Effects of Dietary Fat Sources on the Expression of Lipid-related Genes Involved in the Fatty Acid Profile of Ruminant Meat

Bora Bölükbaş[1,*], Muhammad Waqas[1,2] and Mustafa Salman[1]

[1]Department of Animal Nutrition and Nutritional Diseases, Faculty of Veterinary Medicine, Ondokuz Mayıs University, Samsun, Kurupelit Campus/Atakum, 55139, Türkiye
[2]Department of Poultry Production, Faculty of Animal Production and Technology, University of Veterinary and Animal Sciences, Lahore, Pakistan
*Corresponding author: bora.bolukbas@omu.edu.tr

Abstract

Ruminant meat contains high levels of saturated fats and low levels of polyunsaturated fats and has therefore been targeted for improvement of its fatty acid profile to be consistent with human dietary recommendations. Sources of dietary fat can affect gene expression of enzymes involved in the fatty acid (FA) profile of ruminant meat. The biochemical regulation of the meat's FA profile consists of complicated mechanisms which incorporate both genetic elements and dietary nutrients. The research focus of nutrigenomics is to modulate and monitor this metabolic process. There has been great interest in understanding how transcription factors control lipid and FA metabolism in this context. The available evidence suggests that gene expression is a key metabolic determinant driving ruminant meat FA profile and lipid accumulation. Moreover, the expression of these lipid-related genes is dependent on the composition and nutrient content of the diet. This chapter describes how nutrition influences the gene expressions associated with lipid metabolism and how dietary manipulations may change the fatty acid profile of ruminant meat.

Keywords: Lipogenic genes, Lipogenesis, Meat, Fatty acid, Transcription factors, SREBFs, PPARs

Cite this Article as: Bölükbaş B, Waqas M and Salman M, 2025. Effects of dietary fat sources on the expression of lipid-related genes involved in the fatty acid profile of ruminant meat. In: Şahin T, Ameer K, Abid M and Tahir S (eds), Nutritional Foundations of Holistic Health: From Supplements to Feed Strategies. Unique Scientific Publishers, Faisalabad, Pakistan, pp: 106-111. https://doi.org/10.47278/book.HH/2025.164

A Publication of Unique Scientific Publishers

Chapter No: 25-015

Received: 11-Jan-2025
Revised: 22-Apr-2025
Accepted: 23-May-2025

Introduction

Ruminant meat displays a fatty acid composition that typically creates concerns for health when compared with other available sources of protein. The current perception of ruminant meat as a less healthy protein source emerges because of its elevated saturated fatty acids (SFAs) levels and its unhealthy omega-6 to omega-3 polyunsaturated fatty acids (PUFAs) ratio, which research suggests promotes cardiovascular disease risks and other chronic health issues (Wood, 2017). A growing concern amongst consumers regarding the health implications of the fatty acid composition of ruminant meat leads to a demand for healthier meat products with a more favourable fatty acid composition. Concern rose in prominence from the 2000s onwards, which affected the behaviour of the consumer and led to research work into producing healthier food options. Therefore, reducing the SFA content OR ratio of the meat has been the focus for researchers. The goal is to elevate the levels of some beneficial fatty acids for the sake of human health while reducing the levels of some fatty acids that may adversely affect (Scollan et al., 2023). The FA profile of ruminant meat may be determined by animal lipid metabolism and/or the FA profile of the diet. Some specific rumen bacteria hydrogenate dietary unsaturated fatty acids such as linoleic and linolenic acids to intermediate products such as trans vaccenic acid (TVAC) and conjugated linoleic acid (CLA) isomers, which ultimately give rise to the saturated fatty acid (stearic acid) leading to a high content of SFAs in meat from ruminants. Generally, the increase in the PUFA amount in the tissues is achieved by the suppression of ruminal biohydrogenation (BH), or increases in the PUFA sources consumed from the diet over the BH capacity (Scollan et al., 2023).

Researchers evaluated PUFA-rich feed sources such as vegetable oils (Miltko et al., 2018), fish oil (Marzo et al., 2023), and oilseeds (Bölükbaş & Kaya, 2022) to understand their ability to allow PUFAs to escape rumen biohydrogenation and reach tissues for nutritional benefits. However, multiple scientific experiments to change FA composition in meat by dietary approaches have produced limited success. As reported in a previous review (Ladeira et al., 2018), it is indicated that close to half of the 28 studies considered did not produce substantial variation in ruminant meat FA composition in response to those dietary changes, and only eight of the studies were successful in increasing the level of CLA in meat. Despite many dietary strategies, these findings suggest that achieving both substantial and consistent enhancements in the FA profile of ruminant meat remains a significant challenge. These challenges have created a need to further investigate whether a significant reduction or change in ruminal biohydrogenation can occur and if the muscle tissue will stay patterned for a specific FAs profile, regardless of the rumen profile that is altered. These research questions have led researchers to reveal the relationship between nutrition and genetics.

