Chapter 13

Genetic Factors that Determine the Meat Fatty Acids Composition

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Abstract

In relation the nutritional attributes of beef meat quality, the composition of fatty acid is important not only because it affects the meat palatability, but also it can affect the human health. The fatty acids harmful to human health have received attenuating attention in recent years. Some studies, with taurine breed, have shown that there is a genetic variation for the trait fatty acid profile of the meat and, therefore, the possibility of genetic improvement of this trait in beef cattle. Meantime, in zebu cattle, the genetic parameter estimates for fatty acid profile are scarce. Furthermore, the trait meat fatty acid profile is something difficult and costly to measure and for this kind of trait is indicated the use of genomic selection, which is a type of marker-assisted selection. The objective of this chapter is showing the genetic variability of meat fatty acid profile different cattle breeds and makes an approach of the implement models and methods that use genomic information to improve the fatty acid composition of beef meat.

Keywords: human health, meat quality, genomic selection, GWAS, SNP, genomic regions, *Bos taurus indicus*

1. Introduction

In response to the constant bombardment of health-related stories, there is a continuing and growing concern on the part of the population and public health institutions about excessive consumption of fats, especially fats of animal origin, as well as the type of fat or

fatty acid profile in the meat and their impact on consumer health. The fatty acid profile of intramuscular fat is important for human health, since intramuscular fat cannot be extracted or removed before meat consumption [1]. The composition of fatty acids of intramuscular fat has been widely studied, as it is also related to the succulence, aroma, and tenderness of the meat. For international meat quality standards, the amount of intramuscular fat or marbling deposited on the *longissimus* muscle is the main determinant of the carcass value and predictor of palatability [2].

Although beef is considered a highly nutritious food, being an important source of proteins, micronutrients, and B-complex vitamins, it has a high fat content with undesirable composition, such as high percentage of saturated fatty acids (SFAs). A high intake of SFA is associated with an increase in serum cholesterol and low-density lipoprotein levels (LDLs), which are risk factors for cardiovascular disease [3]. The predominant SFAs (Saturated Fatty Acids) in bovine fat are myristic (C14:0), palmitic (C16:0), and stearic (C18:0) acids [4]. It is noteworthy that C14:0 has a potential to raise serum cholesterol concentrations four to sixfold higher than C16:0 [5].

The fatty ruminant tissue is a natural source of isomers of conjugated linoleic acid (CLA), such as cis–9, trans–11 [6], which is synthesized in the rumen as a consequence of the biohydrogenation process of acids by the microorganisms [7]. CLA has favorable effects on human health, increasing immunostimulatory, antimutagenic, and antioxidant activity [8]. In addition, polyunsaturated fatty acids (PUFAs) present in bovine fat such as linoleic (C18: 2n−6) and linolenic (C18: 3n−3) and monounsaturated fatty acids (AGMI), such as oleic acid (C18: 1, n−9), which offer protection to the cardiovascular system, since balanced consumption of these drugs is associated with a reduction in serum cholesterol levels and an increase in high-density lipoprotein (HDL) [9].

For many years, the composition of fatty acids in meat-producing animals has received considerable interest in view of its implications for human health and meat quality traits [10–12]. Like most traits of economic interest in animal production, the composition of fatty acids is influenced by environmental and genetic factors. A number of studies have demonstrated large changes in fatty acid composition due to alterations in feeding strategies, especially in monogastric animals [13] and in ruminants [11]. However, genetic factors that affect fatty acid composition in cattle have been less investigated, although several studies report differences between breeds for the composition of fatty acids [14, 15]. Despite the differences between breeds for fatty acid composition, they are often confounded by differences in fat deposition or differences in precocity between breeds [1].

