lipoprotein lipase; LT, leukotrienes; MUFA, monounsaturated fatty acids; NSP, non-starch polysaccharides; PGE, prostaglandins; PBMC, peripheral blood mononuclear cell; PPARγ, peroxisome proliferator receptor activator gamma; PUFA, polyunsaturated fatty acids; SCFA, short-chain fatty acids; TNF, tumour necrosis factor; TX, thromboxanes.

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1. Introduction

Fats and oils have assumed considerable importance as raw materials in animal feed due to their ability to provide energy. Nutritionally, they are concentrated sources of energy, providing essential fatty acids (EFA) that are the building blocks for hormone-like compounds (eicosanoids) and are carriers for the liposoluble vitamins A, D, E, and K. Moreover, their physical textures reduce dust in feed mills and increase diet palatability (Wiseman and Garnsworthy, 1997).

The lipids in feedstuffs commonly fed to animals are derived from the storage and structural lipids of animals and plants. More than 90% of dietary lipids are in the form of triacylglycerols, which are composed of a glycerol molecule esterified with 3 molecules of fatty acids.

Fatty acids contribute from 94 to 96% of the total weight of different fats and oils. The length of the carbon chains, the degree of unsaturation and the isomeric form of fatty acids greatly influence both the physical and the chemical characteristics of fat. Fatty acids can be classified as saturated fatty acids (SFA), which contain no double bonds, monounsaturated fatty acids (MUFA), which feature one double bond, and polyunsaturated fatty acids (PUFA), which contain multiple double bonds (ISEO, 2006).

In swine nutrition, fats are traditionally introduced in the diet as high-energy constituents (NRC, 1998). Furthermore, the efficiency of using metabolisable energy from lipids is very high (Noblet et al., 1994) and they have a minimum heat increment compared to other nutrients, reducing summer heat stress (Stahly, 1984).

In addition to the general importance of fat as an energy source, the EFA content is important for maintaining correct body function. Linoleic acid (C18:2 ω-6) and α-linolenic acid (C18:3 ω-3) are essential PUFA because they cannot be synthesised from the body. These acids are the parent compounds of the ω-6 and ω-3 families, respectively (Rooke et al., 2003).

Recent studies have shown that there are several fatty acids that appear to improve body function and may be important to some physiological processes. For this reason, many nutritionists have begun to focus their attention on specific fatty acids for use in feed manufacturing, for their consequent benefit for animal health and for derived products for human consumption (functional food design).

The following fatty acids are discussed in the present study: short- and medium-chain fatty acids for their trophic effect on intestinal mucosa and anti-microbial activity, activity, and ω-3 fatty acids and conjugated linoleic acid for their anti-inflammatory and immunomodulatory activities and for functional food design.

2. Short- and medium-chain fatty acids

Fatty acids with a chain of less than six carbon atoms are called short-chain fatty acids (SCFA), and fatty acids with aliphatic tails of six to twelve carbon atoms are called medium-chain fatty acids (MCFA). The SCFA are the major end products of bacterial fermentative reactions in the colon and are the principal anions in the hindgut of mammals (Pluske et al., 1999). In the absence of dietary supplementation, the concentration of SCFA in the colon is usually within the range of 58–69 mmol/kg of dry matter (DM), although fibre-rich diets may elevate the endogenous production of organic acids to 84–98 mmol/kg of the DM (Hedemann and Bach Knudsen, 2007). The molar ratio of acetate to propionate to butyrate is 50:42:8 in the anterior section of the small intestine and 65:18:17 in the posterior section of the small intestine (Williams et al., 1997), however this ratio will also change depending predominately on the type of diet.

Non-starch polysaccharides (NSP) largely escape digestion in the small intestine and are fermented to different extents by caecal and colonic bacteria (Jensen, 2001). NSP are a major part of dietary fibre, and some studies have reported that increasing fermentable carbohydrate content through the inclusion of wheat middlings, sugar beet pulp, native starch (Bikker et al., 2007; Carneiro et al., 2007) or inulin (Wellock et al., 2008) stimulates SCFA production, enhancing lactic and butyric acid levels in the small and large intestines. Hogberg and Lindberg (2006) reported that diets with different NSP levels (from 147 to 250 g/kg DM) and solubility altered the molar proportions of lactic acid and SCFA as well as the molar proportions of acetic, propionic and butyric acids in the stomach, ileum, caecum and colon of piglets. A recent study indicated that supplementation of a piglet's diet with wheat bran (40 g/kg) and sugar beet pulp (20 g/kg) increases the total amount of SCFA in the colonic digesta (Hermes et al., 2009).

