# Intramuscular fatty acid profiles in farm animals vis-a-vis meat eating and nutritional quality: A Review

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# Abstract

In regards with fast growing meat consumption in modernizing countries in the 20<sup>th</sup> Century, recommendations for a public healthier eating were formulated. It is assumed that an increasing consumption of meat whose fat composition is considered too high in saturated fatty acids (SFA) and too low in Polyunsaturated fatty acids (PUFA), constitutes a public health hazard. The main health risk associated with consumption of meat rich in SFA is that they are reported to contribute to the development of cardiovascular disease in human. This paper aims to review the existing information on some of the most important aspects of intramuscular fatty acid composition and metabolism in farm animals. Trends in healthy eating resulted in selection for leaner animals that has characterized the meat production systems in developed countries, affecting *de facto* meat eating and technological indices. Similar predictions would be drawn for emerging societies thus; more reflections are needed to deal with human health aspects of meat, without affecting its eating quality and technological processing.

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# Introduction

Meat has been identified, often wrongly, as a food having a high fat content and an undesirable balance of fatty acids (Wood and Enser, 1997). This has, in the last half of the 20th Century, attracted considerable investigations on the animal fats, especially for their impact on the human health. Subsequent attention has focussed on the intramuscular fat (IMF) content and composition, as this fat depot is the most closely related to eating quality and healthiness of meat (Tarrant, 1992).

Efforts have been made in controlling the IMF deposition and its fatty acid composition. Particularly, research nowadays has focused on the IMF long chain (LC) polyunsaturated fatty acids (PUFA) as they are of particular relevance to human health requirements. For instance, meat with a high ratio (equal or above 0.4) of PUFA to SFA is considered suitable for human consumption (Department of Health, 1994). It has been suggested that there is more PUFA and MUFA in IFM of beef than other beef fat (Troy et al.,2017). It is assumed that, there is an increasing tendency in the consumption of meat, poultry and other animal products around the globe, following an increasing number of urbanized populations (WHO, 2003). With meat being considered too high in saturated fatty acids (SFA) and too low in Polyunsaturated fatty acids (PUFA), particularly in the long chain (LC) n-3 PUFA, this consumption behaviour remains a public health issue. High levels of saturated fatty acids are considered to predispose consumers to several of the so-called `Diseases of Western Civilisation', notably coronary heart disease (Department of Health, 1994). On the other hand, meat and meat products with higher content in PUFA are prone to rapid oxidative deterioration under refrigeration and freezing during cooking or generally under different processing conditions (Rubén et al., 2019 Love and Pearson, 1970;). Such oxidation can result in production of secondary products such as Malondialdehyde which negatively affects the meat aroma and flavour (Rubén et al., 2019).

Thus, efforts to find ways of controlling in vivo the intramuscular composition of meat in farm producing animals, is more needed to safeguard the healthy consumption of meat in modern societies. However, trends in healthy eating have created a demand for leaner meat (Tarrant, 1992) and, this has resulted in a decline of the fat content which subsequently has adversely affected eating quality and further meat processing (Wood et al., 1996; Tarrant, 1992).The aim of this paper was to review existing knowledge on some of the most important aspects of fatty acid composition and metabolism in farm animals, with emphasis on the factors controlling fat deposition, de novo synthesis of saturated fatty acids (SFA) and the enzymatic elongation

and desaturation pathways responsible for endogenous synthesis of unsaturated FA. The review is however limited to the major fatty acids in intramuscular fat and to the most important indices used in relation to human health considerations, i.e. the P/S ratio (calculated as (C18:2n-6 + C18:3n-3)/(C14:0 + C16:0 + C18:0) and the n-6/n-3 ratio (calculated as the sum of n-6 PUFA/ the sum of n-3 PUFA, including longer chain PUFA (C20-C24)).

# Brief description of fatty acids in animal fats

Fatty acids are hydrocarbons and principal components of most lipids (Gutnikov, 1995).

The naturally occurring fatty acids can be grouped on the basis of the presence of double (=) or sometimes triple  $(\equiv)$  bonds into two broad classes termed saturated and unsaturated fatty acids (Gurr et al., 2002). The most unsaturated fatty acids (UFA) in meat fat may contain one ore more double (ethylenic) bonds and can be into separated monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) (Lobb, 1992). An UFA with a double bond can have two possible configurations, "cis" or "trans", depending on the relative position of the alkyl groups. Most naturally occurring UFA have the cis orientation (Lobb; 1992). Because of their low melting points, UFAs are essential to maintain the gross fluidity of adipose tissue and the fluidity of phospholipids in membranes (Enser, 1984). The polyunsaturated fatty acids are generally categorized into  $\omega$ -6 (n-6) and  $\omega$ -3 (n-3) families (Bézard et al., 1994), depending on the position of the second double bond being a function of the biochemical system (Gurr et al., 2002; Lobb, 1992;). These fatty acids are assembled in different fat (lipid) groups, the most occurring in animal tissues being triacylglycerols, phospholipids and cholesterols (Gurr et al., 2002; Enser, 1984;). Always start with the most recent publication/reference