2. Fatty acid composition influencing human health and meat quality

The fatty acids composition in beef cattle production system has been studied because of its implications for human health and the traits associated with meat quality. There has been interest in to manipulate the fatty acid composition of meat because it has high nutritional value from children to seniors and is a rich source of protein, iron, zinc, complex B vitamins, and essential polyunsaturated fatty acids such as linoleic (C18:2), linolenic acid (C18:3), and

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arachidonic (C20:4) [16]. However, meat also is source of fat in the diet, and the presence of cholesterol, low concentration of polyunsaturated fatty acids, and high concentration of saturated fatty acids has been associated with coronary heart disease, diabetes, obesity, and cancer, as well as the ratio of n−6:n−3 polyunsaturated fatty acids, especially in the formation of blood clots leading to a heart attack [13, 17].

The nutritional properties of meat are largely related to its fat content and its fatty acid composition [11]. Different muscles differ in fat content and may also differ in fatty acid composition, which differs between various tissues, including intramuscular and intermuscular, as well as abdominal and subcutaneous adipose tissue [18, 19]. Moreover, genetic and environmental factors can influence the fatty acid composition of the meat [1, 20]. Differences due to the crossing of breeds and between animals within breeds, species, breeds, or lines can change the fatty acid composition of the meat [21]. But generally, the nature and level of deposit of fatty acids in the muscle depends on the diet, ingestion, intestinal absorption, hepatic metabolism, and lipid transportation [22]. Fatty acids composition can influence the meat quality in the fat tissue firmness (hardness), due to the different melting points of the fatty acids; shelf life (lipid and pigment oxidation) due to the propensity of unsaturated fatty acids to oxidize, leading to the development of rancidity and changing the color, flavor due to the production of volatile, odorous, lipid oxidation products during cooking and the involvement of these with Maillard reaction products and aromas [12, 23].

Wood et al. [20] showed that beef has, on average, 50% of saturated (SFA), 40% of monounsaturated fatty acids (MUFA), and 10% of polyunsaturated fatty acids (PUFA). However, in ruminants, linoleic acid (C18:2 n−6) and α-linolenic acid (C18:3 n−3), which are present in many concentrate feed ingredients, are degraded into monounsaturated and saturated fatty acids in the rumen by microbial biohydrogenation, and only a small proportion (around 10% of dietary consumption) is available for incorporation into tissue lipids. In addition to this, their important role is to work together to regulate immune responses and anti-inflammatory processes. Linolenic acid is also associated with the reduction of coronary diseases and plasma cholesterol and also has anticancer properties. The consumption of saturated fatty acids is associated with an increase in serum cholesterol levels and the risk of coronary heart disease. Especially lauric, myristic, and palmitic fatty acids are responsible for increasing plasma total and LDL cholesterol concentrations, and palmitic acid (C16:0) has the most impact on cholesterol levels, because it raises the levels of LDL.

Long-chain polyunsaturated fatty acids of the omega 3 family also are present in the meat, such as eicosapentaenoic, docosapentaenoic, and docosahexaenoic acids (C22: 6n−3). Eicosapentaenoic acid acts by relaxing the blood vessels and preventing the formation of blood clots. Arachidonic acid, resulting from omega 6 metabolism, leads to constriction of the vessels and formation of blood clots. Although they perform opposite functions, both are necessary for the maintenance of the balance of the organism. Moreover, prostaglandins are lipid autacoids derived from arachidonic acid. They both sustain homeostatic functions and mediate pathogenic mechanisms, including the inflammatory response [24]. Therefore, an omega 6/omega 3 ratio of less than four is recommended. The bovine meat analysis has verified values of the omega 6/omega 3 ratio between 1.5 and 10.4, and the lowest values were found

in the meat of cattle raised in pasture. Disorders that have been suggested to be linked with lack of omega-3 PUFA include hypertension, inflammatory and immune disorders, depression, and neurological dysfunction. Repeatedly, there are a lot of dietary recommendations to reduce the consumption of saturated fatty acids, such as prevention of cardiovascular diseases. On the other hand, some studies have shown beneficial effects of polyunsaturated fatty acids, mainly the n−3 family, CLA, docosahexaenoic acid, and docosapentaenoic acid on the level of serum lipids and their antithrombotic action on platelets and protection against some diseases [25]. Studies also indicate that stearic acid (C18:0) has been shown not to increase total cholesterol or LDL-cholesterol concentrations and slightly changes serum cholesterol levels in humans; however, it is poorly stored in tissues [26].

