Acta Univ. Sapientiae, Alimentaria, **17** (2024) 70–97

Factors influencing marbling in beef cattle. A review

J. Csapó[1,2,3,4]
e-mail: csapo.janos@uni-mate.hu

A. Kari[4]
e-mail: kari.andras@marbleangus.com

[1] MATE Hungarian University of Agriculture and Life Sciences, Institute of Animal Science, H-7400 Kaposvár, 40 Guba S. St
[2] Sapientia Hungarian University of Transylvania, Faculty of Miercurea Ciuc, Department of Food Science, RO-4100 Miercurea Ciuc, 1 Libertății Sq.
[3] University of Debrecen, Faculty of Agricultural and Food Sciences and Environmental Management, Institute of Food Technology, H-4032 Debrecen, 138 Böszörményi St
[4] Total Meat Solutions SRL, 537131 Borzont, nr. 220, Harghita County

Abstract. Marbling in beef is formed by the intramuscular fat (IMF) content of the muscle tissue, which significantly influences the sensory properties and quality of the meat, including tenderness, juiciness, flavour, and colour. The development of IMF in cattle begins approximately six months after conception and steadily increases throughout the animal's lifetime. During foetal development and postnatal growth, adipogenesis and lipogenesis are regulated by various factors and genes. Marbling is affected by breed, sex, genetics, heredity, the cow's nutrition during pregnancy, the feeding of roughages and concentrated energy feeds, their proportions, and the supplementation or deficiency of vitamins A, C, and D. Other influencing factors include castration, early weaning, and these practices combined with high-energy feed strategies. Different management and feeding strategies have been developed to improve IMF accumulation, and combining these approaches can result in significant improvements in IMF deposition. Genetic, management and especially nutritional factors are the primary influences on the IMF content of beef.

Keywords and phrases: beef cattle, feeding, fattening methods, meat quality, marbling, intramuscular fat content, fatty acid composition

1. Introduction

Beef has been an essential part of human nutrition since ancient times. Today, in Anglo-Saxon countries, the per capita annual beef consumption exceeds 35 kg, while in the European Union, the average reaches 25 kg. In Hungary, the annual per capita meat consumption is approximately 50-52 kg, with beef accounting for about 10-11 kg; in the Transylvanian region (Romania), this figure is even more modest, barely reaching 5 kg. Despite this, beef production has a strong tradition. In the Middle Ages, the Carpathian Basin was considered a supplier of beef to Europe (*Horn*, 2013; *Horn & Stefler*, 2017; *Stefler & Mihalecz*, 2020). Several factors contributed to the decline of beef production in Hungary and the Carpathian Basin at that time. These include social and economic changes, wars, economic crises, and restructuring of land use, all of which significantly reduced pasture areas. Additionally, population decline also contributed to the decreased demand for beef (*Pogácsás*, 2012).

The quality of beef is primarily influenced by marbling and intramuscular fat content (IMF), alongside protein content. IMF refers to the visible fat within the muscle tissue, located between muscle fibres. Marbling manifests as white flecks or streaks visible on the cross-sectional surface of the meat, which are caused by fat deposits between muscle fibres (*Lee et al.*, 2018; *Nguyen et al.*, 2021). The IMF content in meat determines its flavour, taste, and tenderness; increased marbling positively affects sensory properties such as juiciness, colour, tenderness, and flavour. Due to its higher content of polyunsaturated fatty acids (PUFA), IMF is considered healthier for humans, prompting numerous recent studies aimed at improving marbling in ruminant meat (*Nguyen et al.*, 2018; 2021; *Ladeira et al.*, 2018; *Chen et al.*, 2019). In Japan, Australia, and South Korea, the marbling score (MS) is the most important parameter used to assess beef quality.

To identify the levels of marbling, the following criteria were established: Low marbling is characterized by little visible fat between muscle fibres, with meat colour being light red or pink, typical of leaner meats. Moderate marbling features visible fat deposits between muscle fibres that do not extend throughout the entire meat mass. The meat colour is bright red, with fat appearing white or pale yellowish. High marbling shows fat integrated throughout the surface of the meat, which may be darker red in colour (*Cheng et al.*, 2015; *Baik et al.*, 2023). Therefore, the degree of marbling can also be inferred from the meat's colour, which in practice can be assessed by comparing it to a colour scale. Light pink indicates lean meat with little marbling, average red corresponds to moderately marbled meat, while darker red or crimson indicates richly marbled meat with high fat content. In cases of extremely rich marbling, the fat's white or slightly yellowish-white colour is visible throughout, characteristic of the highest-quality, premium meats (*Nguyen et al.*, 2018, 2021; *Chen et al.*, 2019). *Figure 1* shows the grades of marbled meat of Hanwoo.

Marbling develops mainly through the hypertrophy (increase in cell size) and hyperplasia (increase in cell number) of IMF cells, processes that occur throughout the animal's life. Foetal and neonatal IMF cell hyperplasia are essential, followed by the hypertrophy of IMF cells in later life stages. The deposition of IMF in beef cattle is complexly influenced by genetics, nutrition, and management practices. Therefore, understanding the mechanisms of adipogenesis (formation of fat cells from preadipocytes) and lipogenesis (synthesis of fat from carbohydrates in adipose tissue or other tissues) is crucial for increasing IMF deposition and improving beef marbling levels (*Wang et al.*, 2009; *Nguyen et al.*, 2021).

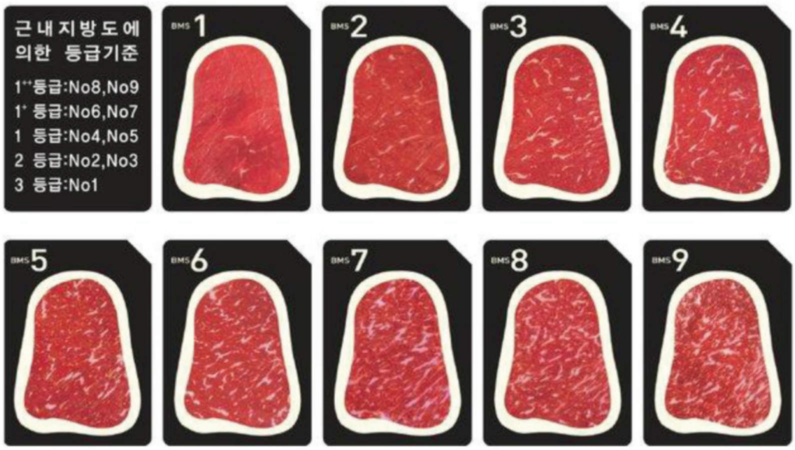

Figure 1. The scores of Hanwoo marbled meat
(*Jo et al.*, 2012; *Chung et al.*, 2018; *Innocencio et al.*, 2023)

In summary, adipogenesis is the process of fat cell formation, during which preadipocytes, or immature fat cells, differentiate into the adipocytes found in adult tissues. Adipogenesis involves the differentiation and development of fat cells. This process is part of lipogenesis, which refers to the accumulation of fat (triglycerides) within fat tissues.

According to *Nguyen et al.* (2021), factors affecting marbling in beef cattle can be categorized into three groups: genetics (breed, genes, inheritance), sex of the animal, nutrition (prenatal nutritional programming, concentrate-to-forage ratio, vitamins), and management practices (castration, age at weaning, age and weight at slaughter).

2. The development and growth of adipose tissue from foetal stage to slaughter in fattening cattle

The first intramuscular fat (IMF) cells develop in the foetus around day 180 of gestation, and the hyperplasia of IMF cells continues until day 250. In contrast, in other fat cells, hyperplasia occurs after early growth, either during the post-weaning period or in the neonatal stage (*Ladeira et al.*, 2018). This difference provides an opportunity to stimulate IMF cell formation without increasing overall fat accumulation in the carcass. During this period, intramuscular adipogenesis is especially active, leading to more IMF deposition and increased marbling levels (*Taga et al.*, 2011).

In IMF accumulation (from day 250 until slaughter), hypertrophy (cell size increase) plays a more significant role than hyperplasia. Intramuscular fat cells continue to grow during the later stages of finishing, whereas the growth of other fat cell types is slow or ceases. For the production of high-quality beef with desirable marbling, animals with high marbling potential are fed in a way that promotes enlargement of fat cell size and increases the amount of IMF between muscle fibres (*Du et al.*, 2017; *Nguyen et al.*, 2021).