### Fat content and fatty acid composition in muscle tissues of farm animals

Intramuscular fat (IMF) refers to the fatty acids present in the intramuscular adipose tissue and in the muscle fibres (Cameron & Enser, 1991). High content in IMF in muscle fibers is also termed as marbling fat in muscle and is associated with increased eating quality of meat (Wood et al.,2004). The level of marbling has been used to grade meat into different categories and it is used as criteria for meat export in different countries (Lonergan et al., 2019). It is currently difficult to increase IMF in muscle and in parallel keep amount of visible fat at minimum level because consumers perceive increased visible fat as an unhealthy sign on meat (Teye et al., 2006). There is a direct positive relationship between meat with IMF above 3 % and eating qualities such as tenderness,

juiciness and flavour (Daszkiewicz et al., 2005). Studies on the effect on IMF on water holding capacity (WHC)

of meat are inconsistent (Watanabe et al., 2017), and the increased IMF at a maximum level of 3.5 % increases acceptability of meat by consumers (Fernandez et al., 1999). Fat content and composition in meat and meat products vary greatly according to the animal species, age of the animal, part of the carcass used and animal feeding, with the later offering relatively good results in singlestomached animals, such as pigs and poultry (Valsta et al., 2005; De Smet et al., 2004;). However, it is widely documented that fat comprises mostly monounsaturated and meat saturated fatty acids (Wood et al., 2008; Valsta et al., 2005).

Available data on muscle and fat tissues indicate that adipose tissue has much higher fatty acid content than muscle fibres but, the fatty acid composition of the two tissues is broadly similar (Wood et al., 2008; Enser et al., 1996;). The major lipid class in adipose tissue (>90%) is riacylglycerol or neutral lipid while in muscle fibres, a significant proportion is phospholipid, which has a much higher PUFA content in order to perform its function as a constituent of cellular membranes (Wood et al., 2008). A a result, long chain n-3 and n-6 PUFA are found in phospholipid but are also detected in pig and sheep muscle neutral lipid and adipose tissue (Cooper et al., 2004; Enser et al., 2000;).

It was reported (Table1) that pigs have much higher proportions of the major PUFA C18:2n-6 in both tissues than cattle and sheep (Wood et al., 2008; Wood and Enser, 1997; Enser et al., 1996). Proportions of linoleic acid (LA, C18:2n-6) in pig are however largely reported to be higher in adipose tissue than muscle (Teve et al., 2006a, 2006b). On the contrary, they were found to be similarly distributed in both tissues by Wood et al. (2008). Subsequently, higher incorporation of LA (C18:2n-6) into pig muscle compared to that of ruminants, produces higher levels of AA (C20:4n-6) by synthesis and, the net result is a higher ratio of n-6/n-3 PUFA in pig compared to beef and lamb (7.22, 2.11 and 1.32 respectively) ( De Smet et al., 2004; Enser et al., 1996; Wood and Enser, 1997;). On the other hand, the ratio of all PUFA to saturated fatty acids (P/S), the target for which is 0.4 or above, is much higher and beneficial so, in pigs (0.58) and other monogastrics, compared with the ruminants (0.11 for beef, 0.15 for lamb) (Kouba et al., 2003; De Smet et al., 2004).

Fatty acid	Beef	Lamb	Pork	
C12:0 (lauric acid)	2.9	13.8	2.6	
C14:0 (myristic acid)	103	155	30	
C16:0 (palmitic acid)	962	1101	526	
C18:0 (stearic acid)	507	898	278	
C18:1-trans	104	231	_	
C18:1-cis (oleic acid)	1395	1625	759	
C18 :2n-6 (linoleic acid)	89	125	302	
C18 :3n-3 (α-linolenic acid)	26	66	21	
C20:3n-6	7	2	7	
C20:4n-6 (arachidonic acid)	22	29	46	
C20:5n-3 (eicosapentaenoic acid)	10	21	6	
C22:5n-3 (docosapentaenoic acid)	16	24	13	
C22:6n-3 (docosahexaenoic acid)	2	7	8	
Total	3835	4934	2255	
P/S 1	0.11	0.15	0.58	
$n-6/n-3^{2}$	2.11	1.32	7.22	

Table1. Fatty acid content of loin muscle (mg/g) in steaks or chops purchased from four supermarkets (Enser et al., 1996; Wood and Enser, 1997).

<sup>1</sup> P/ S: polyunsaturated / saturated fatty acid ratio, i.e. (C18:2n-6 + C18:3n-3)/ (C12:0+C14:0+C16:0)

<sup>2</sup> n-6/ n-3 ratio: calculated as the sum of n-6 PUFA/ the sum of n-3 PUFA, including longer chain PUFA (C20-C24)).

Ruminant meat is described as the most saturated, as a result of enzymatic bio-hydrogenation of unsaturated dietary fatty acids in the rumen (Wood and Enser, 1997; Valsta et al., 2005). For human consumption safety, recommendations for a healthier FA composition of diets and their constituents have been formulated to meet with meat production requirements, e.g. the PUFA/ SFA ratio (or P/ S ratio) should ideally be above 0.45 and the n-6/n-3 PUFA ratio should preferably be inferior to 4 (Department of Health, 1994; Enser et al., 1996).

The second most important PUFA is  $\alpha$ -linolenic acid ( $\alpha$ -LNA, C18:3n-3), with higher proportions in adipose tissue than muscle (Wood et al., 2008). Muscle contains also significant proportions of long chain (C20-22) PUFAs which are formed from  $\alpha$ -LNA (C18:3n-3) (Enser, 1984; De Smet et al., 2004). The important product of this pathway is eicosapentaenoic acid (EPA, C20:5n-3), which has various metabolic roles including eicosanoid production (Wood et al., 2008). It has to be mentioned that variations in these values are controlled by genetic or feeding factors, and should thus not be generalised (De Smet et al., 2004).