To attend the need of good human health, it is necessary to produce meat with a higher ratio of polyunsaturated to saturated fatty acids and a more favorable balance between n−6 and n−3 PUFA. The ratio of n−6:n−3 PUFA is particularly beneficial in cattle, especially from animals that have consumed grass which contains high levels of 18:3 acid. Dietary intake of PUFA from the n−3 series and especially from the n−6 series by the animals favors the production of conjugated isomers of linoleic acid (CLA c9 t11), such as C18:2 cis-9 trans-11 [5], which are synthesized in the rumen as a result of biohydrogenation of fatty acids, performed by microorganisms [7]. Some of these fats, such as CLA (conjugated linoleic acid), could be beneficial to human health. CLA is important in the prevention of specific cancers and in the treatment of obesity, immune functions, and potential beneficial effects on coronary heart disease [8].

In relation to diet, fatty acid composition of concentrate and forage diets is different and leads to different fatty acid compositions in tissues. The presence of the rumen makes fatty acid composition in beef more difficult to manipulate by changing diet, but studies showed that the C18:3 acid, n−3 PUFA concentrations, lipid oxidation, color, and aromas were affected by feeding treatments [23, 24]. Some data demonstrated the feasibility of reducing population cholesterol levels through strategies involving alteration of fat quality within the agricultural and food manufacturing chains. Ruminants consuming fresh pasture, in general, have higher content of unsaturated fatty acid in their meat that those receiving a grain-based concentrate diet. Grass lipids contain high proportions of the unsaturated linolenic acid (C18:3 n−3), and the only way to improve the ratio of PUFA in ruminant meats is by preventing ruminal biohydrogenation or by feeding protected PUFA supplements [27]. For all these reasons, there is an increase interest in research intended to modify the fatty acid composition in meat, especially reducing the concentration of SFA and increasing PUFA.

3. Meat fatty acids profile variation between and within beef cattle breeds

The genetic variability is characterized as the differences between animals within breeds, differences between breeds or lines, and due to the crossing of breeds. The heritabilities and genetic correlations estimate the latter source of variation. The major genes segregation may influence the breed effects, of which the double-muscled gene in cattle is a well-known example [1], and major factors that influence the fatty acid composition of beef are age of animal, diet, and breed type [20]

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Several studies have demonstrated that adipose tissues from *Bos indicus* cattle breeds are less saturated when compared to *Bos taurus* [14, 28, 29]. In this sense, Rossato et al. [29] pointed out that Nelore beef is nutritionally healthier than Angus breed, once it has lower percentages of cholesterol and higher amounts of n−3 fatty acids, CLA precursor (C18:1 *trans*). Bressan et al. [30] showed that the production system has an important influence on beef fatty acid profile when compared animals from *Bos taurus* and *Bos indicus* breeds. The *Bos taurus* animals showed the lower percentage of saturated fatty acids (SFA) and higher percentage for monounsaturated fatty acids (MUFA) in relationship to indicine animals finished at the feedlot system. According to these authors, taurine cattle that was finished under feedlot conditions showed higher ability to desaturate SFA than indicine cattle.