If SCFA and MCFA are supplied as supplements in pigs' diets, the form of SCFA and MCFA supplied is also important due to the weakly acidic nature of these compounds. Given the nature of SCFA and MCFA, pH is considered a primary determinant of efficacy because it influences the concentration of undissociated acid (Davidson, 2001). Evidence of absorption of SCFA and MCFA across the stomach wall in pigs was reported by Argenzio and Eisemann (1996) and was found to depend on the p*K*a of the acid (values at which 50% of the acid molecules are in dissociated form) and on the luminal pH. Dierick et al. (2002) reported that in the upper small intestine, about 80% of the MCFA may be exerting bacteriostatic and bactericidal properties. This characteristic is associated with the much higher antimicrobial strength of the acid undissociated form. As a consequence, several forms of SCFA and MCFA are commercially available, including both uncoated and coated acid products. Uncoated products are powders or liquids that are used to supplement feed or drinking water; however, the

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uncoated acids are easily absorbed by the host, and no effects are expected in the hind parts of the gastrointestinal tract (Thompson and Hinton, 1997; Claus et al., 2007). SCFA and MCFA can be impregnated in or coated on micropearls, from which they are released slowly during transport through the gastrointestinal tract. In these coated or encapsulated products, mineral or lipid carriers are used. One aim of coating or encapsulation is to carry the acids down to the intestinal tract without dissociation in the stomach. The coating or encapsulation of SCFA and MCFA also helps to address bioactivity towards distal parts of the intestine and effectively modulates the intestinal microbiota and mucosal morphology in pigs (Mroz et al., 2006; Defoirdt et al., 2009).

Both SCFA and MCFA have shown physiological activities in the following:

2.1. Cellular metabolism and trophic effect on intestinal mucosa

Usually, colonic enterocytes derive 60–70% of their energetic requirement from SCFA, particularly from butyrate, and Scheppach et al. (1992) has reported that a reduced capacity of intestinal mucosa to oxidise butyrate has been implicated in the pathogenesis of ulcerative colitis. Furthermore, butyrate and propionate are essential for maintaining the normal metabolism of intestinal mucosa (Kruh et al., 1994), regulating cellular growth and proliferation (Treem et al., 1994). Indeed, SCFA derived from a diet supplemented with 10 g/kg tributyrin and 3 g/kg of lactitol (alone or in combination) showed a positive effect on both caecum crypt depth and ileal villus length in piglets (28 days of age). The lactic acid concentration in the caecum was higher in animals fed a lactitol diet than in animals fed other dietary treatments (Piva et al., 2002). Butyric acid, originating from fermented lactitol or from tributyrin, could not be measured due to the rapid absorption rate of *n*-butyrate by the intestinal mucosa; however, shorter crypt depths in pigs fed the supplemented diets were indicative of an availability of *n*-butyric acid for antiproliferative activity (Von Engelhardt et al., 1998). In addition, Gálfi and Bokori (1990) observed that the presence of 1.7 g/kg of sodium butyrate in the diet resulted in a substantial increase in the number of cells (33.5%) constituting the microvilli as well as in the length of microvilli (30.1%) in the ileum of growing pigs.

The increase of crypt cell proliferation, induced by SCFA, can also be explained by the trophic effect of butyrate, which acts through mechanisms not yet completely understood (Blottieres et al., 1999). The effect of SCFA is not restricted to the colon, and SCFA also stimulates cell proliferation and growth of the small intestine. This effect on distant mucosa is likely mediated by a systemic mediatory mechanism (Sakata and Inagaki, 2001).

2.2. Intestinal microbiota

Both SCFA (propionic acid and butyric acid) and MCFA (caprylic acid and caproic acid) have direct antimicrobial activity against *Salmonella typhimurium in vitro*, and a dietary supplementation of 2 g/kg of coated butyrate decreased faecal shedding of *S. typhimurium* in 6-week-old piglets (Boyen et al., 2008). The same study reported that uncoated butyric and caproic acid are rapidly absorbed by epithelial cells along the gastro-intestinal tract so that they are unable to influence *Salmonella* excretion. Messens et al. (2010) reported the effect of MCFA (sodium caproate, sodium caprylate and sodium caprinate) on *Salmonella* and other microbial populations in an *in vitro* caecum model. A dose of 15 mM of sodium caproate had no relevant effect on bacterial populations, while a clear *Salmonella*-inhibiting effect was found with sodium caprylate. Earlier, Skrivanova et al. (2004) found that caprylic acid was the only *Salmonella*-inhibiting compound among 15 fatty acids tested in liquid cultures. SCFA derived from the diet are able to decrease gastro-intestinal pH, which may prevent the colonisation of Enterobacteriaceae (*Escherichia coli*, *Salmonella* spp.) and may stimulate health-promoting bacteria such as *Lactobacillus* (Canibe and Jensen, 2003). Bergsson et al. (2002) suggested that at low pH, the outer lipopolysaccharide membrane of Gram-negative bacteria becomes less dense, allowing MCFA to penetrate into the cell membrane and dissociate into anions once internalised into the neutral pH of the cell cytoplasm. This generation of anions presents problems for bacteria that must maintain a near-neutral cytoplasmic pH and causes cellular energy depletion (Davidson, 2001). A recent study indicated that minimal inhibitory concentration values depend on chain length and are lower for Gram-negative than Gram-positive bacteria (Thormar and Hilmarsson, 2007).