Values for the fatty acid composition of *longissimus dorsi* muscle neutral lipid and phospholipid in pig, indicate that oleic acid (C18:1*cis*-9), the major fatty acid in meat, was much more predominant in neutral lipid. This fatty acid is formed from stearic acid (C18:0) by the enzyme stearoyl Co-A desaturase, a major lipogenic enzyme. On the other hand, LA (C18:2n-6) was found at much higher proportions in phospholipid than neutral lipid (De Smet et al., 2004).

# *De novo* synthesis of fatty acids

Fatty acids are synthesized *in vivo* from any body component "primer" which yields a two-carbon acetyl unit during its metabolism (Enser, 1984), as displayed below;

CH<sub>3</sub>CO-S-CoA + 7HOOC-CH<sub>2</sub>-CO-S-CoA + 14NADPH +14H+

 $\underbrace{\phantom{a}}_{14NADP+}C_{15}H_{31}COOH + 7CO_2 + 6H_2O + 8CoASH + 14NADP +$ 

Figure1. Overall equation for *de novo* fatty acid synthesis (Enser, 1984).

De novo lipogenesis occurs in the cytosol (Drackley, 2000), in which two enzymes are involved: acetyl-CoA carboxylase (ACC) and fatty acid synthetase (FAS) (Enser, 1984; Drackley, 2000; Enser, 1984). Both of them are complexes and catalyze multiple reactions (Gurr et al., 2002). Acetyl-CoA carboxylase adds carbon dioxide to acetyl-CoA (also to 3-hydroxybutyrate in lactating mammary gland of ruminants) to yield malonyl-CoA. The malonyl group and an acetyl group are then transferred from CoA to the fatty acid synthetase complex and condensed to give acetoacetyl-S-enzyme with the release of the carbon dioxide. The enzyme system then carries out sequentially the reduction of the ketoacyl group, dehydration of the hydroxyacyl group and reduction and hydrolysis of an enoyl group (Drackley, 2000; Enser, 1984). The main sites of lipogenesis are adipose tissues and liver, where the major product is palmitic acid (Enser, 1984; Beitz and Nizzi, 1997). In pigs, the lipogenesis activity is more intense in liver than in adipose tissue for piglets before weaning age

Thus, the C18:2n-6/ C18:3n-3 ratio in membrane phospholipids is generally higher than in triacylglycerols, reflecting the preferential deposition of LA (C18:2n-6) in phospholipids and the more equal partitioning of  $\alpha$ -LNA (C18:3n-3) in triacylglycerols and phospholipids, compared to other PUFA (De Smet et al., 2004; Demirel et al., 2004; Wood et al., 2004). On the contrary, the overall n-6/n-3 ratio of membrane phospholipids is lower than the C18:2n-6/C18:3n-3 ratio due to the preferential synthesis of longer chain fatty acids of the n-3 series over the n-6 series (Enser et al., 1998; Wood et al., 2004).

# Fatty acid metabolism in farm animals

Deposited lipids in farm animals originate mostly from dietary fatty acids and *de now* synthesized fatty acids (Warnants et al., 1999; Drackley, 2000; Lizardo et al., 2002). However, variations in dietary fat have no significant effect on fatty acid metabolism in pig (Ding et al., 2003). Consequently, dietary fat has no influence on the composition of *de novo* synthesized FA throughout growth (Lizardo et al., 2002) and by far, on the intramuscular fatty acid content (Enser et al., 2000).

(Fenton et al., 1985), but this becomes the inverse after weaning, where more than 80 % of fatty acids are synthesised *de novo* in adipose tissues, from dietary glucose (O'Hea and Leveille 1969, Chiliard et Ollier 1994, Mourot et al., 1999). In this view, the pig is distinguished from other monogastric species, where *de novo* lipogenesis is mostly occurring in liver tissue.

# Enzymatic synthesis of mono-unsaturated fatty acids

# Role of the stearoyl-CoA desaturase ( $\Delta 9$ desaturase)

The  $\Delta 9$  desaturase complex (EC1.14.99.5), a microsomal enzyme (Enser, 1984; Ozols, 1997) catalyses, in microsomes and peroxisomes, the conversion of SFA in their corresponding MUFA, e.g. palmitic acid (C16:0) and stearic acid (C18:0) to cis-9 palmitoleic acid (cis-9 C16:1) and cis-9 oleic acid (cis-9 C18:1) respectively (Sprecher, 2000; Siebert et al., 2003). The reaction requires acyl-CoA, NADH, NADH-reductase and cytochrome b<sub>5</sub> (Strittmatter et al., 1974), and shows the maximum velocity on the stearic acid (Enser, 1984; Ozols, 1997). For this reason, acetyl-CoA desaturase ( $\Delta 9$ desaturase enzyme) is often referred to as stearoyl-CoA desaturase (SCD) (Siebert et al., 2003). The major product of  $\Delta 9$  desaturation in animal tissues is oleic acid, with smaller quantities of palmitoleic acid (Enser, 1984). Acetyl-CoA carboxylase is under short-term metabolic control and longer-term hormonal and dietary regulation (Oshino and Sato, 1972; Enser, 1984; Ozols, 1997).

# Role of the elongase enzyme

Since palmitic acid is the major product of fatty acid synthetase, except in the mammary gland, other

mechanisms are required to produce longer or shorter fatty acids (Enser, 1984). Two elongation pathways exist which extend the chain by 2C unit at a time, predominantly in the endoplasmic reticulum membrane. In the mitochondria, the elongation process uses acetyl-CoA and NADH or NADPH for reduction and fatty acyl-CoA substrates in the range of C10 – C14, while in the microsomes, it uses malonyl-CoA and NADPH as source of two additional carbon atoms, acting on C16 and longer chain fatty acids (Enser, 1984; Sprecher, 2000; Siebert et al., 2003). The microsomal fraction, unless using malonyl-CoA, is distinct from fatty acid synthetase which is a cytosolic enzyme (Enser, 1984). Fatty acids can also undergo shortening by sequential removal of two carbon units (Enser, 1984).