Recently, Lemos et al. [31] realized a study to identify regions associated with saturated, mono, and polyunsaturated and n−6 to n−3 ratios, in the *longissimus* thoracis muscle from confined Nelore, using the single-step method. The individual fatty acids with the highest concentration in the intramuscular fat of *longissimus thoracis* found by these authors were C16:0, C18:1 cis-9, C18:1 trans-11, and C18:0, representing 67.3% of its fat composition. These results are in agreement with those reported by some authors [32–34] who observed high levels of palmitic, stearic, and oleic fatty acids (FAs). Some authors [4, 35] also reported that palmitic fatty acid was the predominant FA in beef fat. In Nelore finished in feedlot [34], oleic acid (37.46%) displayed the highest concentration in intramuscular fat. The myristic and palmitic FAs are associated with an increase in circulating LDL cholesterol due to interference with hepatic LDL receptors. The saturated fatty acids were predominant, followed by the MUFAs and PUFAs. Similar results [36] were reported for Nelore cattle, 43.93% (SFA), 42.33% (MUFA), and 12.8% (PUFA). However, studies using taurine [15] and Nelore [34] breeds found similar concentrations for SFA and MUFA, 47 and 47.5%, and 47.23 and 48.34%, respectively.

Information on genetic parameters for carcass and meat traits, fatty acid composition, and genetic-quantitative relationships between these traits is essential to improve meat tenderness and the proportion of fat in the carcass, without harming the fat composition in livestock production. On this concern, some studies have been done to estimate these parameters. In these sense, Feitosa et al. [37] studied the genetic-quantitative relationships between the beef fatty acid profile with the carcass and meat traits of Nelore cattle used a total of 1826 bulls finished in feedlot conditions to analyze the following carcass and meat traits: subcutaneous fat thickness (BF), shear force (SF), and total intramuscular fat (IMF). The fatty acid (FA) profile of the *longissimus thoracis* samples was determined. These authors estimated the heritability, which varied from 0.06 to 0.65 for individual saturated fatty acids (SFA), 0.02 to 0.14 for monounsaturated fatty acids (MUFA), and it ranged from 0.05 to 0.68 for polyunsaturated fatty acids (PUFA). Some traits showed the heritability estimates low to moderate, varying from 0.09 to 0.20, how was the case of Omega 3, Omega 6, SFA, MUFA, and PUFA. For the carcass and meat traits, the heritability estimates for the authors were low (SF (0.06) and IMF (0.07)) unless for BF (0.17) which presented a moderate value.

Aboujaoude et al., [38] in a study to determine genetic parameters for fatty acids in intramuscular fat from feedlot-finished Nelore carcasses, estimated heritability for individual FAs ranged from 0.01 to 0.35. The heritability estimates for myristic (0.25 ± 0.09), palmitic (0.18 ± 0.07), oleic (0.28 ± 0.09), linoleic (0.16 ± 0.06), and α-linolenic (0.35 ± 0.10) FAs were moderate. Stearic,

elaidic, palmitoleic, vaccenic, conjugated linoleic acid, docosahexanoic, eicosatrienoic, and arachidonic FAs had heritability estimates below 0.15. Heritability estimates for beef fatty acids were also estimated by Cesar et al. [34] in a study with Nelore breed. The estimates varied from low (<0.10 for lauric, palmitc acid, cis-vaccenic acid, cis-12 octadecenoic, vaccenic acid, eicosanoic acid, aicosatrienoic acid, arachidonic acid, eicosapentaenoic acid, and atherogenic index, respectively) to moderate (up to 0.29 for intramuscular fat, myristic acid, myristoleic acid, palmitoleic acid, margaric acid, heptadecenoic acid, stearic acid, oleic acid, trans-6,7,8 octadecenoic, trans-10,11,12 octadecenoic, linoleic acid, octadecenoic acid, α-linolenic acid, γ-linolenic acid, eicosapentaenoic acid, docosahexaenoic acid, SFA, MUFA, PUFA, Sn−3, Sn−6, and n−6:n−3). For pentadecylic acid, cis-13 octadecenoic, cis-15 octadecenoic, trans-16 octadecenoic, and eicosadienoic acid, the heritability estimates were zero. Differently of these author and working with taurine breed, Tait et al. [39] (Angus) and Nogi et al. [40] (Japanese Black cattle) found the estimates of heritability for IMF fat deposition and composition traits are higher when compared with the results above. The lower values of heritability reported for the populations of some studies could be explained by the reduced sample size [41] or lower amount of genetic variation in the population [42].

