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Fat Deposition, Fatty Acid Composition, and Its Relationship with Meat Quality and Human Health

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Abstract

The consumer’s profile has changed, and in recent years, there has been a greater concern for the nutritional quality of meat, especially in relation to fat that compose it. The meat fat composition can contribute to the onset of cardiovascular disease. On the other hand, fat is an essential component in the human diet, as well as providing energy; it contains essential fatty acids (FAs) that must be present in food. The meat nutritional properties are largely related to its fat content and fatty acid composition. In addition, fat gives flavor to food, helps in the absorption of vitamins, and plays an important role in the immune response, for humans, and animals. The fat nutritional and sensory quality in meat that is determined by the fatty acid composition can affect the degree of fat saturation, the storage stability, and flavor. There are several factors that can influence the fatty acid composition, such as animals’ species, breed, sex, and diet, causing various changes in carcass, as well as in tissues and chemical meat composition.

Keywords: animal production, animal fat, lipid composition, flavor, polyunsaturated fatty acids, human nutrition
1. Introduction

Meat provides important nutrients for the human diet, including vitamin B, minerals such as iron, and the essential fatty acids [1, 2]. The fat deposition in muscles and the meat fatty acid (FA) composition are factors that affect the meat quality and primarily influence flavor, juiciness, and tenderness [3–5]; therefore, they are important in meat industry. The fat also assists in the transport and absorption of fat-soluble vitamins A, D, E, and K by the intestine and plays an important role in the immune response, both in humans and in animals [6]. Furthermore, fat is related to the quality; protects the carcass from the cold; is considered a visual attractive, striking the meat acceptability by the consumer; and is associated with human health issues [7, 8].

For consumers, flavor and nutritional value are important attributes for meat quality and can influence the purchasing power [9]. However, currently, there is a growing concern not only about the fat excessive consumption but also its composition and impact on health, particularly those of animal origin [10]. The fatty acid profile of intramuscular fat is important for human health, since the intramuscular fat cannot be extracted or removed before consumption of meat [11]. The high consumption of saturated fatty acids (SFAs) is associated with elevation of serum cholesterol and low-density lipoproteins (LDL) which are risk factors for the occurrence of cardiovascular diseases [12]. For these reasons, the animal products are criticized, as they have a high SFA content and labeled as harmful to health [6, 13].

These concerns are based on recommendations in health authorities and nutritionists that support the notion that saturated fat from meat has negative impacts on health. However, in most cases, this information is widespread in digital media and disseminated without scientific support to “crucify” especially red meat, making it the villain to health. Therefore, further clarification of the actual impact of the meat and fat consumption to human health, considering other indirect factors related to its consumption, which can harm human health, such as physical inactivity, obesity, and intake of alcoholic beverages, among others, become necessary.

2. Literature review

2.1. Fat deposition

The development of adipose tissue also begins at the pre-birth, around the third month of pregnancy, when embryonic cells derived from the mesenchyme, like fibroblasts, differentiate to give rise to adipoblasts or primitive cells from adipose tissue. After differentiation, there is no way a cell return to the initial state. Once formed, the adipoblasts undergo an exponential multiplication phase forming preadipocytes [14]. Lipoprotein lipase (LPL) is the enzyme responsible for breaking down the triglycerides, caused by fatty acids, and glycerol circulation, endothelial and synthesized by the adipocyte level, also acts as a cell flag, since, when expressed, it stimulates a new wave hyperplastic adipose tissue [14]. After the occurrence of
this new wave of proliferation, new adipocyte proliferation inhibitor cell signalers, such as glycerol-3-phosphate dehydrogenase (GPDH) and fatty acid synthase (FAD), are detected. The cells then receive the signal to initiate the accumulation of lipids, when they become termed themselves adipocytes [14].

During differentiation, preadipocytes undergo morphological changes as well as the selective expression of certain genes. The sequential expression of certain transcription factors, such as the CCAAT/enhancer-binding protein factor, SREBP/sterol regulatory element-binding protein, and the family of transcription factors PPAR/proliferator-activated receptor peroxisome, have a key role in the conversion stages of adipocytes [15].