Researchers demonstrate that dietary fat sources impact gene expressions that control lipogenesis and lipolysis, thereby changing the pattern of intramuscular lipids (Ladeira et al., 2016). Dietary fatty acids, including PUFAs, show interactivity with peroxisome proliferator-

activated Receptors (PPARs) through binding processes that drive lipid oxidation pathways. This leads to higher concentrations of n-3 PUFAs in the muscle tissue of ruminants fed with n-3 PUFA-rich diets through downregulated activity of genes that handle PUFA desaturation (Dewhurst & Moloney, 2013; Ladeira et al., 2018). Conversely, diets rich in saturated fatty acids activate desaturase gene expressions through stearoyl-CoA desaturase (SCD) and develop unfavorable FA profiles in meat.

In this chapter, it is aimed to show the interaction of fat sources used in studies carried out to improve the meat fat profile in ruminants with some lipogenic genes and transcription factors, and to emphasize the results of dietary strategies used for this purpose. In addition, this chapter will explain the functions of some genes involved in fat metabolism in ruminants and their effects on the meat fatty acid profile and provide a perspective on new dietary strategies to increase beneficial fatty acids in meat.

Main Transcription Factors Regulating Fatty Acid Metabolism

Effective nutritional strategies to enhance ruminant meat FA profiles depend heavily on transcription factors that manage lipid metabolism. In studies aiming to improve the FA profile of meat in ruminants through dietary manipulations, two main approaches have been emphasized. The first approach relates to the quantity of FA that can be absorbed and delivered to tissues following ruminal biohydrogenation. The second approach focuses on the effects of FA as metabolic regulators, which either directly alter the production and accumulation of FA in tissues or influence biological reactions that occur in animals, including gene expression. Studies addressing these topics typically integrate nutrition and gene expression; thus, they are referred to as nutrigenomic, as they explore the influence of nutrition on gene expression within metabolic pathways.

The formation of adipose (fat) tissue in ruminants encompasses the processes of adipogenesis (fat cell formation) and lipogenesis (fat synthesis). Adipogenesis is a process that takes place during the prenatal stage and involves mesenchymal stem cells differentiating into pre-adipocytes. Once pre-adipocytes make their commitment, they move through terminal differentiation to develop intracellular lipid droplets that then generate mature adipocytes (Abebe et al., 2023). The procedure called lipogenesis creates and deposits fatty acids and triglycerides primarily within fat tissue but also occurs to some extent in liver cells (Ladeira et al., 2018). The process becomes most active during postnatal development and fattening periods, while it absorbs circulating substances, including glucose and acetate. The fatty acids are produced from these substrate materials via de novo synthesis enzymatic pathways that contain fatty acid synthase (FASN) and acetyl-coenzyme A carboxylase (ACACA). After being synthesized or taken up by adipocytes, they become possible substrates for transformation through the stearoyl-CoA desaturase enzyme (SCD1). The fatty acids produced and desaturated by these enzymatic pathways are ultimately converted to triglycerides and stored in the tissues for energy reserve (Bionaz et al., 2020).

Dietary modifications during fattening phases show that lipogenesis-related genes have a stronger effect on meat quality than adipogenesis-related genes. The main reason for this phenomenon is that fat cell development finishes largely during fetal development (Liu et al., 2020). Interventions with diet improve meat quality during fattening because they control genes which drive fat production processes (Abebe et al., 2023). Yet adipogenesis and lipogenesis are an integral part of lipid deposition and metabolism in ruminants. Adipogenesis forms the requisite number of adipocytes present for lipid storage and lipogenesis creates adipocytes and provides for FAs and triglycerides synthesis and storage in these adipocytes.

FA mobilization and lipolysis form central processes that determine the fatty acid composition of meat. Adipocyte-stored triglycerides yield free FAs on hydrolysis, which then enter either energy production pathways or re-esterification cycles. The enzyme system, recognized as carnitine palmitoyltransferase (CPT), plays its required role as the transporter that moves fatty acids into the mitochondria in lipolysis processes (Bionaz et al., 2020). The system of CPT maintains the transport of long-chain fatty acids (LCFA) through the CPT1 and CPT2 enzymes across the mitochondrial membrane. CPT1 converts long-chain acyl-CoA into long-chain acylcarnitine, which can then enter mitochondria. CPT 2 converts it back into long-chain acyl-CoA inside the mitochondria, so that it can enter the β-oxidation pathway for energy production.

Higher rates of lipid creation or fatty acid consumption, when combined with diminished fatty acid breakdown, promote muscle tissue lipid accumulation and changes its fatty acid structure. A changed balance between muscle cell fat synthesis and breakdown affects both the accumulation and composition of intramuscular fat deposits (Ladeira et al., 2018).

In ruminants, lipogenic and lipolytic processes depend on key transcription factors PPARs alongside SREBPs. PPARs enhance adipocyte development along with lipid accumulation through activation of gene expressions related to FA uptake and synthesis. The subtype SREBP-1c inside the SREBPs family functions to control fatty acid and triglyceride production gene pathways, including FASN, ACACA, and SCD. The combined action of critical transcription factors determines the amount and distribution of intramuscular lipids, which affects the quality of ruminant meat. Abebe et al., 2023).