Adipogenesis is a complex, tightly regulated process involving two distinct phases: the transformation of mesenchymal stem cells (MSC) into preadipocytes, and adipogenic differentiation. Lipogenesis, the process of endogenous fatty acid (FA) synthesis, is regulated by various factors (*Csapó*, 2004). Fat synthesis begins either through de novo FA synthesis or by uptake of dietary fatty acids, followed by triglyceride synthesis, which is then incorporated into adipose tissue. The extent of fat synthesis in animals is primarily influenced by their diet. In ruminants, precursors for FA biosynthesis include acetate and glucose; subcutaneous fat cells preferentially utilize acetate, while intramuscular fat cells use glucose for fat production (*Csapó*, 2004; *Du et al.*, 2015).

FA uptake into cells is facilitated by various proteins, including fatty acid translocases, fatty acid transport proteins, and fatty-acyl-CoA-synthetase-related fatty-acid-binding proteins (*Ladeira et al.*, 2016). De novo FA synthesis involves enzymes such as acetyl-CoA carboxylase and fatty acid synthase (FAS). Subsequently, FA can be converted into unsaturated fatty acids via stearoyl-CoA desaturase (SCD). During lipolysis, FA are transported into mitochondria via the carnitine-palmitoyltransferase enzyme as acylcarnitine, then reconverted into acyl-CoA, which enters β-oxidation for energy production (*Csapó*, 2004; *Nguyen et al.*, 2017). The synthesis and breakdown of fatty acids influence IMF deposition: increased lipogenesis and FA uptake, along with decreased lipolysis, result in greater IMF accumulation.

In foetal, neonatal, and early post-weaning stages, nutritional status significantly affects adipogenesis and the number of fat cells stored in adipose tissue. Proper feeding during pregnancy and ensuring the dam's nutritional needs are maximized can increase the potential for IMF biosynthesis in the foetus (*Du et al.*, 2013; *Nguyen et al.*, 2021).

3. Main factors influencing beef marbling

The main factors affecting the marbling of beef from fattening cattle are: nutrition, including the optimal provision of nutrients during the foetal period to establish marbling; the ratio of concentrated feeds to roughage during the fattening process;

adequate supply of proteins and energy; vitamin intake, especially vitamins A, C, and D. Genetic factors also play a significant role, including breed, specific genes, and heritability, as well as the sex of the cattle. Lastly, technological factors, such as castration, age at weaning, slaughter age, and body weight, influence marbling (*Schmidt*, 1995, 2003; *Nguyen et al.*, 2021).

3.1. Nutritional factors

In many countries around the world, beef cattle husbandry is fundamentally dependent on grazing. Pasture-based beef production, relying on grazing land and crop by-products, can be carried out with minimal investment. The longer the grazing period and the shorter the feeding season based on harvested feed, the higher the likelihood that beef production will be profitable (*Horn & Stefler*, 2017; *Stefler & Mihalecz*, 2020).

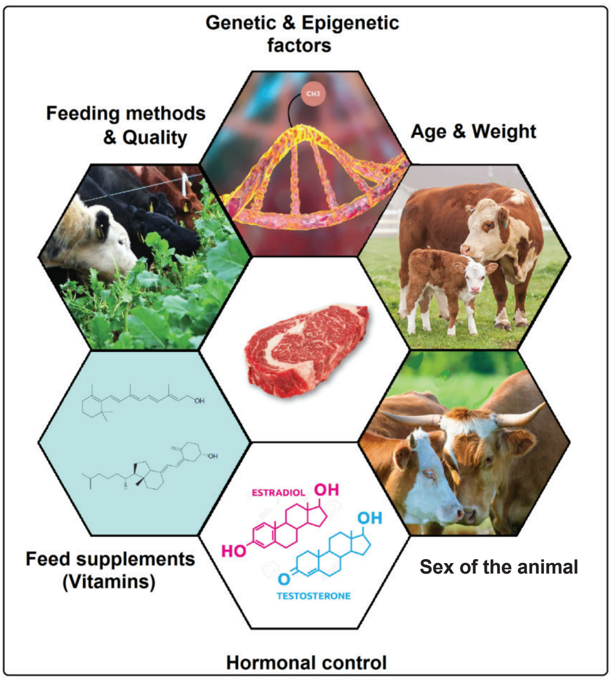

Figure 2. The main biological factors of marbling (based on *Tan & Jiang* (2024))

Pasture-based beef husbandry also plays an important role in landscape and environmental conservation, helping to maintain ecological balance. Without grazing, the condition of grasslands deteriorates, with increased dominance of weeds and invasive species, making the pastures less useful and leading to a decline in local fauna. Conversely, overgrazing also threatens grassland health. Maintaining balance requires conscious livestock management and farming strategies (*Schmidt*, 2003; *Horn & Stefler*, 2017; *Stefler & Mihalecz*, 2020). *Figure 2* shows the main biological factors of marbling (*Tan & Jiang,* 2024). *Table 1* shows a summary of beef quality and yield characteristics (*Baik et al.*, 2023).

Table 1. Summary of beef quality and yield characteristics

Criteria	**Items or indicators**
Beef quality characteristics	
Marbling	Marbling score, marbling size (fine, coarse)
Physiochemical traits	pH, cooking loss, shear force, meat colour, fat colour, texture, maturity
Sensory traits	Tenderness, flavour, juiciness, taste, odour, appearance, overall acceptance
Beef quantity characteristics	
Yield traits	Carcass weight, eye muscle area, backfat thickness
Other considerations	
Economic efficiency	Income
Social consideration	Rural development
Environmental consideration	Carbon footprint, animal welfare
Safety issue	Antibiotic

Source: Baik et al., 2023

3.1.1. The role of nutrition during pregnancy in establishing marbling

Nutritional management of cows during embryonic and foetal stages influences foetal development significantly, impacting the future performance and meat quality of the offspring. Both under- and overfeeding the mother can affect intramuscular adipogenesis in the foetus. The foetal stage is particularly critical because it determines the differentiation of stem cells into muscle, fat, or collagen (*Du et al.*, 2013, 2015; *Ladeira et al.*, 2018). Mesoderm-derived stem cells (MSCs) differentiate into fibroblasts (connective tissue) and preadipocytes (fat cell precursors). Since fibrogenesis and intramuscular adipogenesis are competitive processes, increased adipogenic differentiation reduces fibrogenic differentiation, leading to improved meat tenderness and marbling scores (MS) (*Du et al.*, 2017; *Yamada et al.*, 2020; *Nguyen et al.*, 2021).

If the nutrition of calves during late foetal and neonatal stages is inadequate, fewer intramuscular preadipocytes are formed, significantly limiting the deposition of intramuscular fat (IMF) during fattening. Providing pregnant cows with high-energy diets can promote foetal fat tissue development, which later facilitates IMF accumulation in the offspring. Optimal nutrition during pregnancy subsequently enhances intramuscular adipogenesis, enabling increased IMF content in beef. However, some studies suggest that the impact of foetal nutrition on marbling and intramuscular fat deposition in offspring is minimal, as later feeding conditions tend to overshadow early effects (*Nguyen et al.*, 2021).

There was no significant difference in MS between offspring of cows fed differently during grazing from the 80th day of pregnancy to calving. For Angus cows, limiting dietary energy during late pregnancy did not significantly affect the MS of castrated offspring (*Robinson et al.*, 2013).

The contradictory effects of foetal nutrition on the marbling of offspring's skeletal muscles are difficult to interpret because many factors influence foetal nutrient supply during pregnancy and lactation performance after calving. It is clear, however, that optimal, high-energy diets fed to cows during pregnancy and early life increase fat deposition in calves, as such feeding promotes the growth of adipose tissue by increasing both the number and size of fat cells in the offspring (*Du et al.*, 2017; *Greenwood & Bell*, 2019; *Nguyen et al.*, 2021).

3.1.2. The effect of high-energy, concentrated feed and total mixed ration on marbling

Feeding beef cattle with high-energy, concentrated feed increases the IMF content of the skeletal muscles compared to those fed with low-energy feed; therefore, increasing net energy intake is essential for fat accumulation (*Hwang & Joo*, 2017). Feeding cattle with high-energy, starch-rich diets is one of the best ways to increase the net energy intake because these feeds are broken down into simple sugars in the digestive system, resulting in the production of volatile fatty acids (acetic, propionic, butyric acids), which are primary substrates for fat and protein synthesis and serve as main energy sources for ruminants. Angus crossbreds fed with concentrates had higher MS than those fed only with total mixed ration (*Hwang & Joo*, 2017).