The deposition of intramuscular fat is apparently regulated by different factors when compared with those regulating fat depositions in fatty tissues, such as subcutaneous, metabolic differences existing between them. Intramuscular adipocytes have higher activity of the enzymes hexokinase and phosphofructokinase. The subcutaneous adipose tissue exhibits higher levels of lipogenic enzymes such as NADP-malate dehydrogenase, fosfogluconate-6-dehydrogenase, and glucose-6-phosphate dehydrogenase, showing unique roles in lipid metabolism [16, 17].

The adipose tissue mass, therefore, is controlled by the balance between cell proliferation (hyperplasia) and increased cell size (hypertrophy). The uptake of free fatty acids in the cytosol full of lipid droplets in triacylglycerol contributes to adipocyte hypertrophy [14]. In ruminants, adipocytes play an important role as energy reserve, and occasioning changes in animal fat deposition in accordance with their physiological state, such as during pregnancy or termination phase. In addition, adipocytes act as true endocrine cells, secreting several hormones and endocrine signals which are directly related to animal production. Among these substances, leptin, IGF-1, interleukins, and resistin, among others, stand out [18].

The deposition of fat in cattle, as well as other animal species, is reflected by nutrition and sex and used for the genetic group [19]. Thus, there is a wide interest in manipulating the chemical composition of meat, through the regulation of its biosynthesis. For better understanding of the effects of nutrition on lipid metabolism and consequently on the quality of meat, recent research has made association between gene expression and nutrition area known as nutrigenomics [20–23].

Gene expression is the process whereby information contained in the DNA structure is transmitted to the mRNA and protein products [24]. The binding of specific transcription factors to specific DNA sequences controls this process. The key transcriptional factors involved in lipid metabolism regulatory elements are proteins related to sterol (SREBP-1c) [25], the activated receptor peroxisome proliferator-γ (PPAR), and proliferator-activated receptor peroxisome-α (PPARα). These genes were associated with the synthesis and oxidation of fatty acids in the different organs and tissues of the animal body [26, 27].

The interactions between the nutrients that compose the diet and the synthesis and activity of lipogenic enzymes can illustrate the numerous possibilities regarding lipid deposition in adipose tissue. This is possible because the biological activity displayed by certain dietary fatty
acids can stimulate or inhibit specific lipogenic genes encoding enzymes [22]. For example, sources of polyunsaturated fatty acids (PUFAs) can increase transcription of genes that encode the lipoprotein lipase enzyme (LPL); the connector transporter to fatty acid 4 (FABP4), PPARα [28], and PPAR [26]; and decrease expression of the gene encoding stearoyl-CoA desaturase (SCD1) [21] and SREBP-1c [29].

The oleic acid concentration presents in the meat bovine fat if dependent of the expression of stearoyl-CoA desaturase (SCD) and its activity. SCD has been identified and reported as one of the genes associated with fatty acid composition of beef. This is a limitation of SFA responsible for the conversion of monounsaturated fatty acids (MUFA) in mammalian adipocytes. The composition of the fatty acids stored in fat deposits reflects the previous action SCD substrates such as stearic acid and palmitic acid [30]. Accordingly, higher levels of concentrate feed in the finishing period of the animals confined result in a higher concentration of oleic acid and MUFA in the intramuscular fat [31]. Although the adipogenic mechanism is extremely complex, several genes were identified and confirmed as being responsible for fatty acid composition in beef [20, 32–41].

2.2. Fatty acid composition and its relationship with human health

Besides its importance for the sensory characteristics of the meat, the fat content and their FA composition are relevant to the quality, especially for issues related to human health [42, 43]. The composition of the FA of animal origin can be influenced by diet (forage and grain), by the digestive system, and by the biosynthetic processes of the animal [44]. In ruminants, the FA’s profile is not a direct reflection of FA composition from the feed due to the complex reactions of biohydrogenation caused by rumen microorganisms [8, 14, 42].

Furthermore, the FA composition may also be different depending on the breed, species (Table 1) [13, 45], and sexual condition [46, unpublished data]. Wood et al. [13] showed that the meat has an average 50% of SFA, 40% of MUFA, and 10% of PUFA acids. The meat FAs are mainly medium to long chain, from 12 to 22 carbon atoms, with the basic structure CH₃-(CH₂)ₙ-COOH. Low concentrations of FA short-chain C8–C10 are observed in mutton fat [13].