Peroxisome Proliferator-activated Receptors (PPARs)

As essential nuclear transcription factors, PPARs play a key role in governing lipid metabolism processes (Ladeira et al., 2018). The PPAR proteins establish functional bonds with fatty acids, especially PUFAs, which then combine operationally with the retinoid X receptor. When PPAR-RXR forms together to adhere to selected target gene promoters, it turns genetic expression on and off for those genes. All three PPAR types, PPARα, PPARγ, and PPARδ, stimulate genes that handle fatty acid absorption along with production while controlling the formation and lipid storage of adipocytes (Bionaz et al., 2015). PPARα activates genes for fatty acid translocation and beta-oxidation while showing low expression in muscle tissue and elevated levels in FA oxidation-heavy tissues such as the liver and heart (Bionaz et al., 2020). PPARγ acts as a vital adipogenesis regulator because it shows high expression levels in adipose tissue necessary for adipocyte differentiation. PPARγ regulates genes for lipid synthesis and storage, plus adipocyte-specific combinations, which help create adipose tissue through this regulation (Abebe et al., 2023). According to Bionaz et al., (2020) dietary fatty acids show varied capabilities to activate PPAR isotypes and found PUFAs bind more effectively to PPAR-α. The PPARα activation through n-3 LCFA leads to modified expression levels and operations in genes concerned with FA metabolism during synthesis, transport, and beta-oxidational pathways in mitochondria and peroxisomes (Rodríguez-Cruz and Serna, 2017).

PUFAs are the most potent endogenous and natural activators of the PPAR family, and especially the PPAR-α subtype is sensitive to activation by fatty acids (Bionaz et al., 2020). The effect of various PUFA sources creates differential impacts on PPAR-α expression levels. The n-3 PUFAs cause an upregulation in PPAR-α expression, while the n-6 PUFAs lead to downregulation in PPAR-α expression. Ebrahimi et al. (2015) reported that PPAR-α gene expression increased in the livers of goats fed diets rich in α-linolenic acid (LA), whereas SCD gene expression decreased. On the other hand, PPAR-α expression decreased and SCD expression increased in beef cattle fed diets rich in linoleic acid as a source of n-6 PUFA (Oliveira et al., 2014). Consistent with these studies, Ebrahimi et al. (2018) reported that as omega-6/omega-3 ratios increased in goat diets, SCD expression increased in goat muscles, but PPAR-α expression decreased. The findings from these studies further support the hypothesis of Waters et al. (2009) that dietary n-6 PUFA and CLA sources are negatively correlated with PPAR, whereas n-3 PUFA sources are positively correlated.

Sterol Regulatory Element-binding Proteins (SREBPs)

SREBPs are one of the main transcription factors that control genes encoding de novo synthetic enzymes in the pathway of lipogenesis. There exist three main SREBP-family members named SREBP-1a, SREBP-1c and SREBP-2. In adipose tissue, SREBP-1c, known as SREBF1, functions as the major isoform that governs the expression of FA synthesis genes, including FA synthase (FASN), acetyl-CoA carboxylase (ACACA), and stearoyl-CoA desaturase (SCD) (Ladeira et al., 2018). SREBP up-regulation elevates FA synthesis in the muscle, which raises intramuscular fat content to improve meat quality according to Teixeira et al. (2017).

In contrast to their action on PPARs, dietary FAs do not directly bind to SREBPs, the effect of dietary FAs on SREBPs is indirect because it is through SCD. It has been shown that long-chain n-3 PUFAs contribute to the decrease in SREBP 1c levels (Kyriakaki et al., 2024). It is possible that decreased lipogenic gene expression and thus intramuscular fat accumulation in ruminants is due to decreased expression of SREBP-1c (Zhang et al., 2023). As previously mentioned, the addition of PUFA to ruminant diets increases PPARα activation, while exerting the opposite effect on SREBP1. Although both genes are associated with lipid metabolism, they play distinct physiological roles. PPAR acts as a transcription factor regulating fatty acid oxidation and energy production, whereas SREBP is responsible for lipogenesis and cholesterol synthesis. PUFA, as natural ligands of PPARα, directly activate this gene, enhancing beta-oxidation and supporting energy production. In contrast, PUFA inhibits the proteolytic activation and nuclear translocation of SREBP, thereby suppressing lipogenesis. As a result, genes that are implicated in the production of FAs and triglycerides exhibit decreased expression, reflecting an adaptive response that prioritizes energy production over energy storage in the presence of PUFA (Ebrahimi et al., 2015).

The process by which omega-3 PUFAs inhibit lipogenic gene production remains unknown. The expression levels of SREBP-1c may decrease because omega-3 PUFAs reduce the activity of enzymes involved in lipid synthesis, including phosphatidic acid phosphatase and 1,2-diacylglycerol acyltransferase (Kyriakaki et al., 2024). Long-chain n-3 PUFAs demonstrate specific nuclear SREBF1 suppressive abilities that cause transcriptional reduction alongside increased mRNA degradation. Exposure to this intervention leads to decreased expressions of lipogenic genes ACACA and FASN in the muscle tissue which results in lower levels of de novo fatty acid synthesis products (Ladeira et al., 2018). Research into gene transcription showed that PUFAs increase PPAR levels while the same compounds decrease SREBP levels. According to Ladeira et al. (2019), The gene expression levels of PPAR-α and SREBF1 show opposing interactions within bovine muscle tissue. Their results showed dietary PUFAs enhanced PPAR gene expression while diminishing SREBF1 gene expression, resulting in higher levels of n-3 PUFA in the cattle's meat.