Comparing these values with another study that was accomplished with a great number of animals [31], the estimate of linolenic FA heritability, for example, was similar to that found by Cesar et al. (2014) (0.13) and lower than that reported by Nogi et al. [40] (0.58). However, higher estimates have been reported for linolenic acid in other studies (0.21) [39] and also for palmitoleic acid (0.15) [34] and (0.49) [43]. Higher heritability estimates were reported for linoleic FA, 0.34 and 0.58, respectively, in the intramuscular fat of Japanese Black cattle, suggesting that genetic influence on linoleic acid varies among breeds [40]. Recently, authors also estimated high heritability for SFA (0.54) and MUFA (0.54) and, therefore, concluded that there is sufficient genetic variation in the fatty acid profile of cattle subcutaneous fat to respond to selection [33]. Therefore, these results suggest that it is possible to change the beef lipid composition of intramuscular fat of different cattle breeds' through selection. This information is important for breeding programs that aim at improving the beef fatty acid composition.

4. Genetic markers and metabolic pathways associated with meat fatty acids profile

The fatty acid metabolism is a complex process, which includes lipolysis of dietary fat and biohydrogenation in the rumen, *de novo* synthesis of fatty acids by rumen bacteria, absorption and transport of fatty acids by the host animal, *de novo* synthesis in tissues host, elongation and desaturation in animal tissues, hydrolysis of triglycerides and esterification, oxidation of fatty acids, or metabolism to other components [44–46].

In ruminants, the fatty acid synthesis occurs mainly in the adipose tissue, except during the lactation, when the mammary gland becomes the predominant organ [47]. The main point about control of the fatty acids synthesis is the acetyl-CoA carboxylase, and it seems that the

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endocrine control is very similar in, at least, adipose tissue (insulin activation, inhibition of catecholamine) of ruminants and nonruminants [48].

The principal precursor of fatty acid synthesis in ruminants is the acetate, which should be converted into acetyl-CoA by the action of acetyl CoA synthetase and subsequently incorporated into fatty acids. The conversion of acetate to acetyl-CoA is performed in adipose tissue, which is the largest synthesizer fatty acids in ruminants [49]. Some studies have been carried out to evaluate gene expression pattern in cattle for fatty acid composition and also identified genomic regions and metabolic pathways involved in those process, aiming to improve the beef fatty acid profile. In this sense, Berton et al. [50] studied the gene expression profile in Nelore cattle with extreme phenotypes for intramuscular fatty acid composition, found the *ACSM3* (acyl-CoA synthetase medium-chain family member 3) gene as differentially expressed for linoleic, monounsaturated, polyunsaturated, saturated, and omega-3 acids, participates in the metabolism of lipids and in metabolic pathways that involves the precursor acetyl-CoA metabolism. Also, the *ACSS1* (acyl-CoA synthetase short-chain family member 1) gene acts in the transformation of acetyl-CoA into fatty acids, through chemical reactions and metabolic pathways involving acetyl-CoA, being differentially expressed ($q < 0.05$), for saturated fatty acids such as palmitic, stearic, oleic, and total saturated acids.

Some studies has been realized in attempt do identify and describe the genes which play this important role on the beef fatty acids metabolic pathways. In a previously study, Lemos et al. [31] found several regions close to QTL (Quantitative Trait Loci) associated with saturated, polyunsaturated, and monounsaturated fatty acid groups in the meat of Nelore cattle. These regions have found interesting PCGs (pyruvate candidate genes) that are involved in lipid metabolism, such as receptors for reproductive hormones, transport and use of fatty acids and cholesterol, elongation factors and synthesis of long-chain fatty acids in different species, constituents of cell membranes, biosynthesis and hydrolysis of phospholipids and membrane constituents, energy metabolism, and protein kinase synthesis. The ELOVL5 (ELOVL fatty acid elongase 5) gene, among the many identified, is the most prominent. It is located on chromosome BTA23 at 25 Mb and associated with arachidonic acid (C20: 4 n−6). ELOVL genes are responsible for the elongation of long-chain fatty acids, which encode enzymes that play an important role in the elongation of long-chain fatty acids. The FASN (fatty acid synthetase) enzyme responsible for fatty acid synthesis is located on the BTA19 chromosome between 51,384,922 and 51,403,614 bp, variations of this enzyme were related to the fatty acid composition of Angus beef [51]. In mammals, *FASN* synthesizes the fatty acids that contain up to 16 carbon atoms, and the genes of the *ELOVLs* group produce long-chain fatty acids with 18 carbon atoms or more [13].