2.3. Immune system

Butyrate has been found to profoundly impact the immune system (Weber and Kerr, 2006). One mechanism acting via butyrate (2 mM sodium butyrate) may modulate the immune response *in vitro* by increasing the expression of the suppressor of cytokine signalling in peripheral blood mononuclear cells (PBMC) (Weber and Kerr, 2006). Another mechanism in which butyrate (1 mM sodium butyrate) could impact lymphocyte function is through a cAMP-dependent pathway (De Castro et al., 2005). In summary, the anti-inflammatory mechanism of butyrate is related to its ability to differentially regulate cytokine expression and secretion by porcine PBMC.

2.4. Growth performance in the post-weaning phase

Due to the above-mentioned activities, SCFA and MCFA may be useful in post-weaning piglets because weaning is considered a stressful event that is associated with depressed feed intake, growth performance and elevated incidence of enteric disease (Odle et al., 1996). At weaning, the feed is suddenly changed from sow milk to pelleted dry feed; however, the gut

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secretory capacity is not yet capable of digesting the new diet, and a marked reduction of feed intake generally occurs in the in the first few days. This reduction causes a diminished small intestine overall mass and mucosal component with dramatic reduction of the intestinal villi (Pluske et al., 1997; Owusu-Asiedu et al., 2003). The villus atrophy impairs digestive and absorptive functions of the gut, contributing to poor performance after weaning (Pluske et al., 1997). After weaning, piglets are often susceptible to diarrhoea and immunodepression (Van Beers-Schreurs et al., 1998; Frydendahl, 2002), resulting in both lower daily weight gain and higher mortality. During the last decade, much research has been directed towards increasing intestinal SCFA and MCFA content through different nutritional strategies, especially in post-weaning piglets (Decuypere and Dierick, 2003). Manzanilla et al. (2006) reported that in early-weaned piglets, dietary sodium butyrate (0.3 g/kg) improved feed efficiency. Furthermore, Kotunia et al. (2004) reported an improvement in growth performance of nursery piglets that received milk formula supplemented with sodium butyrate (3 g/kg of dry matter). In addition, Gálfi and Bokori (1990) reported a positive influence on body weight gain and feed conversion rate in pigs fed diets containing 1.7 g/kg of sodium butyrate. The use of feed supplement containing SCFA and MCFA is proposed as a valuable alternative to in-feed antibiotics and can be used to promote growth as well as serve as a preventive and curative treatment for gastrointestinal diseases (Mroz, 2005; Decuypere and Dierick, 2000).

3. Omega-3 fatty acids

EFA are fatty acids that cannot be made endogenously by humans and other animals; therefore, they must be obtained exogenously from dietary sources (Beare-Rogers et al., 2001). There are two families of EFA: ω-3 (or omega-3 or n-3) and ω-6 (omega-6 or n-6). Linoleic acid (C18:2 ω-6; LA) and α-linolenic acid (C18:3 ω-3; ALA) are the parent compounds of the ω-6 and ω-3 families, respectively (Rooke et al., 2003). Many vegetable oils, such as corn, sunflower and soybean oils, are rich in ω-6 fatty acids, mainly as LA, but linseed is a rich source of ALA. In humans, dietary ALA can be metabolised to long-chain eicosapentaenoic (EPA) and docosahexaenoic acid (DHA) in the liver (Holub, 2002). This conversion is limited, and in humans, it is estimated that only 8% of ALA is converted to EPA and even less to DHA (less than 4%) (Burdge et al., 2002). In pigs, it was estimated that only 40% of dietary ALA was deposited in the body. Of this quantity, 63% was deposited as ALA, 28.5% was metabolised to EPA and 0.9% to DHA, which suggests that this conversion is more efficient in pigs than in humans (Kloareg et al., 2007).