CLA-enriching dietary variables likely downregulate the SREBF1 gene resulting in reduced lipogenesis by lowering key lipogenic enzyme expression and activity (Bionaz et al., 2015). CLA functionality extends to the direct suppression of the SCD1 gene which ultimately lowers monounsaturated fatty acid production. Research shows that in ruminants, PUFAs together with omega-3 PUFAs and CLA effectively suppress SREBP-1c's expression and activity, where it functions as the main SREBP transcription factor for lipogenesis.

The Fatty Acid Synthesis Genes

The primary regulation of de novo FA synthesis in ruminants involves two lipid-connected genes, specifically FASN and ACACA, which direct the process. During de novo synthesis, FASN operates as a critical enzyme that facilitates the conversion of acetyl-CoA, together with malonyl-CoA, into palmitic acid. The ACACA protein functions as an essential enzyme promoting the rate-limiting carboxylation reaction from acetyl-CoA to malonyl-CoA in fatty acid synthesis (Otto et al., 2023). After its formation as the last product of FA synthesis, the palmitic acid compound can experience further modifications. The compound's carbon structure allows for lengthening through elongation steps or transformation into unsaturated fatty acids with the helper enzyme desaturase. The three principle desaturases in animal tissues are Δ5 desaturase (FADS1), Δ6 desaturase (FADS2), and Δ9 desaturase (SCD). The FADS1 and FADS2 genes encode enzymes that synthesize PUFAs from 18-carbon precursors, including linoleic acid. On the other hand, Δ9 desaturase (SCD) produces monounsaturated fatty acids (palmitoleic and oleic, respectively) from their saturated parent fatty acids (palmitic and stearic, respectively). (Abebe et al., 2023; Waters et al., 2009). Additionally, SCD mediates the conversion of trans vaccenic acid into CLA. Vaccenic acid desaturation by SCD supplies the bulk (over 80%) of the total CLA present in the tissues. Since increased expression of SCD may increase the level of CLA in muscle tissue, which has a positive impact on human health (Scollan et al., 2023).

In ruminants, FADS1 and FADS2 do not play as significant a role as they do in monogastric animals, primarily because their substrates, PUFAs, are largely saturated through ruminal biohydrogenation. In contrast, SCD plays a more direct role by converting saturated FAs into monounsaturated FAs. According to Ladeira et al. (2018), the expression of the SCD gene can be viewed as a marker for intramuscular fat accumulation. Moreover, there were strong relationships between SCD polymorphisms and monounsaturated FA content as well as CLA levels in intramuscular fat.

The FA profile of ruminant meat can be modified by dietary factors such as dietary FA composition through modulation of the lipogenic gene expressions. Dietary FAs, in particular PUFAs, can regulate the expression of these lipogenic genes through subsequent regulation of

SREBPs. PUFA intake decreases SREBP-1c expression and leads to lower expression of lipogenic genes ACACA and FASN, which increases de novo FA synthesis (Herdmann et al., 2010). According to Otto et al. (2023), FASN gene activity showed negative correlation patterns with n-3 PUFA levels. The dietary intake of higher n-3 PUFA blocks SREBF1 activation along with lipogenic gene expression and de novo lipogenesis formation (Hiller et al., 2011).

Research demonstrates that n-3 polyunsaturated fatty acids suppress SCD1 gene activity among multiple animal species (Ladeira et al., 2018; Abebe et al., 2023). The decrease of SCD1 expression transforms meat fatty acid profiles by raising saturated fat amounts plus CLA isomers like vaccenic acid while leading to drops in monounsaturated fatty acids, including oleic acid and palmitoleic acid (Orrù et al., 2010). It has been demonstrated by Herdmann et al. (2010) that bulls fed greater n-3 PUFA diets have less SCD1 expression in muscle tissue, lower CLA isomers in muscle tissue, and lower oleic acid in muscle tissue. Additionally, growing cattle-fed diets rich in PUFA (palm oil or soybean oil) downregulated the SCD1 in the subcutaneous adipose tissue. (Choi et al., 2015). It was reported that SCD, FABP4, and ACAC genes were upregulated in the muscles of fattening cattle whose diets were supplemented with soybean seeds with high linoleic acid content, and high SCD1 expression increased the amount of CLA in the muscles (Oliveira et al., 2014). Ladeira et al. (2019) detected a significant positive correlation between SCD expression and SREBF1 and also reported increases in SCD expression in the muscle tissue of cattle fed cottonseed. The study led by Choi et al. (2013) showed that oleic acid, together with linoleic acid, reduced SCD1 gene activity within bovine tissues. The research shows monounsaturated fatty acids alongside polyunsaturated fatty acids as inhibitors of SCD1 gene expression in adipose tissue. Analysis of the collected data shows that dietary fatty acid profile influences SCD1 gene expression levels, demonstrating that reduced expression of this lipogenic gene matches declines in monounsaturated fatty acids and polyunsaturated fatty acids concentrations.