In general, the meat fat of the ruminant has a higher concentration of SFA and lower polyunsaturated:saturated relationship compared to nonruminant meat. This fact is due to the FA of biohydrogenation process unsaturated on rumen by the action of microorganisms [46–48]. However, not all SFAs are considered hypercholesterolemic (which increase the levels of bad cholesterol (LDL)). The most undesirable FA, according to French et al. [49], would be myristic acid (C14:0), which represents only 3% of total FA in meat [50]. Howsoever, the main SFAs present in beef intramuscular fat are the palmitic (C16:0) and stearic (C18:0) acids, which make up more than 50% of the total lipid composition [51–53]. The presence of SFA in beef is the main cause of concern and associations of human health with cardiovascular disease and obesity, by influencing cholesterol blood levels [54].

However, palmitic FA has lower hypercholesterolemic effect and stearic FA (43% of total SFA in meat [50], has no effect because it becomes oleic acid (C18: 1 n-9) in the body [55], and thus does not influence blood cholesterol levels. The intramuscular fat beef also has a higher
<table>
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<th>12:0</th>
<th>14:0</th>
<th>16:0</th>
<th>18:0</th>
<th>Total trans</th>
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<th>18:2n6</th>
<th>18:3n3</th>
<th>20:4n6</th>
<th>20:5n3</th>
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ND = not detected.
Source: Woods and Fearon [44].

Table 1. Major fatty acids of milk, beef, lamb, pork, poultry, and eggs (g/100 g total FA).
overall concentration of MUFA, mainly oleic acid and polyunsaturated fatty acids (PUFAs). Oleic acid may decrease the circulating concentration of LDL cholesterol in humans and is considered a “healthy” fat [56–61]. Higher oleic acid values are desirable for having hypcholesterolemic action, with the advantage of not lower HDL cholesterol (good cholesterol), and act to protect against coronary heart disease [50].

The relation between n6 and n3 is particularly beneficial (balanced) in meat from ruminants. These FAs have several effects on the immune and inflammatory response. The n-3 FA has suppressive effects such as inhibition of lymphocyte proliferation, antibody production, and cytokine expression of adhesion molecules and activation of natural killer cells (NK). The n-6 FA has both effects: inhibitory and stimulating the immune response [60]. The balance of daily intake of foods that are sources of FA n-6 and n-3 is important in human health, and recommendations vary according to some authors and countries. The trend of convergence of the n-6:n-3 ratio of FA is in the range from 4:1 to 5:1 [61–63]. The essential FAs include the n-3 and n-6 families, which are not biologically synthesized by humans, but they are necessary for biological processes and therefore should be eaten in the human diet.

After n-3 ingestion, the FA biosynthesis of eicosapentaenoic acid—C20:5 (EPA) and docosahexaenoic acid—C22:6 (DHA) occurs in the body. The first FA is involved in cardiovascular protection in adults [64], and the second is essential for brain development and visual system, associated with maternal and child health [65].

The arachidonic acid (C20:4 n-6) and EPA give rise to eicosanoids, thromboxanes, prostaglandins, and leukotrienes. Their presence in the bloodstream can provide vasoconstrictor responses or vasodilator, stimulation or inhibition of platelet aggregation, and pro effects or anti-inflammatory drugs [66, 67].

The conjugated linoleic acid (CLA) is a representative of micro-components in animal products, with a mixture of FA, which occurs as intermediate biohydrogenation of PUFAs [68]. This substance is interesting to act as a powerful natural anticarcinogenic and reduce atherosclerosis and diabetes [69].

The red meat consumption and cardiovascular disease, obesity, and colon cancer are mainly due to the saturated fat content [70, 71]. On the other hand, more recent studies indicate that processed meats, not the red fresh beef, increase the risk of cardiovascular disease and obesity [72]. However, other researchers have shown the benefits of lean meat as part of a healthy diet [73–75]. Furthermore, the meat with higher fat content produces lower levels of mutagenic heterocyclic aromatic amines, especially pasture-fed animals [76], indicating that the consumption of beef presents additional benefit.

According to Oostindjer et al. [77], data on associations between red meat intake and colorectal cancer are inconsistent, and the underlying mechanisms are unclear. Therefore, it is unlikely that moderate consumption of red meat as part of a balanced diet increases the chances of cardiovascular disease or colon cancer [78].