# Omega-3 and omega-6 long chain PUFA metabolism

The most important PUFA belong to n-6 and n-3 PUFA groups, and are derived from their respective metabolic precursor's linoleic acid (LA, C18:2n-6) and  $\alpha$ -linolenic

acid (a-LNA, C18:3n-3) (Bézard et al., 1994). Vertebrates lack  $\Delta 12$  and  $\Delta 15$  ( $\omega 3$ ) desaturases and so cannot form C18:2n-6 and C18:3n-3 from C18:1n-9. Therefore, C18:2n-6 and C18:3n-3 cannot be synthesized de novo by animal cells and hence, must be provided as essential fatty acids (EFA) in the diets (Enser, 1984; Bézard et al., 1994; Tocher et al., 2003). These dietary essential fatty acids can be further desaturated and elongated to form the physiologically essential C20 and C22 PUFA, arachidonic acid (AA, C20:4n-6), eicosapentaenoic acid (EPA, C20:5n-3) and docosahexaenoic acid (DHA, C22:6n-3) (Bézard et al., 1994; Sprecher, 2000). Two possible routes for the production of C22:6n-3 from C20:5n-3 and C22:5n-6 from C20:4n-6 are described (Fig.4), where  $\Delta 6$ ,  $\Delta 5$  fatty acid desaturases and malonyl-CoA-dependant chain elongase are critical enzymes (Bézard et al., 1994; Sprecher et al., 1995; Tocher et al., 2003; Agaba et al., 2004).

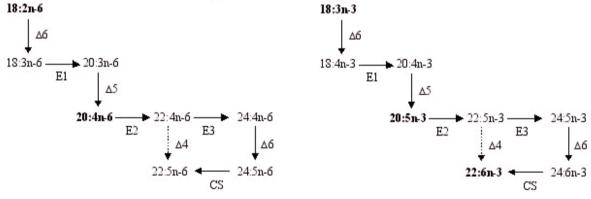


Figure2. Pathways for the biosynthesis of C20 and C22 PUFA from C18:2n-6 and C18:3n-3 (Bézard et al., 1994; Sprecher et al., 1995; Tocher et al., 2003; Agaba et al., 2004).

 $\Delta 6$ ,  $\Delta 5$  and  $\Delta 4$  represent microsomal fatty acyl desaturase activities, E1, E2 and E3 denote microsomal fatty acyl elongase activities and CS denotes peroxisomal chain shortening ( $\beta$ -oxidation). The dotted lines indicate secondary pathways for which there is no direct evidence in vertebrates (Drackley, 2000; Tocher et al., 2003).

Reactions occur in the microsomal fraction of the adipose cells and the same enzymes act on the n-3 and the n-6 fatty acid series (Bézard et al., 1994; Drackley, 2000). Originally the insertion of the last,  $\Delta 4$ , double bond in C22:6n-3 was assumed to occur through direct  $\Delta 4$  desaturation of its immediate precursor C22:5n-3 (Tocher et al., 2003). It has been however shown in rat liver that, the C22:5n-3 is further chain elongated to C24:5n-3 which is then converted by  $\Delta 6$  desaturase enzyme to C24:6n-3, then by a chain shortening reaction in the peroxisomes, to C22:6n-3 (Sprecher et al., 1995). This pathway has also been demonstrated in pigs (Li et al., 2000), in baboons (Su et al., 1999 a, b) and in humans (Burdge and Wootton, 2002). There is a competition for desaturase and elongase enzyme activities between n-6 and n-3 PUFA, with however a preference for the n-3

PUFA synthesis pathway (Mohrhauer and Holman, 1963), in which  $\Delta 6$  desaturase appears to be the ratelimiting step (Sprecher et al., 1995; Sprecher, 2000; Burdge and Wootton, 2002). Long chain PUFA are important in membrane structure as major components of phospholipids for the integrity and fluidity of intracellular and plasma membranes. In this regard, they modulate activity of membrane-bound receptors, enzymes, molecule carriers and ionic channels (Kinsella, 1991; Bézard et al., 1994).

# Inner factors affecting the variation in intramuscular fatty acid composition: Effect of fat content on intramuscular fatty acid composition

The overall fat content of the animal and muscle have an important impact on fatty acid proportions because of the different fatty acid compositions of neutral lipids and phospholipids (Wood et al., 2008). In pig, IMF content was reported to be positively correlated to the total and most of the individual SFA and MUFA proportions, while showing a negative relationship with all PUFA proportions, except C18:3n-3, leading to a decrease in the P/S ratio (Cameron and Enser, 1991; De Smet et al., 2004). In lean animals or animals fed a low energy diet, the lower cis-9 C18:1 and higher C18:2n-6 content of phospholipids has a major influence on total muscle fatty acid composition (Wood et al., 2008). There are evidences that animals with a lower IMF content do have lower de novo fatty acid synthesis and consequently, show greater relative incorporation of the strictly essential dietary fatty acid C18:2n-6 into their tissues.

### Genetic variability Breed differences

Breeds or genetic types with a low concentration of total lipid in muscle, in which phospholipids are in high

proportion, present higher proportions of PUFA in total lipid (Wood et al., 2008). Also, leaner breeds are notable in having high muscle lipid (marbling fat) content relative to subcutaneous fat compared with other breeds (Cameron et al., 2000). Evidences showed breed significant source of variation for both the thioesterase. stearoyl-CoA desaturase and elongase indices in the longissimus muscle of pigs (Zhang et al., 2007) and of cattle (Oka et al., 2002).