The Fatty Acid Uptake and Transport Genes

De novo FA synthesis, along with dietary fatty acids from the bloodstream, serve as the main pathways for adipocyte triglyceride accumulation. Specific lipoproteins with triglyceride content undergo breakdown by the enzyme lipoprotein lipase (LPL), which produces free fatty acids (FFAs). Cells and tissues receive FFAs via the mediatory action of targeted transport proteins. There are three main groups of fatty acid transporters that transport fatty acids into cells: fatty acid translocase (CD36), fatty acid transport proteins (FATPs), and fatty acid binding proteins (FABPs). In addition, free fatty acid receptors (FFARs) are sensors for specific FFAs and make a link between dietary fatty acids and metabolic and gene regulatory pathways. These receptors have been involved in the modulation of the activity of genes like CD36 and FABP4, which are genes that indirectly indicate the accumulation of FA in meat (Kimura et al., 2019).

FABP4 (fatty acid-binding protein 4) functions as the main fatty acid transport protein expressed in muscle cells and adipocytes, where it modulates fatty acid deposition, influencing both meat marbling and quality. According to Jurie et al. (2007), FABP4 can be used as an intramuscular adipocyte marker. Intracellular transporter FABP4 is a very important FFA carrier in metabolic pathways to store or produce energy. Research shows that animals consuming high-energy diets express LPL and FABP genes at higher levels than animals following low-energy diets (Oliveira et al., 2014). Increased intake of dietary energy causes levels of circulating lipoproteins to elevate. Levels of FABP4 increase as a consequence of increased LPL activity. Accordingly, Yang et al. (2017) demonstrate that when yaks consume high-energy diets, they show greater expression levels in fatty acid synthase genes (ACACA, FASN, SCD) along with FABP4, which creates changed fatty acid compositions within their longissimus muscle. These findings were consistent with observations that beef cattle fed a soybean diet showed higher gene expression levels of both LPL and FABP4 (Oliveira et al., 2014). The soybean diet's higher linoleic acid levels caused the observed difference and changed PPAR-α expression, according to researchers. Hydrophobic ligands, along with fatty acids, activate transcription factors from the PPAR family, including PPAR-α, PPARβ, and PPARγ. The activity of these transcription factors results in increased expression of the FABP4 gene, which shows the highest expression within adipocytes (Pećina and Ivanković, 2021). The dietary fatty acids absorbed by the small intestine may regulate the expression of the PPAR-α gene through the positive relationship with the expression of the LPL and FABP4 genes. Therefore, if one of these genes is being expressed, the others would be expected to be similarly expressed. However, Otto et al. (2023) reported that the ribeye muscle of lambs receiving n-3 PUFA in their diet showed reduced FABP4 gene expression. Despite matching energy content between the diets provided to the animals, the authors linked reduced FABP4 gene expression to variations in fatty acid deposition.

These findings suggest that transport of FA genes, particularly FABP4, is intimately connected to FA production in ruminant tissues. Understanding the control of these genes can help us modify the FA composition of meat to meet customer needs for healthier meat products. Fatty acid synthesis, transport, and oxidation pathways in ruminants' adipose tissues have been shown in Figure 1.

Influence of Dietary Fatty Acids on Gene Expression

By strategically supplementing cattle diets with targeted dietary fats, it is possible to produce meat that is higher in CLA and n-3 PUFAs and lower in SFA content and fatty acid composition that better matches current human dietary guidelines (Rizzieri et al., 2018). Recent studies have shown that CLA accumulation concurrent with tissues appears to be limited by the apparent inhibitory effect of n-3 PUFA on CLA synthesis in tissues (Waters et al., 2009). Through activation of PPARs, n-3 PUFAs suppress expression of SCD (Ebrahimi et al., 2015). CLA synthesis is limited by reduced SCD activity because SCD is an essential enzyme that converts trans-vaccenic acid into CLA, as mentioned above (Oliveira et al., 2014). Moreover, n-3 PUFAs may inhibit lipogenesis-associated transcription factor SREBF to decrease the expression of FASN and ACACA, which are also required for de novo FA synthesis. Taken together, these metabolic effects render it difficult to simultaneously increase CLA and n-3 PUFA levels in meat.

In contrast, another fat sources, such as those rich in linoleic acid (e.g., sunflower oil and soybean oil), increase SCD and has a less direct and indirect effect on PPAR activation (Herdmann et al., 2010). Due to the lower capacity of n-6 PUFAs to activate PPAR than n-3 PUFAs, linoleic acid, an n-6 PUFA, has a lower suppressive effect on SCD expression (Ladeira et al., 2018). These fat sources coupled with high starch diets promote lipogenesis through upregulation of genes such as SREBF, FASN and ACACA that offset the inhibitory action of PPAR on SCD (Velliquette et al., 2009). In addition, feeding with fats containing linoleic acid enhances the ruminal biohydrogenation, stimulating the

availability of trans vaccenic acid, an SCD substrate used in CLA production (Teixeira et al., 2017). Therefore, incorporation of these fat sources into ruminant diets creates an environment favoring retention or even further stimulation of SCD enzymatic activity, to increase synthesis of CLA independently of any limited stimulation of PPAR activity. The balance between SCD and PPAR activity showcases the need to choose and formulate dietary fat sources carefully, in order to achieve optimal SCD and PPAR activity. The constrained manipulation of dietary fat sources and their appropriate ratios is thus crucial for achieving intended FA profile modifications in meat.