2.3. The influence of diet on the meat fatty acid composition

The animal’s diet has been demonstrated as one of the factors determining the different changes in carcass composition and tissue as well chemistry of meat cuts [79]. The concentrated and
bulky proportions and their respective sources are some of the factors which determine the quantity and quality of lipids present in animal products [80, 81].

The biohydrogenation process of unsaturated FA that happens in the rumen, and the composition of FAs in the ruminant’s meat, can be affected by breed, diet composition, and management [8, 13, 42, 45, 82]. Still, the factors that influence the chemical and physical components present in the meat can mention the age, sex, and anatomical location of cutting and the muscle [83]. Comparisons between eight different meat cuts showed that composition of breast fatty acids presented lower concentrations of stearic and palmitic acids, lower myristic concentrations, and higher MUFA concentrations represented by oleic acid [84].

The age specifically affects the MUFA content by means of SCD gene expression and enzyme activity [85]. Typically, the MUFA:SFA relationship increases with age, in muscle neutral lipids, and total fat of cattle [13, 85]. The inclusion of sources of MUFA in animal diet improves milk, meat, and eggs FA profile by increasing the proportion of MUFA:SFA, reducing the proportion of n6:n3 FA and increasing CLA levels in ruminant products [44]. However, one should take precautions as the addition of these sources of FA in animal diets may result in some adverse effects. For example, large quantities of MUFAs in the diet can affect ruminal activity, reducing milk production, and the concentrations of fat and protein, while the increase in PUFA levels in meat could result in lower maintenance and worse taste in meat products [44].

French et al. [46] observed that the longissimus dorsi muscle in ruminants fed with grasses showed a higher CLA production, two to three times as compared with the meat of ruminants fed with feedlot diets with high grain content. Accordingly, several subsequent studies have shown that the use of forage in the diet significantly increases the percentage of CLA, especially cis-9 and trans-11, up to twice the total fatty acids found in meat from animals which received greater proportion of grain in the diet [86–89].

The use of grain in cattle feed feedlot during the termination period is directly responsible for difference between FA compositions. Cattle fed with grain increases the absolute mono-unsaturated and saturated fat content of the meat while simultaneously decreasing absolute content of n-3 [89, 90].

Accordingly, Ferrinho et al. [91] observed differences in FA composition as a function of the cottonseed inclusion level in the diet. The total SFAs were not affected by diet, but differences were observed for branched chain fatty acids (BCFA), cis- and trans-monounsaturated fatty acid (MUFAcis/trans), unconjugated (nc) dienes, and in some individual PUFA. The BCFA and MUFAcis levels were higher in meat from cattle fed with the control diet compared with those receiving cottonseed.

Similarly, Diaz [92] reported that FA composition observed in longissimus dorsi and quadriceps femoris of lambs resulted in low percentage of stearic acid and high palmitic and linoleic acid values when compared to animals maintained on pasture. This difference is due to the FA composition in the diet, since fodder contains higher levels of linolenic FA and precursor n-3 series fans. In contrast, the concentrate has a high content of linoleic acid, the precursor of the n-6 series [93].

Likewise, Pelegrini et al. [94] evaluated the FA profile of sheep meat terminated at pasture or confinement observing a higher content of PUFAs in animals kept on pasture. This variation of the fat composition is responsible for the characteristic flavor of the meat of animals whose diet was based on pasture or concentrated [92].
In monogastric domestic animals, it is possible to change the composition of the FA of meat in the diet, since the FA in the diet is absorbed by the intestine unchanged and embedded tissues. Linoleic acid, for example, is not synthesized, and the concentrations present in the tissues respond rapidly to changes in diet. In contrast, MUFAs and SFAs are synthesized and are less influenced by the diet [95].

Morel et al. [96] studied the effect of fat sources in the diet on the FA profile in the pigs’ meat and reported that diets rich in PUFAs increase the levels of linoleic acid (18,2) and linolenic acid (C18:3) in muscle *longissimus dorsi* and subcutaneous fat. The composition of the poultry carcasses can also be altered by the type and amount of FA diet. Supplementation with unsaturated FA enables the deposition of these tissues in poultry [97]. Broilers require high energy concentrations in the feed, making it necessary to use oils, which eventually will influence the meat FA composition [98]. Increasing the proportion of n-3 series in the diet may have a beneficial effect regarding the nutritional quality of poultry meat and then decrease the levels of total lipids and cholesterol [97].