Commonly available dietary sources of EPA and DHA include certain types of algae, fish oils and seafood. Table 1 shows the EFA content of some vegetable and fish oils. In swine diets, the ratio of ω-6/ω-3 can fluctuate from 4:1 to 11:1 and is related to feed composition. This ratio tended to be high in feed composed of cereal grains and raw protein materials, which are naturally rich in ω-6 fatty acids (Wilfart et al., 2004). Haak et al. (2008) reported ω-6/ω-3 ratios of 8:1, 2.5:1 and 1.5:1 in pig diets based on barley, wheat and soybean meal that differed with respect to the inclusion of animal fats, fish oil and crushed linseed, respectively. Kouba et al. (2003) reported ω-6/ω-3 ratios of 7:1 and 1:1 in both a control diet (composed of wheat, soybean meal, barley and fat blend) and a high-linseed diet, which contained 6% whole crushed linseed, respectively. The dietary inclusion of vegetable oils, such as rapeseed oil, is able to decrease the ω-6/ω-3 ratio to 4.7:1 (Htoo et al., 2008).

The ω-3 PUFA play a critical role in human health in relation to their anti-atherogenic, anti-thrombotic, anti-carcinogenic, and anti-inflammatory activities; they also contribute to improvements in cardiac and vascular functions (Simopoulos, 2009). However, the prevalence of health problems in farm animals is related to acute respiratory or gastrointestinal diseases rather than chronic problems. The ω-3 PUFA activity in modulating mediators of humoral and cellular immunity may present many possible benefits in livestock.

In pig nutrition, the following physiological properties are of major interest:

Table 1
Essential fatty acid content (g/100 g) of a number of selected vegetable oils, fish oils and marine algae.

	LA ω-6	ALA ω-3	AA ω-3	EPA ω-3	DHA ω-3
Vegetable oils[a]					
Linseed oil	15.5	53.1	–	–	–
Sunflower oil	64.9	0.3	–	–	–
Rapeseed oil	20.5	9.8	–	–	–
Soybean oil	53.1	7.4	–	–	–
Palm oil	9.9	0.3			
Fish oils[a]					
Salmon oil	1.2	0.6	0.9	12	13.8
Sardine oil	1.3	0.9	1.6	16.9	21.9
Anchovy oil	1.1	0.8	0.3	18.3	8.5
Cod liver oil	1.3	0.5	1.1	11	10.8
Herring oil	1.1	0.7	0.3	6.8	5.8
Menhaden oil	1.1	0.8	0.6	12.2	7.9
Dried marine algae[b]	0.3	0.25	–	6.9	17.1

[a] Adapted from INRA (2002).
[b] Adapted from Sardi et al. (2006).

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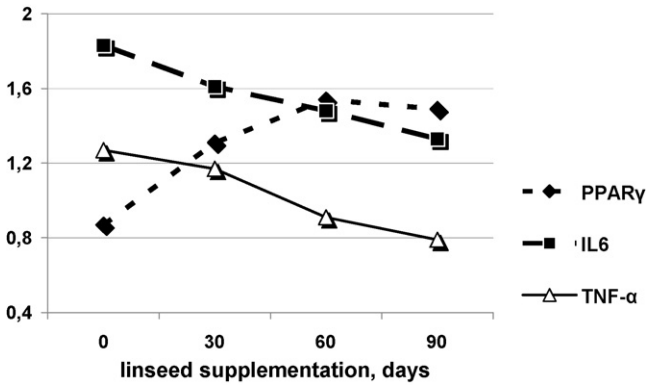

Fig. 1. Effect of dietary supplementation with linseed on swine muscular PPARγ, TNFα and IL-6 gene expression. Adapted from Zhan et al. (2009).