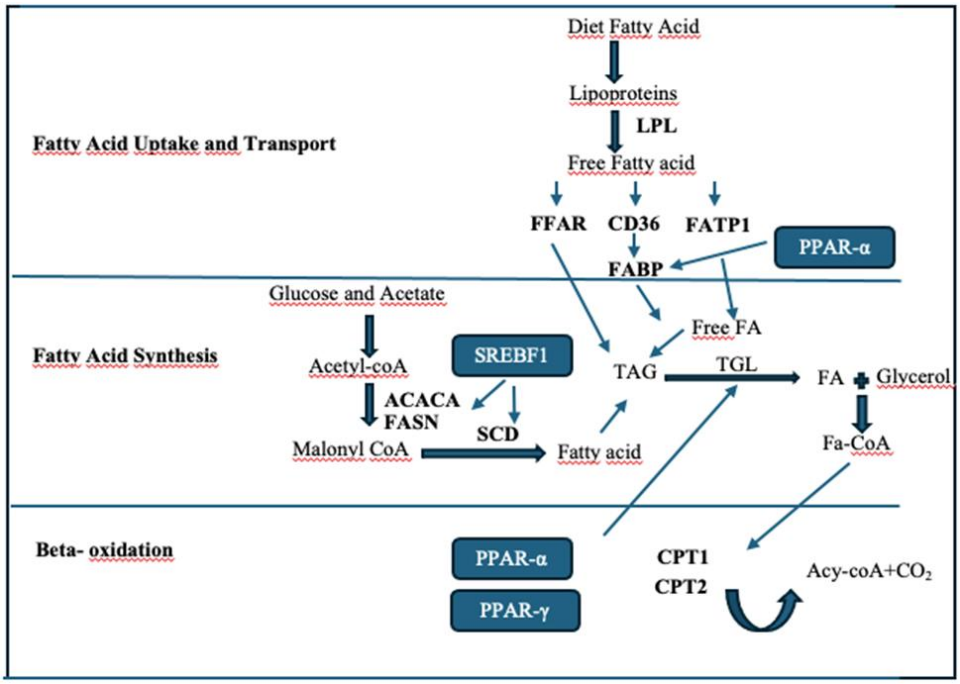

Fig. 1: Fatty acid synthesis, transport, and oxidation pathways in ruminant adipose tissues. LPL: Lipoprotein lipase; TAG: Triglyceride; Transport genes= FFAR: Free fatty acid receptors; FATP: Fatty acid transport protein; CD36: Fatty acid translocase; FABP: Fatty acid-binding protein / Oxidation genes= CPT: Carnitine palmitoyltransferase; PPAR: Peroxisome Proliferator-activated Receptor / Fatty acid synthesis genes= SREBF1: Sterol Regulatory Element-binding Proteins; SCD: Stearoyl-CoA desaturase; ACACA: Acetyl-CoA carboxylase; FASN: Fatty acid synthase.

Conclusion

Dietary manipulations that alter the availability or absorption of particular fatty acids will directly affect gene expression, including expression of genes encoding enzymes of fatty acid synthesis, desaturation, and transport. Ultimately, the coordinated modulation of these lipid-related genes establishes the FA composition of ruminant meat. The deposition of these beneficial FAs can be increased in muscle tissues if supplemented to ruminant diets with n-3 PUFAs from fish oil, linseed, and algae. However, the simultaneous accumulation of n-3 PUFAs and CLA appears to be limited, as n-3 PUFAs decrease the expression and activity of SCD, the major enzyme responsible for converting trans-vaccenic acid into CLA. Conversely, dietary fat sources rich in linoleic acid, an n-6 PUFA, can enhance SCD activity and promote the synthesis of CLA in ruminant tissues. The strategic inclusion of these n-6 PUFA-rich fat sources in ruminant diets while balancing the overall FA profile can help achieve the desired improvements in the healthfulness of the final meat product. Ultimately, a comprehensive understanding of the relationship between ruminal biohydrogenation and the regulatory mechanisms of lipid-related genes in ruminants is crucial for the successful manipulation of the FA composition of meat to meet consumer preferences and nutritional guidelines. By elucidating these complex regulatory pathways, researchers and industry can develop more targeted dietary strategies to optimize the fatty acid profile of ruminant-derived meat, meeting the increasing consumer demand for healthier and more desirable meat products.

References

Abebe, B. K., Wang, H., Li, A., & Zan, L. (2023). A review of the role of transcription factors in regulating adipogenesis and lipogenesis in beef cattle. *Journal of Animal Breeding and Genetics*, 141(3), 235.

Bionaz, M., Osorio, J., & Loor, J. J. (2015). Nutrigenomics in dairy cows: Nutrients, transcription factors, and techniques. *Journal of Animal Science*, *93*(12), 5531-5553.