In additional, we employed the ingenuity pathway analysis (IPA) online software to detect the canonical pathways involving the genes of the above study. No canonical pathway was significant (p-value < 0.05). A large proportion of the pathways acted on fucose and cholesterol biosynthesis, and peroxisome proliferator-activated receptors alpha (PPARa) activation, which would provide valuable insights into explaining the molecular mechanism of lipid metabolism. As one of the pathways showed on canonical pathway, the PPAR alpha has a great role in the regulation in the fatty acids metabolism. Peroxisome proliferator-activated receptors (PPARs) are nuclear hormone receptors that are activated by fatty acids and their derivatives

and play an essential physiological role in the regulation of adipocyte tissue development lipogenesis and skeletal muscle lipid metabolism [52]. Doran et al. [53] performing the study genome-wide association studies (GWAS) in Holstein-Friesian cattle identified PPAR signaling pathway as the biological pathway more significantly involved in the performance of carcass traits, suggesting that PPARs play a key role in the control of carcass weight, carcass fat, and carcass conformation traits.

Li et al. [54] sampled spleen tissues from grain-fed and grass-fed Angus steers and performed a comparative study of gene expression using RNA-Seq method. Based on the DEGs (differentially expressed genes), they identified potential mechanisms, by implemented a functional analysis, that could contribute to the difference observed between both groups. The authors have detected 123 DEGs between grass-fed and grain-fed spleen of Angus cattle. In the grass-finished group, 87 were up-regulated, while the other 36 decreased their gene activity. Based on these genes, they identified 9 significant molecular networks and 13-enriched biological pathways through performed an IPA (ingenuity pathway analysis). The pathways, Nur77 signaling in T lymphocytes and calcium-induced T lymphocyte apoptosis, which are immune related, contain a pair of genes HLA-DRA and NR4A1 with dramatically altered expression level.

In a recent study, Berton et al. [50] analyzed the gene expression profile of intramuscular muscle in Nelore cattle with extreme values of fatty acid and identified several genes associated with fatty acid metabolism, such as those involved in intra- and extra-cellular transport of fatty acid synthesis precursors in intramuscular fat of *longissimus thoracis* muscle. The authors found some genes that play important traits on the metabolic pathways of fatty acids, such as precursors in the synthesis of fatty acids (CSM3 (Chromosome segregation in meiosis protein 3) and ACSS1); deposition of saturated fat in adipose tissue (DGAT2); support in insulin synthesis, stimulating both glucose synthesis and the entry of amino acids into cells (GPP and LPL); and synthesis and degradation of ketone bodies used in the synthesis of ATP (BDH1).

5. Genomic selection and genome-wide association studies for beef fatty acid composition

Marker-assisted selection (MAS) is recommended to increase the annual genetic gain for traits of economic importance in several animal species [55]. In this kind of selection, molecular information from markers is used together with phenotypic data of production and pedigree to select the animals. This way, MAS provides possibility to improve difficult and/or high cost measurement traits, such as the meat fatty acids composition. Some studies in several countries have mainly used microsatellite as genetic marker to study the fatty acids composition in taurine breeds [56]. However, genotype using microsatellite markers is expensive and just a small proportion of the total genetic variance can be show for the markers, limiting the progress or genetic gain [57]. Sequencing of the bovine genome has led to the discovery of thousands of single-nucleotide polymorphism (SNP) markers and subsets of SNPs that can characterize the bovine genome with a wider range and lower cost [58]. In bovine, genome-wide association studies (GWAS) and genomic selection have been done using high-density SNP chips, with thousands of genetic markers for traits related to milk or meat quality, as the fatty acid composition [59–61].