3.1. Modulation of inflammatory response

Both ω-6 and ω-3 fatty acids are stored in cell membranes and have two primary functions: as structural components and as substrates for the production of eicosanoids, such as prostaglandins (PGE), thromboxanes (TX) and leukotrienes (LT) (Calder, 2007). The PUFA ω-6 and ω-3 metabolic pathways are linked, and they are metabolised by the same set of Δ^6 and Δ^5 desaturases and elongases; therefore, they compete for the same set of enzymes. The LA is converted to arachidonic acid (AA, 20:4, ω-6), which is the precursor of the 2 series of PGE and TX as well as the 4 series of LT. ALA is converted to EPA (20:5, ω-3), which is the precursor of the 3 series of PGE and TX as well as the 5 series of LT. The long-chain fatty acids AA and EPA are also converted to their respective eicosanoids, which play an important role in atherosclerosis, coronary heart disease, bronchial asthma, and other inflammatory conditions (Das, 2006). The PGE of the 2 series regulates the production of pro-inflammatory cytokines, whereas the PGE of the 3 series results as anti-inflammatory eicosanoids (Bagga et al., 2003). To encourage the production of anti-inflammatory PGE and to discourage the production of inflammatory PGE, AA should be reduced in the diet, and an appropriate amount of ω-3 fatty acids should be consumed (Boyce, 2007). The substitution of lard with menhaden fish oil (70 g/kg feed) in the sows' late gestation and lactation diet reduced *in vitro* eicosanoid release by nursing piglets' immune cells (Fritsche et al., 1993). In addition, Lauridsen et al. (2007) reported a lower production of the 2 series of PGE and TX in the alveolar macrophages of suckling piglets from sows fed 80 g/kg of fish oil.

In addition, ω-3 PUFA and their metabolites are natural ligands for peroxisome proliferator receptor activator gamma (PPARγ). PPARγ is known to play a fundamental role in immune response through its ability to inhibit the expression of inflammatory cytokines and to direct the differentiation of immune cells towards anti-inflammatory phenotypes (Martin, 2009). Marion-Letellier et al. (2008) reported that ω-3 PUFA not only reduced the secretion of the pro-inflammatory cytokines interleukin 6 and 8, but also enhanced the expression of PPARγ. Data from a recent trial (in pigs fed 100 g/kg of linseed) have documented a decrease of tumour necrosis factor-α (TNF-α) gene expression through a PPARγ-dependent mechanism (Huang et al., 2008). In addition, Zhan et al. (2009) reported that the supplementation of pigs' diets with 100 g/kg of linseed causes increased expression of PPARγ and a decrease of TNF-α expression in muscle (Fig. 1).

3.2. Improvement in reproductive performance

Swine nutritionists have focused primarily on the effect that ω-3 PUFA may have on litter size, piglet pre-weaning mortality and boar fertility. Mateo et al. (2009) reported that piglets born and reared on sows fed a diet supplemented with ω-3 PUFA (10 g/kg of a marine source of ω-3 from day 60 of gestation to day 21 of lactation) have a higher weight at weaning compared to controls. In the same study, a higher concentration of colostral immunoglobulin (Ig) of class G in sows fed ω-3 PUFA diets was observed. In addiction, Rooke et al. (2001a) reported a decrease in piglets' pre-weaning mortality in animals born from sows fed 16.5 g/kg of salmon oil from mating to weaning.

Pig spermatozoa contain a significant amount of DHA, and it is probable that DHA is essential for optimal fertility in boar. Supplementation of boars' diets with 30 g/kg of tuna oil, containing 25% DHA, may improve sperm characteristics, including concentration, vitality and the proportion of spermatozoa with progressive motility and a normal acrosome score (Rooke et al., 2001b).

3.3. Improvement in nutritional characteristics of meat and meat products (functional foods)

In Western diets, ω-6 fatty acids are the predominant PUFA and the increased ω-6/ω-3 ratio most likely contributes to a high incidence of cardiovascular disease as well as inflammatory disorders (Simopoulos, 2009). The importance of ω-3 PUFA in the diet and the need to return to a more physiological ω-6/ω-3 ratio (of about 5:1) rather than the ratio provided by

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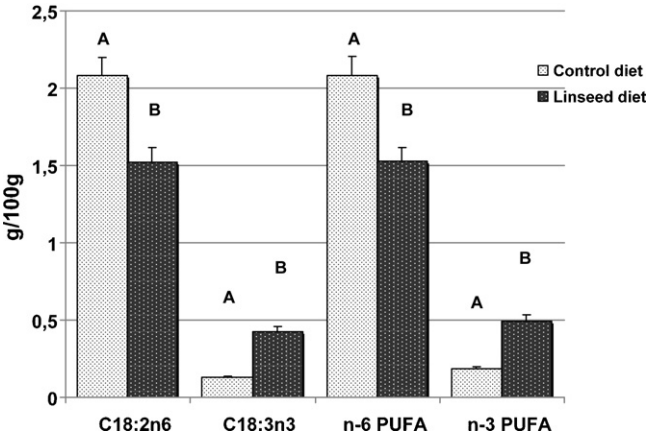

Fig. 2. Effects of linseed supplementation on fatty acid content of a whole slice of dry-cured ham (A, B differ for P<0.01). Adapted from Musella et al. (2009).