Bionaz, M., Vargas-Bello-Pérez, E., & Busato, S. (2020). Advances in fatty acids nutrition in dairy cows: from gut to cells and effects on performance. *Journal of Animal Science and Biotechnology*.

Bölükbaş, B., & Kaya, İ. (2022). Crude glycerin and waste sesame seed in the diets of growing lambs: impacts on growth performance, nutrient digestibility, ruminal fermentation, carcass characteristics, and meat fatty acid profile. In Turkish Journal of Veterınary and Anımal Sciences (Vol. 46, Issue 5, p. 675). *Scientific and Technological Research Council of Turkey* (TUBITAK).

Choi, S. H., Park, S., Choi, C. W., Li, X. Z., Kim, K. H., Kim, W. Y., Jeong, J., Johnson, B. J., Zan, L., & Smith, S. B. (2015). The Expression of Adipogenic Genes in Adipose Tissues of Feedlot Steers Fed Supplementary Palm Oil or Soybean Oil. *In Asian-Australasian Journal of Animal Sciences, 29(3), 404*

Choi, S. H., Silvey, D. T., Johnson, B. J., Doumit, M. E., Chung, K. Y., Sawyer, J. E., Go, G., & Smith, S. B. (2013). Conjugated Linoleic Acid (t-10, c-12) Reduces Fatty Acid Synthesis de Novo, but not Expression of Genes for Lipid Metabolism in Bovine Adipose Tissue ex Vivo. *In Lipids, 49, (1) 15.*

Dewhurst, R. J., & Moloney, A. P. (2013). Modification of animal diets for the enrichment of dairy and meat products with omega-3 fatty acids. *In Elsevier eBooks*, 257.

Ebrahimi, M., Rajion, M. A., Goh, Y. M., Farjam, A. S., Oskoueian, E., & Jafari, S. (2015). Diet high in α-linolenic acid up-regulate PPAR-α gene expression in the liver of goats. *In Electronic Journal of Biotechnology*, 18(3), 210.

Ebrahimi, M., Rajion, M. A., Jafari, S., Jahromi, M. F., Oskoueian, E., Sazili, A. Q., Goh, Y. M., & Ghaffari, M. H. (2018). Effects of dietary n-6: n-3 polyunsaturated fatty acid ratios on meat quality, carcass characteristics, tissue fatty acid profiles, and expression of lipogenic genes in growing goats. *PloS one*, *13*(8), e0188369.

Herdmann, A., Nuernberg, K., Martin, J., Nuernberg, G., & Doran, O. (2010). Effect of dietary fatty acids on expression of lipogenic enzymes and fatty acid profile in tissues of bulls. *Animal*, *4* (5), 755-762.

Hiller, B., Herdmann, A., & Nuernberg, K. (2011). Dietary n-3 Fatty Acids Significantly Suppress Lipogenesis in Bovine Muscle and Adipose Tissue: A Functional Genomics Approach. *Lipids*, *46*, 557-567.

Jurie, C. C., Cassar-Malek, I., Bonnet, M., Leroux, C., Bauchart, D., Boulesteix, P., Pethick, D. W., & Hocquette, J.-F. J.-F. (2007). Adipocyte fatty acid-binding protein and mitochondrial enzyme activities in muscles as relevant indicators of marbling in cattle1. *Journal of Animal Science*, *85* (10), 2660-2669.

Kimura, I., Ichimura, A., Ohue-Kitano, R., & Igarashi, M. (2019). Free Fatty Acid Receptors in Health and Disease. *Physiological Reviews,* 100(1), 171.

Kyriakaki, P., Mavrommatis, A., & Tsiplakou, E. (2024). The Interaction of Microalgae Dietary Inclusion and Forage-to- Concentrate Ratio on the Lipid Metabolism-Related Gene Expression in Subcutaneous Adipose Tissue of Dairy Goats. *Animals*, *14* (22), 3291.

Ladeira, M. M., Oliveira, D. M. de, Schoonmaker, J. P., Chizzotti, M. L., Barreto, H. G., Paiva, L. V., Coelho, T. C., Neto, O. R. M., Gionbelli, M. P., & Chalfun-Júnior, A. (2019). Expression of lipogenic genes in the muscle of beef cattle fed oilseeds and vitamin E. *Agri Gene*, *15*, 100097.

Ladeira, M. M., Schoonmaker, J. P., Gionbelli, M. P., Dias, J. C. O., Gionbelli, T. R. S., Carvalho, J. R. R. de, & Teixeira, P. D. (2016). Nutrigenomics and Beef Quality: A Review about Lipogenesis. *International Journal of Molecular Sciences*, *17* (6), 918.

Ladeira, M. M., Schoonmaker, J. P., Swanson, K. C., Duckett, S. K., Gionbelli, M. P., Rodrigues, L. M. A., & Teixeira, P. D. (2018). Review: Nutrigenomics of marbling and fatty acid profile in ruminant meat *Animal*, *12* (p2), p282-p294.

Liu, S., Huang, J., Wang, X., & Ma, Y. (2020). Transcription factors regulate adipocyte differentiation in beef cattle. *Animal Genetics*, *51* (3), 351-357.