Breed differences reported for beef meat are often confounded by differences in fatness. Several authors made corrections for the effect of fatness by including it as a covariate in the statistical analyses or compared breeds at similar carcass fat levels, and still found significant differences in individual fatty acid concentrations between breeds, as well as in the triacylglycerols and in the phospholipids fraction (De Smet et al., 2004). Specific differences breed in the n-6/ n-3 ratio and in the levels of longer chain fatty acids C20: 5n-3 and C22:6n-3 that probably could not be attributed to differences in the fat level, have also been reported in cattle (Choi et al., 2000).

#### Implication of major genes

Some major genes may also be implicated in genetic variability on fat content and fatty acid composition (De Smet et al., 2004). In pig, only minor effect of the stresssusceptibility genotype on the subcutaneous and intramuscular fatty acid profiles were found by Piedrafita et al. (2001) and De Smet et al. (2004) while Hartmann et al. (1997), reported a significantly higher P/S ratio in muscle and adipose tissue for stress-susceptible pigs compared to normal pigs. But, the genotype effect in this case might take into consideration a confound effect of fat content variations (De Smet et al., 2004), since relatively small differences in fatty acid composition were

found between pigs with and without the RN- allele (Johansson et al., 2002). Polymorphisms in the H-FABP gene have also been associated with variability in intramuscular fat content, largely independent of backfat thickness (Gerbens et al., 1999; Gerbens et al., 2000). In a QTL mapping study, Pérez-Enciso et al. (2000) pointed out that, the metabolism and (or) deposition rate of C18:2n-6 in pig, is under control of a OTL situated on chromosome 4. Also, in cattle, the Belgian Blue beef breed is well known for its extreme carcass leanness and the accompanying high P/S ratio in the intramuscular fat, due to the high selection effort on conformation and to the associated high frequency of double-muscled animals caused by a mutation in the myostatin gene. The intramuscular fatty acid composition was examined in the three myostatin genotypes (double-muscling, *mh/mh*; heterozygous, mh/+; normal, +/+) by Raes et al. (2001). Results suggested a markedly higher P/S ratio as well as higher proportions of LA (C18:2n-6), α-LNA (C18:3n-3), EPA (C20:5n-3) and Docosapentaenoic acid (DPA, C22:5n-3), for the double-muscled animals compared with the normal and heterozygous ones.

### Quantitative genetic variations

Within-breed, quantitative genetic variations in the proportion of the major FA in backfat and intramuscular fat were reported in several studies. Sellier (1998) and Cameron and Enser (1991) cited a high heritability of the intramuscular lipid content (h2 around 0.50 and 0.53 respectiely) and of subcutaneous fat firmness traits related to FA composition in pig. Average heritabilities for the major intramuscular fatty acids are estimated between 0.25 and 0.50, except for C18:0 and C18:3n-3 with values of 0.73 and 0.62 respectively (De Smet et al., 2004; Cameron and Enser, 1991). Similarly, heritability ranging between 0.24 and 0.73 for C18:2n-6 was found for intramuscular FA by Cameron and Enser (1991).On the other hand, negative correlations between C16:0,C18: 0 and C18:1 proportions and carcass lean weightwere found, at genetic and phenotypic level, whereas the proportion of C18:2n-6 showed opposite correlations for the inner layer for IMF (Cameron, 1990; Cameron and Enser, 1991).

Reports of genetic parameters for fatty acid composition traits in other species are scarce. Heritability estimates for individual fatty acids and their summations, desaturation and elongation indices, melting point and marbling were reported to be low to moderate (0.14-0.33), in adipose tissue samples (subcutaneous and muscle) of crossbred cattle (Hereford dams × seven sire breeds) (Pitchford et al., 2002). Genetic correlations between fatty acid composition and carcass traits were found not significant, allowing the authors to conclude that simultaneous improvement in carcass and meat quality traits is feasible.

**Sex factor** : Studies showed a higher IMF content, higher proportions of total SFA and MUFA as well as lower proportions of total n-6 PUFA in intramuscular to fbarrows compared to gilts (Zhang et al., 2007).Huang and Horrobin (1987) studied the effect of sex on the distribution of long-chain n-3 and n-6fatty acids in essential fatty d-deficient rats fed C18:2n-6concentrate and/or C20:5n-3 and C22: 6n-3-rich fishoil,and observed a greater incorporation of the sum of total of long-chain essential fatty acids (EFA;C20: 4n-6,C20:5n-3 and C22:6n-3) in females than in males.

### Conclusion

Trends in healthy eating, in modern societies, have created a demand for leaner meat in respect with healthy eating guidelines. This evolution in a decline of the fat content may adversely affect eating quality and further meat processing. Thus, a dilemma arises between eating quality indices and human health aspects in evolution of meat production, e.g. the desire to reduce PUFA content of intramuscular fat, from a technological perspective,

### References

Agaba, M., Tocher, D., Dickson, C. A., Dick, J. R., & Teale, A. J. (2004). ZebrafishcDNA encodingmultifunctional fatty acid elongase involved in production of eicosapentaenoic (20:5n-3) and docosahexaenoic (22:6n-3) acids. Marine Biotechnology, 6, 251-261.

Beitz, D. C., & Nizzi C. P. (1997). "Lipogenesis and lipolysis in bovine adipose tissue." In Rumen microbes and digestive physiology in ruminants (eds. Onodera R., Itabashi H., Ushida K., Yano H., Sasaki, Y.), pp. 133-143.