the current Western diet is now clear (EFSA, 2010). The consumer, for health reasons, increasingly prefers products with a higher PUFA content (especially ω-3 fatty acids) because of their beneficial effects in preventing certain diseases; therefore, there has been much interest in ways to manipulate the fatty acid composition of meat in order to produce functional food (Coates et al., 2009). It is possible to enhance the concentration of beneficial ω-3 PUFA in pig tissues through the use of different fat sources in feed because lipids in the meat of monogastric animals reflect the nature of dietary fat (Wood et al., 2003). However, the technological and sensory characteristics of pork meat are affected by its fatty acid profile. The dietary supplementation of ω-3 PUFA (50 g/kg extruded linseed) leads to meat suitable for fresh consumption but not for long time-cured pork, due to oxidative phenomena (Cannata et al., 2010). In swine, linseed and its by-products are often chosen as a source of ω-3 fatty acids because ALA, which is readily available in linseed, is less susceptible to oxidation; therefore, it produces fewer quality and storage problems than fish oils fatty acids (Van Oeckel et al., 1996). Moreover, supplementation of fish oils and fish products can be costly and increases the risk of flavour taints and rancidity in the meat (Wood et al., 1999). The ω-3 PUFA supplementation requires an adequate amount of antioxidants that can be incorporated into pig diets to avoid the oxidative phenomena.

The long-term feeding of pigs with 25 g/kg rapeseed oil increased ALA content in the *Longissimus Dorsi* muscle as well as in the seasoned ham (Corino et al., 2002c; Pastorelli et al., 2003). Corino et al. (2008a) and Musella et al. (2009) also reported an increase in ALA and EPA content and a reduction in the ω-6/ω-3 ratio in meat for fresh consumption (*Longissimus Dorsi* muscle) as well as in dry-cured product (Parma ham) from pigs fed 50 g/kg of extruded linseed (Fig. 2).

Taking into account the fact that in the EU, the per capita pork meat consumption per year is about 43.4 kg (Eurostat, 2007), ω-3 enriched pork products could help consumers meet health recommendations without having to change their dietary habits. Additional studies are needed to clarify the source and the optimal amount of dietary ω-3 PUFA to improve the pork fatty acid profile without affecting the technological and sensory characteristics of the meat and meat products.

4. Conjugated linoleic acid

Conjugated linoleic acids (CLA) are a group of positional and geometric isomers of linoleic acid that are characterised by the presence of conjugated dienes and differ in both the position and the stereochemistry of their double bonds. Naturally occurring CLA originate mainly from bacterial isomerisation and biohydrogenation of PUFA in the rumen and the desaturation of *trans*-fatty acids in the adipose tissue and mammary gland (Griinari and Bauman, 1999). Several CLA isomers are abundant in foods derived from ruminants, and in beef and dairy products, 80% of the CLA isomers are represented by the *cis*-9, *trans*-11 isomer (Fritsche and Steinhardt, 1998). In synthetic CLA preparations, which are used in dietary supplements and as functional food ingredients, the *cis*-9, *trans*-11 and *trans*-10, *cis*-12 isomers predominate, often in 1:1 ratios (Larsen et al., 2003). These two isomers, which have been used in experimental studies as a mixture, represent the most widely investigated CLA isomers.

Interest in CLA arose in its anticarcinogenic action, but there is an increasing amount of scientific literature concerning the biological effects and properties of CLA (Belury, 2002; Pariza, 2004). Numerous biological effects of CLA are due to the separate action of the most studied isomers, *cis*-9, *trans*-11 and *trans*-10, *cis*-12. It is also likely that some effects are induced and/or enhanced by these isomers acting synergistically. Although the *cis*-9, *trans*-11 isomer is mainly responsible for anticarcinogenic effects, the *trans*-10, *cis*-12 isomer reduces body fat, and it is referred to as the most effective isomer affecting blood lipids. With regard to the immune system, it is not clear whether individual isomers of CLA may act similarly or differently (Churruca et al., 2009). Some detrimental effects of the *trans*-10, *cis*-12 isomer have also been reported in terms

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of altered blood lipid composition and impaired insulin sensitivity in humans (Tricon et al., 2005). At present, evidence regarding the effectiveness of CLA in humans is not clear, and isomer-specific effects need further investigation.