Marzo, D. D., Bozzo, G., Ceci, E., Losacco, C., Dimuccio, M. M., Khan, R. U., Laudadio, V., & Tufarelli, V. (2023). Enrichment of Dairy-Type Lamb Diet with Microencapsulated Omega-3 Fish Oil: Effects on Growth, Carcass Quality and Meat Fatty Acids. *Life*, *13* (2), 275.

Miltko, R., Majewska, M., Bełżecki, G., Kula, K., & Kowalik, B. (2018). Growth performance, carcass and meat quality of lambs supplemented different vegetable oils. In Asian-Australasian Journal of Animal Sciences (Vol. 32, Issue 6, p. 767). *Asian-Australasian Journal of Animal Sciences*, *32* (6), 767.

Oliveira, D. M. de, Chalfun-Júnior, A., Chizzotti, M. L., Barreto, H. G., Coelho, T. C., Paiva, L. V., Coelho, C. P., Teixeira, P. D., Schoonmaker, J. P., & Ladeira, M. M. (2014). Expression of genes involved in lipid metabolism in the muscle of beef cattle fed soybean or rumen-protected fat, with or without monensin supplementation1. *Journal of Animal Science*, *92* (12), 5426-5436.

Orrù, L., Cifuni, G. F., Piasentier, E., Corazzin, M., Bovolenta, S., & Moioli, B. (2010). Association analyses of single nucleotide polymorphisms in the LEP and SCD1 genes on the fatty acid profile of muscle fat in Simmental bulls. *Meat Science*, *87* (4), 344-348.

Otto, J. R., Pewan, S. B., Edmunds, R. C., Mwangi, F. W., Kinobe, R. T., Adegboye, O. A., & Malau-Aduli, A. E. O. (2023). Differential expressions of FASN, SCD, and FABP4 genes in the ribeye muscle of omega-3 oil-supplemented Tattykeel Australian White lambs. *BMC genomics*, *24* (1), 666.

Pećina, M., & Ivanković, A. (2021). Candidate genes and fatty acids in beef meat, a review. *Italian Journal of Animal Science*, *20*(1), 1716-1729.

Rizzieri, R. A., Costa, C. F., Melo, G. F., Müller, L., Perdigão, A., Zanata, M., Pacheco, R. D. L., Legako, J. F., Millen, D. D., Martins, C. L., & Arrigoni, M. D. B. (2018). Fatty Acid Profile of Nellore Bulls Supplemented With Different Fat Sources during Feedlot Finishing. *Meat and Muscle Biology*, *2*(2).

Rodríguez-Cruz, M., & Serna, D. S. (2017). Nutrigenomics of ω-3 fatty acids: Regulators of the master transcription factors. *Nutrition*, *41*, 90-96.

Scollan, N. D., Dannenberger, D., Nuernberg, K., Richardson, I., Mackintosh, S., Hocquette, J.-F., & Moloney, A. P. (2023). Enhancing the nutritional and health value of beef lipids and their relationship with meat quality. *Meat Science*, *97*(3), 384-394.

Teixeira, P. D., Oliveira, D. M. de, Chizzotti, M. L., Chalfun-Júnior, A., Coelho, T. C., Gionbelli, M. P., Paiva, L. V., Carvalho, J., & Ladeira, M. M. (2017). Subspecies and diet affect the expression of genes involved in lipid metabolism and chemical composition of muscle in beef cattle. *Meat Science*, *133*, 110-118.

Velliquette, R. A., Gillies, P. J., Kris-Etherton, P. M., Green, J. W., Zhao, G., & Heuvel, J. P. V. (2009). Regulation of human stearoyl-CoA desaturase by omega-3 and omega-6 fatty acids: Implications for the dietary management of elevated serum triglycerides. *Journal of Clinical Lipidology*, *3* (4), 281-288.

Waters, S. M., Kenny, D. A., Killeen, A. P., Spellman, S., Fitzgerald, A., Hennessy, A. A., & Hynes, A. C. (2009). Effect of level of eicosapentaenoic acid on the transcriptional regulation of Δ-9 desaturase using a novel in vitro bovine intramuscular adipocyte cell culture model. *Animals*, *3* (5), 718-727.

Wood, J. D. (2017). Meat Composition and Nutritional Value. In *Lawrie´ s Meat Science* (pp. 635-659). Woodhead Publishing.

Yang, C., Liu, J., Wu, X., Bao, P., Long, R., Guo, X., Ding, X., & Yan, P. (2017). The response of gene expression associated with lipid metabolism, fat deposition and fatty acid profile in the longissimus dorsi muscle of Gannan yaks to different energy levels of diets. *PLoS One,* 12(11), e0187604.

Zhang, T., Li, C., Huang, L., Song, N., Cao, Y., Loor, J. J., Luo, J., & Shi, H. (2023). Regulation of stearoyl-coenzyme A desaturase 1 by trans-10, cis-12 conjugated linoleic acid via SREBP1 in primary goat mammary epithelial cells. *Journal of Agricultural and Food Chemistry*, *67* (5), 1463-1469.