In a study using oil in chicken diet with the aim to evaluate the effect of different dietary lipid sources, the author reported that the chickens fed with the offal fat diet showed a higher percentage of MUFAs in the carcass and significant values of the palmitoleic acid. Besides, the linoleic acid was found to have high concentration in soybean oil [99], which confirms that the FA profile in the substrate is influenced by dietary fat sources used [100]. Subsequently, the effects of CLA supplementation in poultry diet during growth, diets containing different percentages of CLA ranging from 0% to 1.5%, were evaluated. It was observed that as increased levels of CLA in the diet, CLA is increased accumulation-in meat and decreased abdominal fat of poultry [101].

### 2.4. Genetic factor that influence the fatty acid composition

There is a growing market demand for healthier fat sources, and several strategies have been used to improve the meat FA profile, such as dietary manipulation and animal breeding. However, the high cost to obtain the phenotypic information and the fact that this trait can be only obtained after slaughter limits the genetic improvement through traditional selection. Although FA profile is not considered selection criteria, genomic selection is an important tool to improve the genetic progress of this trait, since the animal can be availed early in life, even at birth, reducing the generation interval and low cost [32]. In this sense, Cesar et al. [37] and Aboujaoude et al. [35] reported that selection for beef FA profile in Zebu cattle is very feasible, since there is additive genetic variation for most beef fatty acids in Zebu cattle. Therefore, information on the genetic differences between breeds and genetic parameters to develop breeding programs are essential. Thus, estimates of heritability and genetic and phenotypic correlations are key attributes. Differences in the fatty acid composition between purebred and crossbred cattle has been extensively evaluated on different production systems. In contrast, genetic studies reporting parameters (heritability and genetic correlations) for fatty acid profile are plentiful for monogastric animals, particularly pigs but, however, are still scarce in cattle, or the number of data used is limited [102].

However, estimates of parameters of genetic or genetic variability within breeds for fatty acid composition have been widely studied. Currently, the availability of genomic data for selection of traits associated with meat quality and lipid profile in cattle has increased [103],...
since there is a collection of information by research institutions, especially in Nellore herds [32, 35, 37, 104].

Heritability estimates for the meat fatty acid profile have been different in magnitude and, as a result, probably different in populations and used data structure, applied estimation methods, sampled tissue, etc. Furthermore, when comparing the estimates obtained in different breeds, differences in the activity of enzymes related to fatty acid desaturation can influence the estimated genetic variability [105]. Heritabilities and genetic correlations to fatty acid proportion were estimated to correspond to some studies and observations of the phenotypic level compared to the level of intramuscular fat [11].

Methods such as SNP-BLUP (single nucleotide polymorphism-best linear unbiased predictor) have been proposed to predict the genomic breeding values. This method allows to obtain less biased and applicable genomic evaluations, which is the most viable method when considering the computational cost [32].

Various fatty acids were identified positively and negatively in different biological processes in the skeletal muscle and other tissues. Knowing the biological processes associated with fatty acid content in the skeletal muscle and identifying differentially expressed genes (DEG) and functional pathways related to the regulation of gene expression associated with the fatty acid profile contribute to the understanding of how some FAs modulate metabolism and may have a protective function for health [36] as well as its potential for use in animal selection.

2.5. Effects of fatty acids on meat quality

The proportions of intramuscular fat present in the meat as well as its composition are associated with the juiciness, flavor, tenderness, and overall acceptability [106]. Besides these traits, the meat shelf life (pigment and lipid oxidation) is influenced by the composition thereof.

The FAs are involved in various technological aspects of meat quality because they have different fusion points. Groups of fat cells containing fat solidified with a high fusion point are whiter than when it contains liquid fat with a lower fusion point. This fat has another color, and appearance quality is affected by the FA [8]. The adipose tissue of ruminants is naturally firmer than that of pigs because the FA profile is more saturated. In bovine finishing period, the concentration of SFA in relation to the unsaturated increases, but beyond a certain level of fat in the animal, this ratio decreases. In fatty cattle the fat is soft, mainly due to an increase in relation to the oleic stearic and palmitic acids [107].