Nutritional regulation by CLA in pigs represents a novel and important approach in relation to the following factors:

4.1. Effect on growth performance

The effects of CLA on pig growth performance are controversial (Dugan et al., 2004; Corino et al., 2006) and are related to animal weight as well as the dose and length of CLA supplementation. Only one study has reported an improved average daily gain after increasing CLA levels from 1.2 to 10 g/kg (as a replacement of corn) in pig diets (Thiel-Cooper et al., 2001). Improved feed conversion efficiency in pigs was observed when CLA levels (55% total CLA, 25% *cis*-9, *trans*-11 and 30% *trans*-10, *cis*-12 isomers) in pigs' diets were increased from 1.25 to 10 g/kg (as a replacement to soybean oil) (Ostrowska et al., 1999). In addition, Wiegand et al. (2002) reported that the dietary substitution of soy oil with 12.5 g/kg of CLA (60% total CLA, 27% *cis*-9, *trans*-11 and 20% *trans*-10, *cis*-12 isomers) improved feed conversion efficiency in pigs.

In contrast, Dugan et al. (1997) reported that 20 g/kg feed (50% total CLA, 15% *cis*-9, *trans*-11 and 6% *cis*-8, *trans*-10 isomers) of CLA supplement (as a replacement of sunflower oil) did not improve growth performance in pigs from 61 to 106 kg of live weight. Furthermore, our previous study in heavy pigs with a slaughter weight of about 160 kg demonstrated no effect of 7.5 g/kg (50% total CLA, 24.5% *cis*-9, *trans*-11, 25.5%. *trans*-10, *cis*-12 isomers) of dietary CLA oil (as replacement to sunflower oil) on growth performance (Corino et al., 2008b).

4.2. Influence on lipid metabolism

CLA have many interesting and unique biological properties compared to common unsaturated fatty acids. Among the biological effects of CLA is the reduction of fat deposition in various mammalian species (Domeneghini et al., 2006; House et al., 2005). A reduction of acetyl-CoA carboxylase activity was observed in the adipose tissue of pigs fed 5 g/kg of dietary CLA (65% total CLA, half *cis*-9, *trans*-11 and half *trans*-10, *cis*-12) from 97 to 170 kg of live weight (Corino et al., 2003). Moreover, an *in vitro* study reported a decrease in the expression of the lipoprotein lipase (LPL) gene in stromal vascular cell cultures from adipose tissue treated with 50 mmol/L of a CLA mixture (Zhou et al., 2007). The plasma triacylglycerol concentration was increased in pigs fed CLA, suggesting lower uptake of lipids (Ostrowska et al., 1999).

One way of decreasing fat deposition is to decrease the proliferation of preadipocytes, as observed in the adipose tissue of heavy pigs supplemented with 7.5 g/kg of CLA oil (50% total CLA, 24.5% *cis*-9, *trans*-11, 25.5% *trans*-10, *cis*-12 isomers) (Corino et al., 2005; Di Giancamillo et al., 2007). A decrease in adipocyte size and an increase in adipocyte apoptosis have also been reported (Corino et al., 2005; Di Giancamillo et al., 2009).

CLA feeding may be associated with changes in the expression of key genes for fatty acid metabolism. In particular, the decreased expression of sterol CoA desaturase (SCD) may increase the SFA level in the adipose tissue of pigs, as observed in pigs fed 5 g/kg feed of CLA (Corino et al., 2003). In a recent study, we observed that the antiadipogenic effects of CLA are associated with both a decrease in leptin content and the enhancement of a noradrenergic mechanism, possibly via enhanced catecholamine release at the local level (Di Giancamillo et al., 2009). To better understand the mechanism of action of the two isomers and provide insight into the regulation of adipose tissue metabolism, additional studies on the CLA-altered fat stores are needed.

4.3. Immune system modulation

There is evidence to support an immunological effect of CLA isomers in different species (Sebedio et al., 1999). An increase in the colostral IgG, IgA and IgM concentrations in sows supplemented with 5 g/kg of CLA powder (32% *cis*-9, *trans*-11 and 31% *trans*-10, *cis*-12 CLA isomers in free fatty acid form) as well as in the serum IgG concentration of nursing piglets was observed by Corino et al. (2009) (Fig. 3). This result confirmed the immunomodulatory effects of CLA isomers in piglets fed 5 or 10 g/kg of dietary CLA (65% total CLA half *cis*-9, *trans*-11 and half *trans*-10, *cis*-12) as described by Corino et al. (2002a); a similar finding was reported by Bontempo et al. (2004) in sows fed 5 g/kg feed of CLA powder (32% *cis*-9, *trans*-11 and 31% *trans*-10, *cis*-12 CLA isomers in free fatty acid form) and in nursery piglets. Furthermore, dietary CLA supplementation showed an improvement in non-specific immunity (Corino et al., 2002a; Bontempo et al., 2004) and also in the anti-inflammatory activity, associated with the inhibition of AA biosynthesis and PPAR activity, like PUFA ω-3 (Turek et al., 1998). There is also evidence that CLA increases lymphocyte proliferation (Chew et al., 1997) and CD8 lymphocyte subsets in pigs (Bassaganya et al., 2001; Lai et al., 2005).