Wagyu cattle slaughtered at 31 months showed higher IMF content in the longissimus muscle (LM) if they were fed high-energy concentrate diets from 4 to 10 months of age, compared to those fed only grass (*Khounsaknalath et al.*, 2021). It was concluded that angiogenic growth factors, along with the ratio of concentrate to roughage, influence fat storage differently in fattened Wagyu steers.

Animals fed with high-energy diets are believed to have stimulated intramuscular preadipocytes, resulting in higher MS values in their meat compared to animals on lower-energy diets. It is also hypothesized that the ratio of concentrate to roughage significantly affects the expression of adipogenic genes in fat stores (*Li et al.*, 2018).

In Hanwoo cattle, however, a negative correlation was found between the concentrate/total mixed ratio and IMF content. In this case, the ratio of barley silage to concentrate during the fattening period did not cause significant differences in MS among Hanwoo steers (*Yang et al.*, 2020). When bulls were fed whole corn without concentrates, higher IMF content was observed in the LM compared to those fed ground corn and corn silage. It is believed that a high-energy diet decreased ruminal pH, altered rumen microbiota, and shifted biohydrogenation pathways, leading to increased synthesis of trans10-cis12 conjugated linoleic acid (t10,c12 CLA) at the expense of cis9-trans11 CLA. The trans10-cis12 linoleic acid isomer reduces the expression of genes involved in fatty acid synthesis, which is the main reason for decreased de novo fatty acid synthesis in bovine preadipocytes, while promoting the expression of genes related to fatty acid oxidation. Overall, this inhibits fatty acid synthesis and promotes fatty acid breakdown and β-oxidation (*Obsen et al.*, 2012; *Bionaz et al.*, 2012).

Research on feeding residual moist grains after distillation found that increasing the proportion of moist grains in the diet raised the levels of polyunsaturated fatty acids with 18 or more carbons and trans fatty acids in the muscle tissue. However, no significant differences in saturated or unsaturated fatty acids were observed with vitamin E supplementation (*Senaratne et al.*, 2009; *De la Fuente et al.*, 2009; *Luciano et al.*, 2011; *Juárez et al.*, 2012; *Nguyen et al.*, 2018).

3.1.3. The role of transcription factors in marbling

Transcription factors are proteins that regulate gene transcription to mRNA, thereby influencing cell function and development. The formation of marbling, i.e. the fat layer in meat, is closely related to meat quality and flavour and is governed by multiple factors, including genetic, environmental, and biochemical processes. The role of transcription factors in marbling development can be summarized as follows: Some transcription factors participate in the formation and differentiation of fat and adipose tissue by stimulating adipocyte formation and lipid metabolism processes, thus contributing to the development of marbling (*Liu et al.*, 2020; *Abebe et al.*, 2024a–b). Other transcription factors regulate the growth of adipose tissue, influencing meat fat content and quality. They also control genes involved in energy metabolism, which affect fat and muscle development, indirectly impacting marbling (*Ueda et al.*, 2025). These transcription factors operate at different levels across various genetic lines and individual animals, which may explain differences in meat marbling among breeds. In summary, transcription factors play a central role in the development of fat cells, fat accumulation, and overall meat quality (*Luscombe et al.*, 2000; *Buchlet et al.*, 2003; *Goodrich & Kugler*, 2003).

3.2. The role of vitamins in the development of intramuscular fat content in muscle tissue

3.2.1. The effect of retinol (vitamin A) on IMF

Vitamin A (retinol) plays a crucial role in the overall health, growth, and productivity of cattle. It is essential for vision, skin formation, immune system function, and reproduction (*Wang et al.*, 2016; *Peng et al.*, 2021). In feed, the provitamin of vitamin A, carotene, is present in higher amounts, which the body converts into vitamin A with the help of the enzyme carotenoidase. Retinoic acid, a metabolite of vitamin A, is significant in the development of preadipocytes and the differentiation of fat cells. Using an *in vitro* adipogenesis model with mesenchymal stem cells (MSCs), it was found that retinoic acid promotes the development of MSC adipogenic cells (*Dani et al.*, 1997; *Wang et al.*, 2016).

It has also been established that vitamin A limits IMF deposition by reducing the hyperplasia of fat cells, which can occur even after 14 months of age or during finishing periods. Therefore, vitamin A influences the differentiation of fat cells rather than fat accumulation itself. Specifically, vitamin A appears to restrict IMF deposition but does not significantly affect subcutaneous fat stores (*Kruk et al.*, 2018; *Peng et al.*, 2019). Recent studies have shown that restricting vitamin A during the finishing period increased marbling in Angus calves and Wagyu cattle, although no significant effects were observed in Hanwoo calves or crossbred Angus calves (*Pickworth et al.*, 2012).

The health status and marbling score (MS) of cattle are influenced by age and the duration of vitamin A deprivation or supplementation. Calves treated with 45 µg (150,000 IU) of vitamin A exhibited higher IMF content at slaughter compared to untreated calves. Early vitamin A supplementation enhances beef production efficiency and increases marbling. Conversely, vitamin A restriction in Wagyu cattle at different slaughter times either increased MS or had no effect at all (*Wang et al.*, 2016; *Harris et al.*, 2018).

Continuous restriction of vitamin A during the late finishing phase is not recommended, as it can cause joint inflammation, muscle oedema, severe liver diseases, blindness, and decrease growth rate, ultimately impairing carcass quality. Experts suggest that during the initial finishing phase, vitamin A content in concentrated feed should be between 3,520 and 15,400 IU/kg, and in later stages between 3,300 and 7,260 IU/kg. It has been determined that plasma retinol concentrations in fattening beef fed a vitamin-A-restricted diet should not fall below 300 IU/l (*Oka et al.*, 1998; *Kawachi*, 2006).

3.2.2. The effect of L-ascorbic acid (Vitamin C) on IMF

The liver of cattle can synthesise vitamin C, so it is generally not supplemented in their diet (*Mwangi et al.*, 2019). Vitamin C plays an important role in collagen synthesis, redox reactions, and fertility treatments. Due to its positive effect on preadipocytes, it promotes adipogenesis. For example, Hanwoo steers showed increased MS when fed a diet supplemented with coated vitamin C with saturated palm oil, and rumen-protected vitamin C improved MS in Wagyu and Angus-crossed steers (*Kawachi*, 2006). However, in Angus steers, MS did not significantly change with rumen-protected vitamin C supplementation, indicating that the effects depend on the level and duration of supplementation, and further research is needed to clarify these influences (*Pogge & Hansen*, 2013).

3.2.3. The effect of calciferol (Vitamin D) on IMF

The active form of vitamin D, 1,25-dihydroxy-D_3, is an important factor in maintaining calcium homeostasis and responds rapidly to dietary calcium levels. Studies examining vitamin D's impact on IMF deposition in ruminants have found that it inhibits adipogenesis by limiting preadipocyte differentiation (*Mwangi et al.*, 2019). Diets low in vitamin D_3 resulted in higher MS compared to those with higher vitamin D_3 levels. However, dietary vitamin D supplementation has often shown no significant differences in MS across different breeds and crossbred steers (*Knobel-Graves et al.*, 2016; *Reilig & Johnson*, 2003).

In summary, vitamin D supplementation in cattle feed has a more direct impact on bone health and tenderness, but its influence on marbling – the amount of intramuscular fat – is indirect and generally less pronounced than the effects of other factors such as diet composition and breed. Diets of pasture-raised and barn-raised cattle differ markedly: pasture-based diets are typically lower in energy and protein, which can limit marbling development. Vitamin D plays a role in calcium absorption and utilization, which can indirectly influence bone – and potentially muscle – development. Although vitamin D can affect marbling, its impact tends to be more pronounced in barn-raised cattle, where the feeding environment is controlled and supplementation is feasible. Pasture-raised cattle, by contrast, rely more on natural sunlight-driven synthesis of vitamin D, making supplementation effects less significant (*Poltorak et al.*, 2017).