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In dairy cattle, Bouwman et al. [61] performed a genome-wide association analysis using 50,000 SNP markers for the contente of saturated fatty acids (C4:0–C18:0), monounsaturated (C10:1–C18:1), and polyunsaturated (C18:2cis9trans11-CLA), to identify genomic regions associated with individual fatty acids in bovine milk. The authors found 54 regions on 29 chromosomes that were significantly associated with one or more fatty acids. In beef cattle, studies involving genomic association or selection are scarce. Uemoto et al. [60] found 32 SNPs located on the chromosome 19 associated with the amount of oleic acid (C18:1) in the intramuscular fat of the trapezius muscles in Japanese black cattle. The content of oleic acid is positively correlated with the sensorial quality of the meat [62]. In the study of Uemoto et al. [60], the authors used the Illumina BovineSNP50 BeadChip and genotyped only 160 bovines (80 animals with higher values and 80 animals with lower values of oleic acid) selected from 3.356 animals based on corrected phenotype.

Another study with a significantly higher number of animals has been shown for Reecy et al. [59]. They used the BovineSNP50 beadchip (54 k) to genotype 2.285 Angus bulls to analyze the fatty acid concentration of the meat. Effects of SNPs on each trait were estimated using the Bayes C module, considering the probability of a SNP not influencing the trait (π) = 0.90. Depending on the fatty acid considered in the analysis, 2.3–48.5% of observed variance could be explained by an animal's 54 K genotype. According to the authors, long-chain fatty acids appear to be lowly heritable traits with a low proportion of variance accounted by markers, in relation to short-chain fatty acids. They concluded that a large proportion of variation in fatty acid composition is associated with a relatively low number of SNPs. Therefore, genetic progress can be achieved by implementation of whole genome selection to improve fatty acid composition in meat. Similarly, Saatchi et al. [43] found in other GWAS with 2.177 Angus cattle, using a 54-K genotyping panel, 57 genomic regions associated with the fatty acids profile trait in meat. The authors concluded that this large number of genomic regions might indicate the presence of an elaborate molecular mechanism that control fatty acid content in skeletal muscle.

The first genome-wide association study involving intramuscular fat deposition and fatty acid composition in Nelore cattle (*Bos indicus*) was carried out by Cesar et al. [34]. The authors genotyped 386 Nelore steers using a BovineHD BeadChip (770 k) and used Bayesian methods (Bayes B) to identify genomic regions and putative candidate genes that could be involved with fatty acid composition in Nelore. The authors found eight genomic regions (1 Mb windows) for saturated fatty acids that explained more than 1% of genotypic variation for C12:0, C14:0, C16:0, and C18:0. Ten genomic regions for monounsaturated fatty acids, which relates C14:1 cis-9, C16:1 cis-9, C18:1 cis-9, and C18:1 trans-16. For polyunsaturated fatty acids, nine genomic regions which relates C18:2 cis-9 cis12 n−6, C18:2 trans-11 cis-15, C18:3 n−3, C18:3 n−6, C20:3 n−6, C20:5 n−3, and C22:5 n−3. They concluded that intramuscular fat composition is affected by many loci with small effects, and the identification of genomic regions associated to fatty acid composition can lead to selection to improve human nutrition and health.