4.4. Improvement of technological and nutritional characteristics of meat and meat products (functional foods)

The increase in SFA levels in the adipose tissue of pigs fed CLA is fundamental to improving fat firmness as well as for obtaining a dry-cured product of high quality (Dugan et al., 2004). Moreover, the effect of CLA on adipose fatty acid composition also improves the oxidative stability of meat, as observed in the *Longissimus Dorsi* muscle of CLA-fed pigs (Corino et al., 2002b, 2003).

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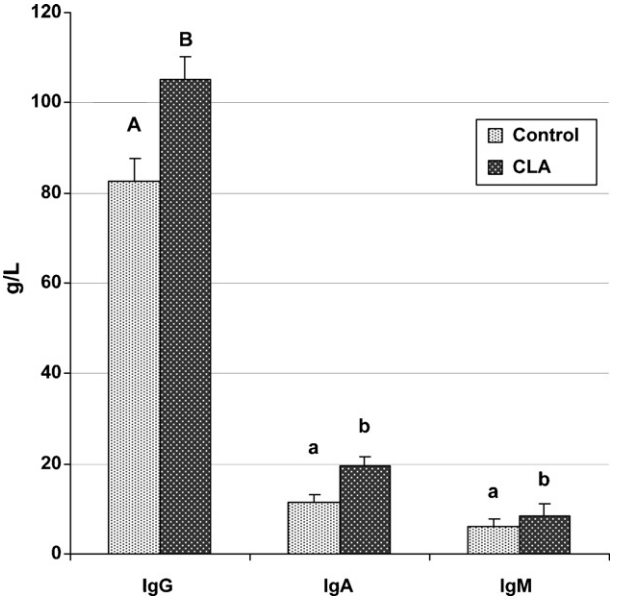

Fig. 3. Colostrum immunoglobulins G, A and M concentration in sows given a control diet or 5 g/kg CLA diet from 7 days before parturition (a, b differ for P<0.05; A, B differ for P<0.01).
Adapted from Corino et al. (2009).

An indirect indicator of fat firmness is the iodine value; therefore, it a measure of unsaturation. Some producers, according to the disciplinary of dry-cured production, recommend a maximum iodine value of 70 for pig subcutaneous adipose tissue to avoid fat quality problems (soft fat). A reduction in the iodine value of 9.1 and 6.8% (compared to a control) was observed in pigs fed 2.5 and 5 g/kg feed of CLA from 97 to 170 kg of live weight (Corino et al., 2003). The same result (−6.7% compared with control) was observed in a subsequent study in pigs supplemented with 7.5 g/kg of CLA for 3 months (Corino et al., 2005).

Given the ability of swine to accumulate relatively high amounts of CLA in their tissues, pork and pork products could become an important vehicle for the delivery of significant amounts of CLA to consumers. Pastorelli et al. (2005) reported an improvement of *cis*-9, *trans*-11 CLA (+75%) and *trans*-10, *cis*-12 CLA (+85%) content in the *Longissimus Dorsi* muscle of pigs fed 2.5 and 5 g/kg feed of CLA. Such results are also evident in fat and muscle of the dry-cured Parma ham from pigs fed 2.5 g/kg feed of CLA (Lo Fiego et al., 2005). The use of a commercial CLA mixture containing both isomers increases their concentration in meat and dry-cured products. The *trans*-10, *cis*-12 CLA isomer, present in a large amount in synthetic mixture and in a negligible amount in food from natural sources, is considered to be "man-made". At present, the use of the single isomer *cis*-9, *trans*-11 as a supplement should be preferred.

5. Conclusion

The biological activities of the above-mentioned fatty acids could be used to improve different phases of swine production. The trophic effect on the intestinal mucosa and the antimicrobial activity of SCFA and MCFA might be beneficial in some circumstances for the preventive and curative treatment of gastrointestinal diseases in the post-weaning piglet. The immune modulation activity of ω-3 PUFA and CLA might improve health and welfare during lactation, post-weaning and reproductive phases. Dietary ω-3 and CLA in the fattening phase may increase the nutritional properties of pork and pork products, which should be recognised as functional foods with new health properties.

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