4. Genetic factors

4.1. Breed

In beef cattle, intramuscular fat (IMF) accumulation is significantly influenced by genetic background in addition to nutrition (*Wang et al.*, 2009; *Nguyen et al.*, 2021). The longissimus muscle (LM) of Wagyu cattle contains the highest amount of IMF, averaging between 31.8% and 37.8%. The second highest IMF content was measured in Hanwoo cattle's LM, ranging from 13.3% to 19.7%. Generally, the IMF content in

Bos taurus cattle is higher than in Bos indicus. The IMF content in Hereford breeds averages around 8.3%, while in Angus it varies between 6.5% and 7.5%, both higher than the approximately 5% observed in Brahman and Nellore breeds (*Teixeira et al.*, 2017; *Flowers et al.*, 2018; *Detweiler et al.*, 2019; *Miguel et al.*, 2011).

What causes these significant differences in IMF content among breeds? The variations in IMF deposition between breeds may be attributed to differences in energy metabolism and fatty acid (FA) synthesis in the liver, as well as the expression of regulatory genes. Higher IMF levels are associated with increased amounts of saturated fatty acids (SFA) and monounsaturated fatty acids (MUFA), whereas polyunsaturated fatty acid (PUFA) levels have shown only minor differences among breeds. The genetic variation in fatty acid metabolism is primarily due to the fact that PUFAs are mainly incorporated into cell membrane phospholipids, while SFAs and MUFAs primarily constitute the triacylglyceride fraction, which is the main lipid fraction responsible for adiposity in tissues (*De Smet et al.*, 2004).

Studies examining IMF incorporation into the muscles of Wagyu and Angus cattle have shown that the improvement in marbling score (MS) in Wagyu is associated with increased mRNA expression early in life, and with enhanced expression of adipogenic markers later on. It has been observed that higher levels of adipogenic markers in the longissimus muscle of Angus correlate with higher IMF content, similar to Nellore cattle. This suggests that, compared to low-marbled beef cattle, breeds producing highly marbled beef have increased IMF associated with enhanced adipogenesis (*Duarte et al.*, 2013; *Martins et al.*, 2015).

4.2. Genotype and heritability

In animals of the same breed, sex, similar age, and diet, the IMF content of skeletal muscles is regulated by different genes. Analysing 20 Hanwoo cattle raised and classified into high and low marbling groups (up to 30 months old), it was found that the group with high marbling exhibited strong expression of the triosephosphate isomerase 1 gene, whereas the low marbling group showed high expression of genes such as troponin T type 1, actin alpha 1, and malate dehydrogenase 2 (*Shin & Chung*, 2016; *Poleti et al.*, 2018). In crossbred Xiangxi x Angus cattle, it was also shown that the high IMF group had significant regulation of the triosephosphate isomerase 1 gene (*Mao et al.*, 2016). In Angus steers, three genes – enolase 3, pyruvate kinase M2, and glucose-6-phosphate isomerase – exhibited higher activity in the LM of cattle with greater IMF content.

Heritability estimates for marbling score (MS) in various beef breeds over long periods have shown wide ranges (0.01–0.88), but most values fall between 0.30 and 0.57, with subsequent studies reporting values between 0.34 and 0.68 (*Utrera & Van Vleck*, 2004). The heritability of MS in Wagyu cattle is particularly high, ranging from 0.63 to 0.68 (*Inoue et al.*, 2015), while in Hanwoo and Angus cattle it varies between 0.46 and 0.61, and 0.35 and 0.61 respectively. For Nellore cattle, heritability estimates range from 0.34 to 0.47, and for Brahman cattle from 0.37 to 0.44. In Korean Chikso cattle, heritability was measured at 0.53 (*Park et al.*, 2020).

The genetic potential of individual animals also significantly influences their capacity to accumulate IMF, as the level of marbling is not uniform across animals within the same breed. Generally, animals with lower IMF deposition potential tend to have lower marbling scores at slaughter, compared to those with higher IMF potential (*Black et al.*, 2015; *Chen et al.*, 2019). Animals with high marbling potential show upregulated mRNA levels associated with adipogenesis, while reduced mRNA levels are linked to myogenesis, which explains the lower MS observed during increased muscle growth in cattle (*Chen et al.*, 2019).

4.3. Sex

The sex of the cattle significantly influences the IMF content of the skeletal muscles. Generally, for the same slaughter weight, age, feeding technology, and time, bulls of the same breed have lower IMF content compared to heifers (*Pethick*, 2004; *Stefler & Mihalecz*, 2020). Studies examining the effect of sex on IMF content have found that it has a significant impact on the FA profile and physical-chemical properties of Qinchuan beef (a premium Chinese beef known for its excellent flavour and texture due to regional breeding and meat processing methods) (*Zhang et al.*, 2010). Sex hormones significantly affect intramuscular fat cell hyperplasia and hypertrophy in cattle. It has also been established that fat cell metabolism can be modified by changing the sex hormone status of the cattle (*Picard et al.*, 2019).

5. Breeding technology

5.1. Castration

Castration of male calves generally leads to a significant improvement in the marbling level of certain cattle breeds' skeletal muscles. Castration significantly increases IMF content in Holstein-Friesian calves, Hanwoo cattle, Chinese Qingyuan cattle, and Nellore steers. Castration is a common practice in Japan for fattening highly marbled Wagyu beef (*Zhang et al.*, 2017; *Gotoh et al.*, 2018). In South Korea, approximately 90.5% of Hanwoo bulls are castrated. Castration can promote an increase in IMF content because it enhances lipid uptake and lipogenesis, while reducing lipolysis. Castration has been shown to increase IMF content, marbling scores, and improve beef quality by upregulating adipogenic gene expression without changing fibrogenic gene expression (*Bong et al.*, 2012; *Park et al.*, 2018a; 2018b).

Surgical castration involves removal of both testes, which leads to increased fat deposition, improved carcass quality, reduced aggressiveness, and enhanced sexual behaviour (*Mueller et al.*, 2019). Recently, alternative methods such as partial castration, immunocastration with gonadotropin-releasing hormone, and chemical castration using substances like sodium chloride, calcium chloride, ethanol, and lactic acid have been employed. In calves, it has been observed that partial castration, compared to traditional methods, positively affects growth performance and meat yield, which can be explained by the testosterone produced by one testis. However, partial castration reduces MS because it inhibits fat cell differentiation and lipid synthesis, whereas immunocastration improves fat deposition and meat quality (*Moreira et al.*, 2018; *Mueller et al.*, 2019).

The timing of castration can also influence marbling; early castration increases marbling, while late castration decreases it. For Nellore cattle, castrated bulls at weaning had higher MS than those castrated at 20 months. There was a negative correlation between IMF content and age at castration in Holstein cattle, although no significant differences were observed in MS immediately after calving or at weaning. In Hanwoo bulls, no significant differences in meat quality were found between bulls castrated at different times (*Chung et al.*, 2018; *Hong et al.*, 2021).

5.2. Weaning age

In traditional breeding systems, calves are weaned from their mothers at 180–220 days of age. Early weaning can be performed as soon as 45 days after calving, and it is considered early if it occurs before 180 days of age (*Stefler & Mihalecz*, 2020). The weaning age influences intramuscular fat (IMF) deposition. When combined with high-energy diets, early weaning is one of the most effective methods to improve beef marbling. Studies on Angus bulls have concluded that calves weaned at 90 days show better feed utilization and higher average daily gain, hot carcass weight, and fat percentage compared to calves weaned at the conventional average of 174 days (*Rasby*, 2007; *Reddy et al.*, 2017).

At 105 days of age, Angus calves weaned and fed on high-energy diets for 148 days showed increased hot carcass weight and carcass yield compared to calves weaned at 253 days and kept with their mothers on pasture. Early weaning at 141 days combined with high-energy feeding increased IMF content in Angus and Angus × Simmental calves compared to the standard weaning at 222 days. Early weaning, along with high-energy diets and activation of adipogenic genes, stimulated the differentiation of preadipocytes and fat deposition in early-maturing animals (*Scheffler et al.*, 2014).

5.3. The effect of age and slaughter weight

In various cattle breeds, IMF content increases with age (*Okumura et al.*, 2012). For example, the IMF content of the longissimus dorsi muscle in Wagyu calves was 23.7% at 20 months and increased to 41.1% by 30 months. Increased IMF levels have also been observed in Angus, Hereford, and Wagyu × Angus cattle as their slaughter age advanced. Holstein-Friesian bulls slaughtered at 26 months had higher IMF than those slaughtered at 20 months (*Wang et al.*, 2019). Similar trends are seen in young Simmental bulls and Holstein calves. The influence of slaughter age on the expression of adipogenic genes has been noted to increase with the animal's age (*Li et al.*, 2018).