Trying to identify regions of the genome associated with saturated, mono, and polyunsaturated fatty acids, Lemos et al. [31] genotyped 1616 Nelore using the high-density Bovine BeadChip (770 k) and the single-step method to perform the GWAS. The authors used the single-step method because it allows to combine the information of genotyped and nongenotyped

animals in the genetic evaluation process, expanding the scope and identification of potential regions associated with loci responsible for variations in the studied traits [63]. Interestingly, the results showed that a total of 31 genomic regions that explain more than 1% of genotypic were found for total saturated fatty acids, C12:0, C14:0, C16:0, and C18:0; 37 genomic regions for monounsaturated fatty acids, which relates to total monounsaturated fatty acids, C14:1, C16:1, C18:1 trans11, C18:1 cis9, and C18:1 trans9 and 40 genomic regions for the polyunsaturated fatty acids group as C20:4 n−6, C18:2 cis-9 cis12 n−6, C18:3 n−3, C22:6 n−3, and C20:3 n−6 cis-8 cis-11 cis-14. Additionally, a total 21 genomic regions accounted for more than 1% of the genetic variance for n−3 and n−6 fatty acids and the n−6:n−3 ratio. The authors could conclude that the identification of such regions and the respective candidate genes should contribute to improve the genetic knowledge regarding the fatty acids profile of Nelore cattle and help to improve the selection of such traits to favor human health.

Some authors have been testing different methodologies to predict the direct genomic value for many traits in livestock production, such as SNP-BLUP (single-nucleotide polymorphisms best linear unbiased predictor), which assumes a normal distribution for SNP effect and common variance for all markers [64]; the LASSO (least absolute shrinkage and selection operator) assumes a double exponential distribution for the SNPs effect [65, 66] and Bayesian methods—BayesC and BayesCπ, which considered a variable with binomial distribution that reports whether a marker (SNP) has (1) or not (0) effect on the trait under study, with π variable probability to be zero and a normal distribution with probability $1-\pi$, assuming that part of the effect markers follows a normal distribution. These methods differ in the assumptions about the genetic model associated with quantitative traits, and the best method is the one that reflects the biological nature of polygenic traits, in terms of genic effects [67].

In this sense, studying an Angus population, Saatchi et al. [43] concluded that genomic selection for beef FA profile using Bayesian models is feasible. Moreover, Onogi et al. [68] evaluated the predictive ability of genomic selection in FA composition of Japanese Black cattle, using single-step genomic-best linear unbiased method. Recently, Chiaia et al. [69] evaluated the genomic predictability for beef fatty profile in Nelore breed and concluded that genomic information can assist in improving FA profile in Zebu animals, since the use of genomic information yielded genomic values for FA profile with accuracies ranging from low to moderate. The authors also concluded that none of the evaluated methods (SNP-BLUP, Bayesian Lasso, BayesC, and BayesCπ) excelled in terms of accuracy; however, the SNP-BLUP method allows obtaining less-biased genomic evaluations; thereby, this method is more feasible when taking account the computational cost. The genomic selection has the potential to increase the genetic gain for hard measure traits, like the FA profile, however, the most suitable model to evaluate those traits are still being studied. The divergence between studies suggests that the difference within the methods is due to the genetic architecture of the trait that is the accuracy tends to increase as the model adjusts itself to the genetic architecture of the trait [70] (Lund et al., 2009). For traits that are affected by moderate to major genes effect, higher accuracies can be reached through Bayesian methods [71]. Traits that are controlled by many genes with small effects, polygenic trait, and the SNP-BLUP method showed better prediction ability [72].

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6. Final considerations

The review was to give a comprehensive approach of current knowledge about the genetic influence on the beef fatty acid profile. Several studies have reported genomic regions and genes that are involving witch the lipid metabolic pathways in cattle and other livestock species. With this information, the elucidation of the genetic basis for the improvement of meat quality traits, with an emphasis on human health, becomes closer to reality. Another contribution is the improvement of the knowledge about the biosynthesis of fatty acids and the selection of animals with better nutritional quality. However, more research with focus on genomic and fatty acid composition needed to improve meat is required since the use of genomic information can produce genomic values for FA profile more accurate. Together, this information can be implanted in future breeding programs for cattle, in order to select animals according to the fatty acid profile of the meat.

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