Japan Scientific Societies Press, Karger, Basel.Bézard, J., Blond, J. P., Bernard, A., & Clouet, P. (1994).The metabolism and availability of essential fatty acids inanimal and human tissues. Reproduction Nutrition andDevelopment, 34, 539-568.

Burdge, G. C., & Wootton, S. A. (2002). Conversion of -linolenic acid to eicosapentaenoic and cosahexaenoic acids inyoung women. British Journal of Nutrition, 88, 411-420.

Cameron, N. D. (1990). Genetic and phenotypic parameters for earcass traits, meat and eating quality traits in pigs. Livestock Production Science, 26, 119-135.

Cameron, N. D., & Enser, M. B. (1991). Fatty acidcomposition of lipid in Longissimus dorsi muscle of Duroc and British Landrace pigs and its relationship witheating quality. Meat Science, 29, 295-307. Castration of piglets was also associated with increased fat deposition in pig (Mersmann, 1984; Mourot et al., 1999; Peinado et al., 2008) and reduces the efficiency of conversion of feed into meat (Wood, 1984).

In cattle, residual sex effects independent of fat content seem to exist for fatty acid composition, and some authors linked them with possible effects of sex hormones on the enzyme systems such as  $\Delta 9$ -desaturase that may interfere in MUFA metabolism (Malau-Aduli et al., 2000; Pitchford et al., 2002; De Smet et al., 2004).

should be balanced by the need to increase ratios of polyunsaturated/ saturated fatty acids (P/S) and n-6/ n-3 PUFA. One would raise a question: What is the point in tropical areas and emerging country?

In any of the cases, there is a huge interest in reflecting on ways to control the fat content and composition in meat (and other animal products), to improve its nutritional, eating quality and technological indices.

Cameron, N. D., Enser, M., Nute, G. R., Whittington, F.M., Penman, J. C., Fisken, A.C., Perry, A. M., & Wood, J.D. (2000). Genotype with nutrition interaction on fattyacid composition of intramuscular fat and therelationship with flavour of pig meat. Meat Science, 55,187-195.

Chiliard, Y., & Ollier, A. (1994). Alimentation lipidiqueet metabolisme du tissu adipeux chez les ruminants.Comparison avec le porc et les rongeurs. INRAProduction Animale, 7 (4), 293-308.

Choi, N. J., Enser, M., Wood, J. D., & Scollan, N. D.,2000. Effect of breed on the deposition in beef muscleand adipose tissue of dietary n-3 polyunsaturaed fattyacids. Animal science. 71, 509-519.

Cooper, S. L., Sinclair, L. A., Wilkinson, R. G., Hallett, K. G., Enser, M., & Wood, J. D. (2004). Manipulation of the n-3 polyunsaturated acid content of muscle and adipose tissue in lambs. Journal of Animal Science, 82,1461-1470.

Daszkiewicz T, Bąk T, Denaburski J. 2005. Quality ofpork with a different intramuscular fat (IMF) content.Pol J Food Nutr Sci; 14/55:31–6.

De Smet, S., Raes, K., & Demeyer, D. (2004). Meat fattyacid composition as affected by fatness and geneticfactors: a review. Animal Research, 53, 81-98.

Demirel, G., Wachira, A. M., Sinclair, L. A., Wilkinson, R. G., Wood, J. D., & Enser,

M. (2004). Effects of dietary n-3 polyunsaturated fattyacids, breed and dietary vitamin E on the fatty acids oflamb muscle, liver and adipose tissue. British Journal ofNutrition, 91, 551-565.

Department of Health, 1994. Nutrition aspects of cardiovascular desease. Report on health and social subjects no. 46. London: H. M. Stationery office.

Ding, S.T., Lapillone, A., Heird, W. C., & Mersman, H. J. (2003). Dietary fat has minimal effects on fatty acid metabolism transcript concentrations in pigs. Journal of Animal Science, 81, 423-431.

Drackley, J. K. (2000). Lipid metabolism. In Farm animal metabolism and Nutrition (Ed D'Mello, J. P. F.), pp 5, 97-119. CAB international.

Enser, M., Hallett, K., Hewitt, B., Fursey, G. A. J., & Wood, J. D. (1996). Fatty acid content and composition of English beef, lamb and pork at retail. Meat Science, 42, 443-456.

Enser, M., Hallett, K. G., Hewitt, B., Fursey, G. A. J, Wood, J. D., & Harrington, G. (1998). The polyunsaturated fatty acid composition of beef and lamb liver. Meat Science, 49, 321-327.

Enser, M., Richardson, R. I., Wood, J. D., Gill, B. P., & Sheard, P. R. (2000). Feeding linseed to increase the n-3 PUFA of pork: fatty acid composition of muscle, adipose tissue, liver and sausages. Meat Science, 55, 201-212.

Enser, M. (1984). The chemistry, biochemistry and nutritional importance of animal fats. In Fats in animal nutrition (Ed Wiseman, J.), pp 23-51.Butterworths, London.

Fenton J. P., Roehrig K. L., Mahan D. C. & Corley J. R. (1985). Effect of swine weaning age on body fat and lipogenic activity in liver and adipose tissue. Journal of Animal Science, 60, 190-199.

Fernandez, X., Monin, G., Talmant, A., Mourot, J., & Lebret, B. (1999). Influence of intramuscular fat content on the quality of pig meat — 1. Composition of the lipid fraction and sensory characteristics of m. longissimus lumborum. Meat Science, 53(1), 59–65. tps://doi.org/10.1016/S0309-1740(99) 00037-6.