A positive correlation exists between IMF content, carcass weight, and muscle mass across different cattle breeds. IMF increases when the hot carcass weight of Angus, Angus × Hereford, and Wagyu × Holstein cattle rises from 100 to 450 kg. In Nellore heifers, a positive relationship was found between muscle mass and slaughter weight. The IMF content in the longissimus muscle significantly increases in Holstein × Limousin bulls and steers as carcass weight increases from 450 to 600 kg. Similar findings have been reported for Angus, Wagyu × Angus, and Hereford cattle (*Nogalski et al.*, 2014; *Greenwood et al.*, 2015).

Nellore heifers slaughtered at higher weights are expected to have higher adipose tissue deposition, including the marbling fraction, in adult animals. Marbling was similar in meat from cows slaughtered at different weights, with values ranging from 7.3 to 6.7. Although the backfat thickness of the carcasses of cows slaughtered at higher weights was greater, this difference was not sufficient to alter the marbling of the meat (*Rodrigues et al.*, 2015).

The amount of myoglobin in the muscle is one of the factors that determines the intensity of the red colour of the meat, and its concentration increases with the aging and/or weight gain of the animal (*Rezende et al.*, 2012). In animals of similar age, slaughtered between 340 and 400 kg, the slaughter weight did not result in differences in the colour and quality of the meat. The texture of the meat was not affected by the slaughter weight, reaching an average of 3.19 points, which corresponds to a medium texture classified between "slightly thick" and "fine" (*Table 2*). It is likely that the genetic homogeneity and uniform age of the animals studied caused the similar meat texture in the experimental groups.

Subjective assessment of the intermuscular fat content of the longissimus dorsi, which estimates the degree of marbling of the meat, showed lower values for animals slaughtered at a slaughter weight of less than 340 kg compared to the other slaughter weight classes, which did not differ from each other and showed results that could be considered highly satisfactory (*Table 2*). Marbling fat refers to the number and size of fat granules between muscle fibres, which is a key parameter for the organoleptic characteristics of meat, since the amount of lipids in meat is closely related to its palatability and juiciness. *Table 2* shows the characteristics of meat from Nellore heifers slaughtered at different body weights.

Table 2. Characteristics of meat from Nellore heifers slaughtered at different weights

Variable	Slaughter weight class (kg)			
	≤ 340	340–370	370–400	≥ 400
pH	5.57	5.57	5.59	5.56
Colour points	2.93	3.30	3.37	3.55
Texture points	3.05	3.30	3.18	3.23
Marbling points	4.72	10.90	9.66	8.78

Source: Rezende et al., 2012

Notes: marbling: 1 to 3 = traces; 4 to 6 = slight; 7 to 9 = little; 10 to 12 = medium; 13 to 15 = moderate; 16 to 18 = abundant.

Differences in IMF content and marbling among animals of different ages and slaughter weights are mainly attributed to genetics, management, and nutrition. Muscles require time to reach appropriate maturity, and extended finishing periods allow animals more time to develop high marbling levels. Once animals reach an optimal slaughter age and weight, muscle growth slows, and feed efficiency declines because less energy is needed for muscle accretion compared to fat deposition. Prolonged finishing can lead to increased subcutaneous fat thickness, negatively affecting yield and quality (*Pethick et al.*, 2004; *Agastin et al.*, 2013).

Every 1% increase in intramuscular fat is estimated to correspond to a 3.0 kg increase in subcutaneous fat in Wagyu, 4.3 kg in Holstein-Friesian, 7.9 kg in Angus, and 10.7 kg in Belgian Blue cattle. Therefore, extending the finishing period to enhance marbling is only recommended for animals with high genetic potential (*Gotoh et al.*, 2009).

Prolonged finishing can decrease carcass quality, reduce economic efficiency by increasing visceral and subcutaneous fat deposits and feed costs, but it can also improve meat tenderness. Technologies producing highly marbled meat in Hanwoo and Wagyu breeds are characterized by high costs and economic inefficiency, as Wagyu cattle, for example, consume highly expensive imported energy-dense feed twice or thrice daily from 11 months until slaughter at 28-30 months of age (*Greenwood*, 2021).

Since consumer demand for higher marbling score (MS) beef has increased, cattle must be fed intensively for longer periods, typically between 100 and 300 days. In South Korea, the average slaughter age for Hanwoo cattle has increased from 30.2 months to 32.5 months in recent years. Japanese Wagyu steers are usually slaughtered at around 29 months of age (*Motoyama et al.*, 2016).

Achieving higher intramuscular fat (IMF) levels promotes the accumulation of less valuable fat in fat depots, which consequently raises production costs and reduces feed efficiency. During the fattening of Hanwoo steers, IMF content increased rapidly between 12 and 28 months of age, with the most significant growth observed between 24 and 28 months. Optimal profitability was achieved when animals were slaughtered at 28 months; beyond this age, profit decreased. Therefore, slaughter age, carcass weight, meat quality, feed costs, labour costs, and carcass price must all be considered to optimize profit (*Lee et al.*, 2013). *Table 3* shows a summary of factors affecting beef quality (*Sakowski et al.*, 2022; *Park et al.*, 2018).

Table 3. Summary of factors affecting beef quality

Factors	**Major beef quality items**
Genetic factors	
Breed	Marbling, sensory, yield, income
Sex	Marbling, sensory, musculature, income
Management factors	
Castration	Marbling, sensory, yield, income
Slaughter age/weight	Marbling, sensory, yield, income
Environments	Marbling, yield
Nutritional factors/feeding system	
Plane of nutrition	Marbling, sensory, yield, income
Roughage : concentrate ratio	Marbling, fatty acid composition, sensory, income
Feeding systems	Marbling, sensory, income

Source: Sakowski et al., 2022; Park et al., 2018

6. Conclusions

In cattle, adipogenesis and lipogenesis responsible for IMF deposition are influenced by factors such as genetics, sex, nutrition, and management practices. Fat cell development begins during early embryonic stages and continues throughout the animal's life. Bos taurus breeds generally produce meat with higher IMF content compared to Bos indicus breeds. The accumulation of IMF is regulated by various related genes, with heritability ranging from moderate to high.

In foetuses and neonatal stages, nutrition and vitamin A supplementation significantly influence the number of intramuscular fat cells, as well as the proliferation and differentiation of preadipocytes and adipocytes. During later growth phases, a higher proportion of concentrated and roughage feeds markedly enhances IMF cell hypertrophy. Dietary restrictions of vitamins A and D, along with vitamin C supplementation, have positive effects on IMF deposition. Castration and early weaning, combined with high-energy diets, are effective strategies to increase marbling, and slaughter age and weight are also positively correlated with IMF content. Wagyu and Hanwoo breeds possess a high marbling potential, often being fattened for extended periods on energy-dense diets. Prolonged finishing increases IMF deposition in muscle but can compromise carcass quality and significantly raise management and feeding costs.

Feeding mature animals excessively energy-rich diets during the late finishing phase affects feed conversion efficiency, leading to an increase in visceral and subcutaneous fat that is less suitable for human consumption. Rising feeding costs further threaten the sustainability of production systems.

In general, increasing marbling tends to contribute to higher feeding costs, as it requires the use of more energy-dense or specially formulated feeds, which are often associated with longer finishing periods. This extension in finishing time raises the overall raising expenses, and in some cases additional treatments may be necessary, further increasing costs. Estimates suggest that feed expenses can increase by 10-20% to achieve higher marbling levels compared to standard finishing, although this largely depends on the specific methods used, the composition of the feed, the breeding conditions, and the targeted quality.

Developing comprehensive technologies that simultaneously address genetics, nutrition, and management factors, as well as improving feeding efficiency, is necessary to enhance marbling levels within a herd. Relying on a single-factor change will not increase the IMF content of beef significantly.

References

[1] Abebe, B. K., Wang, H., Li, A., Zan, L., A review of the role of transcription factors in regulating adipogenesis and lipogenesis in beef cattle. *Journal of Animal Breeding and Genetics*, 141. (2024) 235–256.

[2] Abebe, B. K., Wang, J., Guo, J., Wang, H., Li, A., Zan, L. A review of emerging technologies, nutritional practices, and management strategies to improve intramuscular fat composition in beef cattle, *Animal Biotechnology*, 35. 1. (2024) 1–20.