However, 90% of the volatile compounds in the meat, subjected to a cooking method, arise from the oxidation of unsaturated FA [108]. These volatile compounds contribute to the flavor and odor of meat, and unsaturated FAs are particularly important in the development of flavor [109], since the FA degradation of the n-9 family can produce hexanal, heptenol, decanal, octanal, heptanal, and nonanal. The oxidation of n-3 fatty acids gives rise to 1-penten-3-ol and propanal, and degradation of n-6 fatty acids will form hexanal, pentanal pentylfuran, pentanol, hexanol, 1-octenol, and 2-octenol [110].

Correspondingly, the group of aldehydes (pentanal, hexanal, heptanal, nonanal, octanal, octanal) is the most frequently identified in meat samples submitted to cooking; among them it is possible to highlight hexanal, which represents about 90% of total aldehydes, and it
can be produced from the oxidation of oleic, linoleic, and arachidonic fatty acids and degradation from other aldehydes, such as 2,4-decadienal [111].

The color change is due to the oxidation of oxymyoglobin (red) to metmyoglobin (brown), and this reaction usually occurs along the rancidity. Li and Liu [112] have shown that lipid oxidation products can promote the oxidation of the pigment and vice versa, although the strength of the relationship between these two aspects of shelf life is sometimes low. Antioxidants, in particular α-tocopherol (vitamin E), have been used to retard lipid oxidation and color in addition to prolong the life of meat products [113, 114].

Warren et al. [115] compared the grazing pasture-fed and grain-fed cattle and found that bright red color associated with oxymyoglobin was retained longer, simulating retail condition in cattle fed on pasture. Although the total concentration of unsaturated FA was similar in both groups, the animals were grazing beef with high concentrations of n-3 and the feed grain increased levels of n-6. It was found that antioxidants naturally present in the pasture probably caused higher levels of vitamin E in the tissue of these animals, with benefits to lower lipid oxidation and better color retention.

In studies with sheep, Kasapidou et al. [116] reported that low concentrations of vitamin E in the fabric are associated with lesser amounts of both n-6 and n-3 FAs in tissues. This suggests that the loss of in vivo PUFAs occurs when the antioxidant status is low. It is well known that marbling plays an important role in meat quality and sensory palatability of beef [53]. It has also been shown that in some countries growing score marbling corresponds to more acceptable taste, greater juiciness, bigger texture, and therefore greater palatability and acceptability [51, 117–120].

These results implied that high concentrate grain-fed beef could increase intramuscular fat (IMF) content and the proportion of oleic acid, thus increasing the sensory palatability of Hanwoo beef [53]. Lee et al. [121] reported differences between gene expression of FABP4, SCD, PPARγ, titin, and nebulin in longissimus muscle from high- and low-marbled Hanwoo steers. PPARγ and SCD gene were highly expressed in the low-marbled group, the SCD being related to the FA profile of the meat and the conversion of stearic acid to oleic acid. The SCD gene was associated with fatty acid composition and converts stearic acid into oleic acid. However, the FABP4 gene had a higher gene expression pattern in the high-marbled group relative to the low-marbled group.

3. Final consideration

It is already known that the fat contains essential fatty acids that must be present in the feed, to providing more energy than carbohydrates and proteins. Fat also provides flavor to food, assisting in the transport and absorption of fat-soluble vitamins A, D, E, and K by the intestine and plays a major role in the immune response, both in humans and animals. Thus, fat consumption that contains good fatty acid quality is essential while assisting in reducing the consumption of foods rich in simple carbohydrates, once the excessive intake of these compounds is detrimental to health.
The fatty acid composition of both adipose tissue and domestic animal muscle tissue depends on numerous factors, including intrinsic factors such as species, breed, genetics and age, and extrinsic factors such as food. These factors have direct effects on the meat quality. It is noteworthy also that the digestion of lipids present in the diet depends on the animal species.

Today, the search for healthy foods that meet the requirements of consumers in its qualitative aspect as nutrition, increasing concentrations of CLA, respecting the reasons of PUFA:SFA, n6: n3, stipulated by public health authorities is crucial, in order to prevent the development of cardiovascular disease and a possible incidence of some types of tumors and diabetes, among others.

Given the above, it is noted that the fat deposition and fatty acid profiles have great influence on meat quality evaluations, and its association with human health should be undertaken with caution and greater scientific support. However, additional studies are necessary to elucidate the real impact of fat consumption on human healthy.

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