Genya Watanabe, Michiyo Motoyama, Ikuyo Nakajima, & Keisuke Sasaki. (2018). Relationship between water-holding capacity and intramuscular fat content in Japanese commercial pork loin. Asian-Australasian Journal of Animal Sciences, 31(6), 914–918. https://doi.org/10.5713/ajas.17.0640

Gerbens F., van Erp A. J. M., Harders F. L., Verburg F. J., Meuwissen T. H. E., & Veerkamp J. H. (1999). Effect of genetic variants of the heart fatty acid-binding protein gene on intramuscular fat and performance traits in pigs. Journal of Animal Science, 77, 846-852.

Gerbens F., de Koning D. J., Harders F. L., Meuwissen T. H. E., Janss L. L. G., Groenen, M. A. M., Veerkamp J. H., Van Arendonk J. A. M., & te Pas M. F. W. (2000). The effect of adipocyte and heart fatty acid-binding protein genes on intramuscular fat and backfat content in Meishan crossbred pigs. Journal of Animal Science, 78, 552-559. Gurr, M. I., Harwood, J. L. & Frayn, K. N. (2002). Fatty acid nomenclature. In Lipid Biochemistry 5th Edition (Ed Osney, M .), pp 5, 1-337.Blackwell Science, Oxford, UK.

Gutnikov, G., 1995. Fatty acid profiles of lipid samples. Review. Journal of Chromatography. B (671), 71-89.

Hartmann S., Otten W., Kratzmair M., Seewald M. J., Iaizzo P. A., & Eichinger H. M. (1997). Influences of breed, sex, and susceptibility to malignant hyperthermia on lipid composition of skeletal muscle and adipose tissue in swine. American Journal of Veterinary Research, 58, 738-743.

Huang, Y. S., & Horrobin, D. F. (1987). Sex differences in n-3 and n-6 fatty acid metabolism in EFA-depleted rats. Proceedings of the Society for Experimental Biology andM edicine, 185, 291-296.

Kinsella, J. E. (1991). Linolenic acid: functions and effects on linoleic acid metabolism and eicosanoid-

mediated reactions. In Advances in food and nutritionresearch (Ed Kinsella, J. E.), pp 35, 1-184. Academicpress, San Diego, USA.

Kouba, M., Enser, M., Whittington, F. M., Nute, G. R., & Wood, J. D. (2003). Effect of a high-linolenic acid dieton lipogenic enzyme activities, fatty acid compositionand meat quality in the growing pig. Journal of AnimalScience, 81, 1967-1979.

Lizardo, R., Van Milgen, J., Mourot, J., Noblet, J., &Bonneau, M. (2002). A nutritional model of fatty acid composition in the growing-finishingpig. Livestock Production Sciences, 75, 167-182.

Lobb, K. (1992). Fatty acid classification and nomenclature. In Fatty acid in foods and their health implications (Ed. Chow. C.K.), pp 2957, 1-15. Marcel Dekker INC, New York, USA.

Love J.D and A.M. Pearson. 1970. Lipid Oxidation in Meat and Meat Products-A Review 1. Journal of American oil Chemistr's society. 48, (10): 547-549. https://doi.org/10.1007/BF02544559.

Malau-Aduli, A. E. O., Siebert, B. D., Bottema, C. D. K.& Pitchford, W. S. (2000). Heterosis, sex and breed differences in the fatty acid composition of muscle phospholipids in beef cattle. Journal of Animal Physiology and Animal Nutrition, 83, 113-120.

Mersmann, H. J. (1984). Adrenergic control of lipolysis in swine adipose tissue. Comparative Biochemistry and Physiology, 77, 43-53.

Mohrhauer, H., & Holman, R.T. (1963). Effect oflinolenic acidupon the metabolism oflinoleic acid. Journal of Nutrition, 81,67-74.

Mourot, J., Kouba, M., & Salvatori, G. (1999). Facteurs de variation de la lipogenèse dans les adipocytes et les tissus adipeux chez le porc. INRA Production Animale, 12(4), 311-318.

O'Hea, E.K., & Leveille, G. (1969). Significance of adipose tissue and liver as sites of fatty acid synthesis in the pig and the efficiency of utilisation of various substrates for lipogenesis. Journal of Nutrition, 99, 338-344.

Oka, A., Iwaki, F., Dohgo, T., Ohtagaki, S., Noda, M., Shiozaki, T., Endoh, O., & Ozaki, M. (2002). Genetic effects on fatty acid composition of carcass fat of Japanese Black Wagyu steers. Journal of Animal Science, 80, 1005-1011.

Oshino, N., & Sato, R. (1972). The dietary control of the microsomal stearyl CoA desaturation enzyme system in rat liver. Arch. Biochem. Biophys., 149, 369-377.

Ozols, J. (1997). Degradation of hepatic stearyl CoA\_9desaturase. Molecular Biology of the Cell, 8, 2281-2290.

Peinado, J., Medel, P., Fuentetaja, A., & Mateos, G.G. (2008), Influence of gender and castration of females on growth performance and carcass and meat quality of heavy pigs destined to the dry-cured industry. Journal of Animal Science, 86, 1410-1417.

Pérez-Enciso, M., Clop, A., Noguer, J. L., óvilo, C., Coll,A., Folch, J. M., Babot, D., Estany J., Oliver, M. A., Diaz, I., & Sanchez, A. (2000). A QTL on pig chromosome 4 affects fatty acid metabolism: Evidence from an Iberian by Landrace intercross. Journal of Animal Science, 78, 2525-2531.