[3] Agastin, A., Naves, M., Farant, A., Godard, X., Bocage, B., Alexandre, G., Effects of feeding system and slaughter age on the growth and carcass characteristics of tropical-breed steers. *Journal of Animal Science*, 91. (2013) 3997–4006.

[4] Baik, M., Lee, J., Kim, S. Y., Ranaweera, K. K. T. N., Factors affecting beef quality and nutrigenomics of intramuscular adipose tissue deposition. *Animal Bioscience*, 36. (2023) 350–363.

[5] Bionaz, M., Thering, B. J., Loor, J. J., Fine metabolic regulation in ruminants via nutrient–gene interactions: Saturated long-chain fatty acids increase expression of genes involved in lipid metabolism and immune response partly through PPAR-α activation. *British Journal of Nutrition*, 107. (2012) 179–191.

[6] Black, D., Neville, B., Crosswhite, M., Dahlen, C., Evaluation of implant strategies in Angus-sired steers with high or low genetic potential for marbling and gain. *Journal of Animal Science*, 93. (2015) 5411–5418.

[7] Bong, J. J., Jeong, J. Y., Rajasekar, P., Cho, Y. M., Kwon, E. G., Kim, H. C., Differential expression of genes associated with lipid metabolism in longissimus dorsi of Korean bulls and steers. *Meat Science*, 91. (2012) 284–293.

[8] Buchler, N. E., Gerland, U., Hwa, T., On schemes of combinatorial transcription logic. *Proceedings of the National Academy of Sciences*, 100. 9. (2003) 5136–5141.

[9] Chen, D., Li, W., Du, M., Cao, B., Adipogenesis, fibrogenesis and myogenesis related gene expression in longissimus muscle of high and low marbling beef cattle. *Livestock Science*, 229. (2019) 188–193.

[10] Cheng, W., Cheng, J. H., Sun, D. W., Pu, H., Marbling analysis for evaluating meat quality: Methods and techniques. *Comprehensive Reviews in Food Science and Food Safety*, 14. (2015) 523–535.

[11] Chung, K. Y., Lee, S. H., Cho, S. H., Kwon, E. G., Lee, J. H., Current situation and future prospects for beef production in South Korea – A review. *Asian-Australasian Journal of Animal Sciences*, 31. (2018) 951.

[12] Csapó J., *Biokémia* [Biochemistry]. Scientia Publishing House, Cluj-Napoca. (2004) 1–468.

[13] Dani, C., Smith, A. G., Dessolin, S., Leroy, P., Staccini, L., Villageois, P., Differentiation of embryonic stem cells into adipocytes *in vitro*. *Journal of Cell Science*, 110. (1997) 1279–1285.

[14] De la Fuente, J., Díaz, M. T., Álvarez, I. et al. Fatty acid and vitamin E composition of intramuscular fat in cattle reared in different production systems. *Meat Science,* 82. 3. (2009) 331–337.

[15] De Smet, S., Raes, K., Demeyer, D., Meat fatty acid composition as affected by fatness and genetic factors: A review. *Animal Research*, 53. (2004). 81–98.

[16] Detweiler, R. A., Pringle, T. D., Rekaya, R., Wells, J. B., Segers, J. R., The impact of selection using residual average daily gain and marbling EPDs on growth, performance, and carcass traits in Angus steers. *Journal of Animal Science*, 97. (2019) 2450–2459.

[17] Du, M., Ford, S. P., Zhu, M. J., Optimizing livestock production efficiency through maternal nutritional management and fetal developmental programming. *Animal Frontiers*, 7. (2017) 5–11.

[18] Du, M., Huang, Y., Das, A., Yang, Q., Duarte, M., Dodson, M., Manipulating mesenchymal progenitor cell differentiation to optimize performance and carcass value of beef cattle. *Journal of Animal Science*, 91. (2013).1419–1427.

[19] Du, M., Wang, B., Fu, X., Yang, Q., Zhu, M. J., Fetal programming in meat production. *Meat Science*, 109. (2015) 40–47.

[20] Duarte, M. S., Paulino, P. V. R., Das, A. K., Wei, S., Serao, N. V. L., Fu, X., Enhancement of adipogenesis and fibrogenesis in skeletal muscle of Wagyu compared with Angus cattle. *Journal of Animal Science*, 91. (2013) 2938–2946.

[21] Flowers, S., Hamblen, H., Leal-Gutierrez, J. D., Elzo, M. A., Johnson, D. D., Mateescu, R. G., Fatty acid profile, mineral content, and palatability of beef from a multibreed Angus–Brahman population. *Journal of Animal Science*, 96. (2018) 4264–4275.

[22] Goodrich, J. A., Kugler, S., Transcription factors and their roles in gene regulation. *Nature Reviews Genetics*, 4. 9. (2003) 801–814.

[23] Gotoh, T., Albrecht, E., Teuscher, F., Kawabata, K., Sakashita, K., Iwamoto, H., Differences in muscle and fat accretion in Japanese Black and European cattle. *Meat Science*, 82. (2009) 300–308.

[24] Gotoh, T., Nishimura, T., Kuchida, K., Mannen, H., The Japanese Wagyu beef industry: Current situation and future prospects – A review. *Asian-Australasian Journal of Animal Sciences*, 31. (2018) 933.

[25] Greenwood, P. L. An overview of beef production from pasture and feedlot globally, as demand for beef and the need for sustainable practices increase. *Animal*, (2021) 100295.

[26] Greenwood, P. L., Bell, A. W., Developmental programming and growth of livestock tissues for meat production. *Veterinary Clinics: Food Animal Practice*, 35. (2019) 303–319.

[27] Greenwood, P. L., Siddell, J., Walmsley, B., Geesink, G., Pethick, D., Mcphee, M., Postweaning substitution of grazed forage with a high-energy concentrate has variable long-term effects on subcutaneous fat and marbling in Bos taurus genotypes. *Journal of Animal Science*, 93. (2015) 4132–4143.

[28] Harris, C. L., Wang, B., Deavila, J. M., Busboom, J. R., Maquivar, M., Parish, S. M., Vitamin A administration at birth promotes calf growth and intramuscular fat development in Angus beef cattle. *Journal of Animal Science and Biotechnology*, 9. (2018) 55.

[29] Hong, H., Baatar, D., Hwang, S. G., The difference of castration timing of Korean Hanwoo bulls does not significantly affect the carcass characteristics. *Journal of Animal Science and Technology*, 63. (2021).

[30] Horn, P., A tej és marhahústermelés versenyhelyzete a világ állattenyésztésében. [The competitive situation of milk and beef production in global livestock farming]. *Állattenyésztés és Takarmányozás*, 62. (2013) 308–323.

[31] Horn, P., Stefler, J., A világ állati fehérje ellátása, annak humán-egészségügyi szerepe, figyelemmel a húsmarha tenyésztésre [The world's animal protein supply and its role in human health, with a focus on beef cattle farming]. *Állattenyésztés és Takarmányozás*, 66. 4. (2017) 261–276.

[32] Hwang, Y. H., Joo, S. T., Fatty acid profiles, meat quality, and sensory palatability of grain-fed and grass-fed beef from Hanwoo, American, and Australian crossbred cattle. *Korean Journal for Food Science of Animal Resources*, 37. (2017) 153.

[33] Inocencio, M. A. E., Purnamasari, L., Hwang, S. G., de la Cruz, J. F., Effect of Vitamin A, C, and D on improving intramuscular fat in Hanwoo beef cattle – Review. *Journal of Livestock Science*, 14. (2023) 91–103.

[34] Inoue, K., Honda, T., Oyama, K., Genetic relationships between internal diseases diagnosed at slaughter and carcass traits in Japanese Black cattle. *Journal of Animal Science*, 93. (2015) 2714–2721.

[35] Jo, C., Cho, S. H., Chang, J., Nam, K. C., Keys to production and processing of Hanwoo beef: A perspective of tradition and science. *Animal Frontiers*, 2. 4. (2012). 32–38.

[36] Juárez, M., Dugan, M. E., Aldai, N., Basarab, J. A., Baron, V. S., McAllister, T. A., Aalhus, J. L., Beef quality attributes as affected by increasing the intramuscular levels of vitamin E and omega-3 fatty acids. *Meat Science*, 90. 3. (2012) 764–769.

[37] Kawachi, H., Micronutrients affecting adipogenesis in beef cattle. *Animal Science Journal*, 77. (2006) 463–471.

[38] Khounsaknalath, S., Etoh, K., Sakuma, K., Saito, K., Saito, A., Abe, T., Effects of early high nutrition related to metabolic imprinting events on growth, carcass characteristics, and meat quality of grass-fed Wagyu (Japanese Black cattle). *Journal of Animal Science*, 99. (2021).

[39] Knobel-Graves, S., Brooks, J., Johnson, B., Starkey, J., Beckett, J., Hodgen, J., Effect of vitamin D_3, zilpaterol hydrochloride supplementation, and postmortem aging on shear force measurements of three muscles in finishing beef steers. *Journal of Animal Science*, 94. (2016) 2637–2647.

[40] Kruk, Z., Bottema, M., Reyes-Veliz, L., Forder, R., Pitchford, W., Bottema, C., Vitamin A and marbling attributes: Intramuscular fat hyperplasia effects in cattle. *Meat Science*, 137. (2018) 139–146.

[41] Ladeira, M., Schoonmaker, J., Gionbelli, M., Dias, J. C., Gionbelli, T., Carvalho, J. R., Nutrigenomics and beef quality: A review about lipogenesis. *International Journal of Molecular Sciences*, 17. (2016) 918–939.

[42] Ladeira, M., Schoonmaker, J., Swanson, K., Duckett, S., Gionbelli, M., Rodrigues, L., Nutrigenomics of marbling and fatty acid profile in ruminant meat. *Animal,* 12. s2. (2018) s282–s294.

[43] Lee, S. C., Choi, H. H., Shin, J. S., Kim, K. H., Oh, Y. K., Cheon, D. W., Carcass characteristics and profitability analysis based on slaughter age of Hanwoo steers. *Journal of Animal Science and Technology*, 55. (2013) 315–323.

[44] Lee, Y., Lee, B., Kim, H., Yun, Y., Kang, S., Kim, K., Sensory quality characteristics with different beef quality grades and surface texture features assessed by dented area and firmness, and the relation to muscle fiber and bundle characteristics. *Meat Science*, 145. (2018) 195–201.

[45] Li, X. Z., Yan, C. G., Gao, Q. S., Yan, Y., Choi, S. H., Smith, S. B., Adipogenic/lipogenic gene expression and fatty acid composition in chuck, loin, and round muscles in response to grain feeding of Yanbian Yellow cattle. *Journal of Animal Science*, 96. (2018). 2698–2709.

[46] Liu, S., Huang, J., Wang, X., Ma, Y., Transcription factors regulate adipocyte differentiation in beef cattle. *Animal Genetics*, 51. (2020) 351–357.

[47] Luciano, G., Moloney, A. P., Priolo, A., Röhrle, F. T., Vasta, V., Biondi, L., López-Andrés, P., Grasso, C. S., Monahan, F. J., Vitamin E and polyunsaturated fatty acids in bovine muscle and the oxidative stability of beef from cattle receiving grass or concentrate-based rations. *Journal of Animal Science*, 89. 11. (2011) 3759–3768.

[48] Luscombe, N. M., Berman, H. M., Thornton, J. M., Protein–DNA interactions: From molecules to genomes. *Current Opinion in Structural Biology*, 10. 3. (2000) 327–334.

[49] Mao, Y., Hopkins, D. L., Zhang, Y., Li, P., Zhu, L., Dong, P., Beef quality with different intramuscular fat content and proteomic analysis using isobaric tag for relative and absolute quantitation of differentially expressed proteins. *Meat Science*, 118. (2016) 96–102.

[50] Martins, T. S., Sanglard, L. M., Silva, W., Chizzotti, M. L., Renno, L. N., Serao, N. V., Molecular factors underlying the deposition of intramuscular fat and collagen in skeletal muscle of Nellore and Angus cattle. *PLoS One*, 10. (2015) e0139943.

[51] Miguel, J. A., Ciria, J., Asenjo, B., Pargas, H., Colmenarez, D., Chemical composition of meat in castrated male Brahman cattle in Venezuela. *Journal of Life Sciences*, 5. (2011). 562–568.

[52] Moreira, A. D., Siqueira, G. R., Lage, J. F., Benatti, J. M. B., Moretti, M. H., Miguel, G. Z., Castration methods in crossbred cattle raised on tropical pasture. *Animal Production Science*, 58. (2018) 1307–1315.

[53] Motoyama, M., Sasaki, K., Watanabe, A., Wagyu and the factors contributing to its beef quality: A Japanese industry overview. *Meat Science*, 120. (2016). 10–18.

[54] Mueller, L. F., Balieiro, J. C. C., Ferrinho, A. M., Martins, T. D. S., da Silva Corte, R. R. P., de Amorim, T. R., Gender status effect on carcass and meat quality traits of feedlot Angus × Nellore cattle. *Animal Science Journal*, 90. (2019) 1078–1089.

[55] Mwangi, F. W., Charmley, E., Gardiner, C. P., Malau-Aduli, B. S., Kinobe, R. T., Malau-Aduli, A. E., Diet and genetics influence beef cattle performance and meat quality characteristics. *Foods*, 8. (2019).

[56] Nguyen, D. V., Flakemore, A. R., Otto, J., Ives, S. W., Smith, R. W., Nichols, P. D., Nutritional value and sensory characteristics of meat eating quality of Australian prime lambs supplemented with pelleted canola and flaxseed oils: Fatty acid profiles of muscle and adipose tissues. *Internal Medicine Review*, 3. (2017) 1–21.

[57] Nguyen, D. V., Malau-Aduli, B. S., Cavalieri, J., Nichols, P. D., Malau-Aduli, A. E., Supplementation with plant-derived oils rich in omega-3 polyunsaturated fatty acids for lamb production. *Veterinary and Animal Science*, 6. (2018) 29–40.

[58] Nguyen, D. V., Nguyen, O. C., Malau-Aduli, A. E., Main regulatory factors of marbling level in beef cattle. *Veterinary and Animal Science*, 14. (2021) 100219.

[59] Nogalski, Z., Wielgosz-Groth, Z., Purwin, C., Sobczuk-Szul, M., Mochol, M., Pogorzelska-Przybytek, P., Effect of slaughter weight on the carcass value of young crossbred (Polish Holstein Friesian x Limousin) steers and bulls. *Chilean Journal of Agricultural Research*. 74. (2014) 59–66.

[60] Obsen, T., Faergeman, N. J., Chung, S., Martinez, K., Gobern, S., Loreau, O., Trans-10, cis-12 conjugated linoleic acid decreases de novo lipid synthesis in human adipocytes. *The Journal of Nutritional Biochemistry*, 23. 6. (2012) 580–590.

[61] Oka, A., Maruo, Y., Miki, T., Yamasaki, T., Saito, T., Influence of vitamin A on the quality of beef from the Tajima strain of Japanese Black cattle. *Meat Science*, 48. (1998) 159–167.

[62] Okumura, T., Saito, K., Sowa, T., Sakuma, H., Ohhashi, F., Tameoka, N., Changes in beef sensory traits as somatic-cell-cloned Japanese black steers increased in age from 20 to 30 months. *Meat Science*, 90. (2012) 159–163.

[63] Park, B., Choi, T. J., Park, M. N., Oh, S. H., Estimation of environmental effects and genetic parameters of carcass traits on Chikso (Korean brindle cattle). *Asian-Australasian Journal of Animal Sciences*, 33. (2020) 525.

[64] Park, S. J., Beak, S. H., Jung, D. J. S., Kim, I. H. J., Piao, M. Y., Kang, H. J., Genetic, management, and nutritional factors affecting intramuscular fat deposition in beef cattle – A review. *Asian-Australasian Journal of Animal Sciences*, 31. (2018) 1043–1061.

[65] Park, S. J., Kang, H. J., Na, S., Lee, S. H., Baik, M., Differential expression of extracellular matrix and integrin genes in the longissimus thoracis between bulls and steers and their association with intramuscular fat contents. *Meat Science*, 136. (2018) 35–43.

[66] Peng, D. Q., Lee, J. S., Kim, W. S., Kim, Y. S., Bae, M. H., Jo, Y. H., Effect of vitamin A restriction on carcass traits and blood metabolites in Korean native steers. *Animal Production Science*, 59. (2019) 2138–2146.

[67] Peng, D. Q., Smith, S. B., Lee, H. G., Vitamin A regulates intramuscular adipose tissue and muscle development: Promoting high-quality beef production. *Journal of Animal Science and Biotechnology,* 12. (2021) 34–44.