Piedrafita J., Christian L.L., & Lonergan S.M. (2001). Fatty acid profiles in three stress genotypes of swine and relationships with performance, carcass and meat quality traits. Meat Science, 57, 71-77.

Pitchford, W. S., Deland, M. P. B., Siebert, B. D., Malau-Aduliand, A. E. O., & Bottema, C. D. K., 2002. Genetic variation in fatness and fatty acid composition of crossbred cattle. Journal of Animal Science. 80, 2825-2832.

Raes K., De Smet S. & Demeyer, D. (2001). Effect of double-muscling in Belgian Blue young bulls on the intramuscular fatty acid composition with emphasis on conjugated linoleic acid and polyunsatutated fatty acids. Animal Science, 73, 253-260.

Rubén Domínguez, Mirian Pateiro, Mohammed Gagaoua, Francisco J. Barba, Wangang Zhang, & José M. Lorenzo. (2019). A Comprehensive Review on Lipid Oxidation in Meat and Meat Products. Antioxidants, 8(10). https://doi.org/10.3390/antiox8100429.

Sellier, P. (1998). Genetics of meat and carcass traits. In: Rothschild M.F., Ruvinsky A. (Eds.), The genetics of the pigs. CAB International, Jouy-en-Josas Cedex. pp 463-510. Siebert, B.D., Pitchford, W.S., Kruk, Z.A., Kuchel, H., Deland, M.P.B., & Bottema, C.D.K. (2003). Differences in-9 desaturase activity between Jersey and imousin-sired cattle. Lipids, 38, 539-543.

Sprecher, H., Luthria, D., Mohamed, B.S., & Baykousheva, S.P. (1995). Reevaluation of the pathway for the biosynthesis of polyunsaturated fatty acids. Journal of lipid Research, 36, 2471-2477.

Sprecher, H. (2000). Metabolism of highly unsaturated n-3 and n-6 fatty acids. Lipids, 1486, 219-231.

Strittmatter, P., Spatz, L., Corcoran, D., Rogers, M.J., Setlow, B., & Redline, R. (1974). Purification and properties of rat liver microsomal stearyl coenzyme A desaturase. Proceedings of the National Academy of Science USA, 71, 4565-4569.

Tarrant, P. V., 1992. Production factors affecting meat quality. Paper presented at OECD workshop, June 8–10, Helsinki, Finland.

Teye, G. A., Sheard, P. R., Whittington, F. M., Nute, G. R., Stewart, A., & Wood, J. D., (2006a). Influence of dietary oils and protein level on pork quality. 1. Effects on muscle fatty acid composition, carcass, meat and eating quality. Meat Science, 73, 157-165.

Teye, G. A., Wood, J. D., Whittington, F. M., Stewart, A., & Sheard, P. R. (2006b). Influence of dietary oils and protein level on pork quality. 2. Effects on properties of fat and processing characteristics of bacon and frankfurter-style sausages. Meat Science, 73, 166-177.

Tocher, D.R., Agaba, M., Hasting, N., & Teale, A.(2003). Biochemical and molecular studies of the polyunsaturated fatty acid desaturation pathway in fish. Proceedings of the 26th annual larval fish conference, 211-227.

Troy, D., Tiwari, B., Joo, S., & Troy, D. (2016). Health Implications of Beef Intramuscular Fat Consumption. Korean Journal for Food Science of Animal Resources, 36(5), 577–582. https://doi.org/10.5851/kosfa.2016.36.5.577.

Steven M. Lonergan, David G. Topel, Dennis N. Marple. (2019). The Science of Animal Growth and Meat Technology (Second Edition). Academic Press.

Valsta, L.M., Tapanainen, H., & Männistö, S. (2005). Meat fats in nutrition. Meat Science, 70, 525-530. Warnants, N., Van Oeckel, M. J., & Boucque, C. V. (1999). Incorporation of dietary polyunsaturated fatty acids into pork fatty tissues. Journal of Animal Science, 77, 2478-2490. WHO, 2003. Diet, nutrition and the prevention of chronic diseases. Report of a joint WHO/ FAO Expert consultation. WHO Technical Report Series 916, Geneva.

Wood, J.D. (1984). Fat deposition and the quality of fattissues in meat animals. In: Wiseman J.B. (Eds.), Fat in Animal Nutrition. London, Butterworths. pp 407-435.

Wood, J. D., Brown, S. N., Nute, G. R., Whittington, F. M., Perry, A. M., Johson, S. P., & Enser, M., 1996. Effect of breed, feed level and conditioning time on the tenderness of pork. Meat Science. 44, 105-112.

Wood J.D., & Enser, M. (1997). Factors influencing fatty acids in meat and the role of antioxidants in improving meat quality, British Journal of Nutrition, 78 (1), 49-60.

Wood, J. D., Nute, G.R., Richardson, R.I., Whittington, F.M., Southwood, O., Plastow, G., Mansbridge, R., da Costa, N., & Chang, K.C. (2004). Effect of breed, diet and muscle on fat deposition and eating quality in pigs. Meat Science, 67, 651-667.

Wood, J.D., Enser, M., Fisher, A.V, Nute, G.R, Sheard, P.R., Richardson R.I., Hughes S.I., & Whittington, F.M. (2008). Fat deposition, fatty acid composition and meat quality: A review. Meat Science, 78, 343-358

Zhang, S., Knight, T.J., Stalder, K.J., Goodwin, R.N., Lonergan, S.M., & Beitz, D.C. (2007). Effect of breed, sex and halothane genotype on fatty acid composition of pork longissimus muscle. Journal of Animal Science, 85, 583-591.