[68] Pethick, D. W., Harper, G. S., Oddy, V. H., Growth, development and nutritional manipulation of marbling in cattle: A review. *Australian Journal of Experimental Agriculture*, 44. (2004) 705–715.

[69] Picard, B., Gagaoua, M., Al Jammas, M., Bonnet, M., Beef tenderness and intramuscular fat proteomic biomarkers: Effect of gender and rearing practices. *Journal of Proteomics*, 200. (2019) 1–10.

[70] Pickworth, C., Loerch, S., Fluharty, F., Restriction of vitamin A and D in beef cattle finishing diets on feedlot performance and adipose accretion. *Journal of Animal Science*, 90. (2012) 1866–1878.

[71] Pickworth, C. L., Loerch, S. C., Fluharty, F. L., Effects of timing and duration of dietary vitamin A reduction on carcass quality of finishing beef cattle. *Journal of Animal Science*, 90. (2012). 2677–2691.

[72] Pogácsás, P., *Átalakuló gazdasági régiók a magyar történelemben. I.* [Transforming economic regions in Hungarian history I]. Akadémiai Kiadó, Budapest. 13. 1. (2012) 21–38.

[73] Pogge, D., Hansen, S., Supplemental vitamin C improves marbling in feedlot cattle consuming high sulfur diets. *Journal of Animal Science*, 91. (2013) 4303–4314.

[74] Poleti, M. D., Regitano, L. C., Souza, G. H., Cesar, A. S., Simas, R. C., Silva-Vignato, B., Longissimus dorsi muscle label-free quantitative proteomic reveals biological mechanisms associated with intramuscular fat deposition. *Journal of Proteomics*, 179. (2018) 30–41.

[75] Półtorak, A., Moczkowska, M., Wyrwisz, J., Wierzbicka, A., Beef tenderness improvement by dietary vitamin D_3 supplementation in the last stage of fattening of cattle. *Journal of Veterinary Research*, 61. 1. (2017) 59–67.

[76] Rasby, R., Early weaning beef calves. *Veterinary Clinics of North America: Food Animal Practice*, 23. (2007) 29–40.

[77] Reddy, K. E., Jeong, J., Baek, Y. C., Oh, Y. K., Kim, M., So, K. M., Early weaning of calves after different dietary regimens affects later rumen development, growth, and carcass traits in Hanwoo cattle. *Asian-Australasian Journal of Animal Sciences*, 30. (2017) 1425–1434.

[78] Reiling, B., Johnson, D., Effects of implant regimens (trenbolone acetate-estradiol administered alone or in combination with zeranol) and vitamin D_3 on fresh beef color and quality. *Journal of Animal Science*, 81. (2003). 135–142.

[79] Rezende, P. L. P., Restle, J., Bilego, U. O., Resende Fernandes, J. J., Missio, R. L., Guimarães, T. P., Carcass characteristics of feedlot-finished Nellore heifers slaughtered at different weights. *Acta Scientiarum. Animal Sciences*, 41. (2019) e44826.

[80] Robinson, D., Cafe, L., Greenwood, P., Developmental programming in cattle: Consequences for growth, efficiency, carcass, muscle and beef quality characteristics. *Journal of Animal Science*, 91. (2013) 1428–1442.

[81] Rodrigues, L. S., Moura, A. F., Pacheco, R. F., Paula, P. C., Brondani, I. L., Filho, D. C. A., Características da carcaça e da carne de vacas de descarte abatidas com distintos pesos e grau de acabamento – abordagem meta-analítica. *Ciência Animal Brasileira*, 16. 4. (2015) 508–516.

[82] Sakowski, T., Grodkowski, G., Gołebiewski, M., Genetic and environmental determinants of beef quality – A review. *Frontiers in Veterinary Science*, 9. (2022) 819605.

[83] Scheffler, J., Mccann, M., Greiner, S., Jiang, H., Hanigan, M., Bridges, G., Early metabolic imprinting events increase marbling scores in fed cattle. *Journal of Animal Science*, 92. (2014) 320–324.

[84] Schmidt, J., *A takarmányozás alapjai* [Basic principles of feeding]. Mezőgazda Kiadó, Budapest. (2003) 1–452.

[85] Schmidt, J., *Gazdasági állataink takarmányozása* [Feeding of our farm animals]. Mezőgazda Kiadó, Budapest. (1995) 1–356.

[86] Senaratne, L. S., Calkins, C. R., de Mello Jr., A. S., Carr, T. P., Erickson, G. E., Fatty acid composition of beef from cattle fed wet distillers grains diets supplemented with vitamin E. *Nebraska Beef Cattle Reports*, 513. (2009) 110–112.

[87] Shin, S., Chung, E., Identification of differentially expressed genes between high and low marbling score grades of the longissimus lumborum muscle in Hanwoo (Korean cattle). *Meat Science*, 121. (2016) 114–118.

[88] Stefler, J., Mihalecz, A., Tenyészcél az Aberdeen Angus fajtában [Breeding goal in the Aberdeen Angus breed]. In: *A Brit Húsmarhafajtákat Tenyésztők Egyesülete Tenyésztési Programja* [Breeding Programme of the British Beef Cattle Breeders' Association]. (2020) 1–30.

[89] Taga, H., Bonnet, M., Picard, B., Zingaretti, M., Cassar-Malek, I., Cinti, S., Adipocyte metabolism and cellularity are related to differences in adipose tissue maturity between Holstein and Charolais or Blond d'Aquitaine fetuses. *Journal of Animal Science*, 89. (2011) 711–721.

[90] Tan, Z., Jiang, H. Molecular and cellular mechanisms of intramuscular fat development and growth in cattle. Review. *International Journal of Molecular Sciences*, 25. (2024) 2520.

[91] Teixeira, P. D., Oliveira, D. M., Chizzotti, M. L., Chalfun-Junior, A., Coelho, T. C., Gionbelli, M., Subspecies and diet affect the expression of genes involved in lipid metabolism and chemical composition of muscle in beef cattle. *Meat Science*, 133. (2017) 110–118.

[92] Ueda, S., Kitamura, C., Tateoka, Y., Kanai, A., Suzuki, Y., Fukuda, I., Shirai, Y., Single-nucleus RNA sequencing reveals muscle-region-specific differences in fibro-adipogenic progenitors driving intramuscular fat accumulation. *Metabolites*, 15. (2025) 231.

[93] Utrera, A. R., Van Vleck, L. D., Heritability estimates for carcass traits of cattle: A review. *Genetics and Molecular Research*, 3. (2004) 380–394.

[94] Wang, B., Yang, Q., Harris, C. L., Nelson, M. L., Busboom, J. R., Zhu, M. J., Nutrigenomic regulation of adipose tissue development – Role of retinoic acid: A review. *Meat Science*, 120. (2016) 100–106.

[95] Wang, H., Li, H., Wu, F., Qiu, X., Yu, Z., Niu, W., Effects of dietary energy on growth performance, rumen fermentation and bacterial community, and meat quality of Holstein-Friesians bulls slaughtered at different ages. *Animals,* 9. (2019) 1123.

[96] Wang, Y. H., Bower, N., Reverter, A., Tan, S., De Jager, N., Wang, R., Gene expression patterns during intramuscular fat development in cattle. *Journal of Animal Science*, 87. (2009) 119–130.

[97] Yamada, T., Kamiya, M., Higuchi, M., Fat depot-specific effects of body fat distribution and adipocyte size on intramuscular fat accumulation in Wagyu cattle. *Animal Science Journal*, 91. (2020).

[98] Yang, S. H., Kim, W. H., Kang, S. N., Choi, K. C., Kim, D., A comparison of rice straw and whole-crop barley (*Hordeum vulgare* L.) silage supplements on performance and carcass characteristics of Hanwoo (Bos taurus coreanae) steers. *Applied Sciences*, 10. (2020). 7725.

[99] Zhang, Y. Y., Wang, H. B., Wang, Y. N., Wang, H. C., Zhang, S., Hong, J. Y., Transcriptome analysis of mRNA and microRNAs in intramuscular fat tissues of castrated and intact male Chinese Qinchuan cattle. *PLoS One*, 12. (2017).

[100] Zhang, Y. Y., Zan, L. S., Wang, H. B., Xin, Y. P., Adoligbe C. M., Ujan. J. A., Effect of sex on meat quality characteristics of Qinchuan cattle. *African Journal of Biotechnology*, 9. 28. (2010) 4504–4509.