# Effect of Vitamin A, C, and D on improving intramuscular fat in Hanwoo beef cattle - Review

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# Abstract

Intramuscular fat (IMF) or marbling is commonly used for carcass quality. High IMF was already innate in Hanwoo cattle and was increased with the help of vitamin restriction or administration. Throughout the years, research focused on preadipocyte hyperplasia which helped in the proliferation of intramuscular adipocytes and genes that were responsible for preadipocyte proliferation were enhanced with the administration of vitamin A. Its supplementation in its early stages and restriction in the late stages increased the efficiency of IMF proliferation. When it comes to the supplementation of Vitamin C, the potential it has in improving the fatty acid profile of Hanwoo steers through different modes of administration. On the other hand, varying results regarding the administration of vitamin D suggested that more studies should be conducted before full implementation. Climate, age, dosage, risks, mode of administration, stage of life, efficacy when administered, and fusion with newer technologies should be considered when conducting further studies of these vitamins. Personal preferences, customs, tampering, and purchasing powers were some of the challenges that the Hanwoo cattle producers and consumers should surpass with the help of the improvement in marbling.

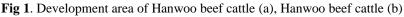
Keywords: Hanwoo cattle; Marbling; Vitamin A; Vitamin C; Vitamin D

# Introduction

Hanwoo beef cattle was initially used as a draft animal until it became meat-type cattle over some time due to genetic improvement that started in the 1970s for it to fit for meat consumption (Jo et al., 2012; Lee et al., 2014). It is a native cattle found in the Korean Peninsula since 2000 B.C. and maintained its pure bloodline (Dela Cruz et al., 2016). There are four types of Hanwoo beef which can be found in Korea: Brown (Major Hanwoo), Black Face (Heukwoo), Black (Jeju Heukwoo), and Tiger color (Chickso) (Jo et al., 2012). According to McTavish et al. (2013), the Asian cattle (Hanwoo and Japanese Black) originated from a hybrid of taurine-indicine type. The taurine-indicine types of cattle have better marbling which affects the tenderness of the meat, and their pure breeding has allowed manipulation of this meat trait.

Throughout the years, the Korean beef cattle breeding program focuses on improving carcass quality rather than quantity (Gajaweera et al., 2017). Tenderness is one of the markers for assessing the quality of beef carcasses and is associated with palatability. According to Hansen et al. (2012), the tenderness of the meat is the easiest trait to manipulate, creating high market demand. The tenderness of the meat is greatly affected by the amount of intramuscular fat across the carcass. Intramuscular fat (IMF) or marbling is commonly used for carcass quality determination in Korea, Japan, Australia, and the United States (Figure 1) (Park et al., 2018). The high level of marbling is achieved through increasing levels of concentrated feed with an extended finishing period and generally use steers and heifers instead of bulls, combined with an intensive grain-based feeding system (Joo et al, 2017).





IMF deposition occurs when there is hyperplasia (increase in cell number) and hypertrophy (increase in cell size) of intramuscular cells throughout their life (Cheng et al., 2015; Harris et al., 2018). Longissimus and semimembranosus muscles are often used in studies regarding intramuscular fat deposition since both comprise 90% muscle fibers and 10% connective tissues, adipose tissues, vascular, and nervous tissues (Harris et al., 2018; Chen et al., 2019). This depends on the breed and post-slaughter meat-processing technique (Herault et al., 2014; Listrat et al., 2014). Other parts that are used for studies include longissimus lumborum, biceps femoris, infraspinatus, supraspinatus, and semitendinosus, which are skeletal muscles (Harris et al., 2018; Chen et al., 2019).

There are several benefits in improving the IMF of the Hanwoo meat carcass. High IMF of Hanwoo beef is suited for the Goigui or the traditional barbecue method for meat in Korea. The preference for Hanwoo meat stems from the right amount of fat and meat across the carcass (Figure 2 and 3). The IMF content of beef varies depending on feeding time, finishing diet, and breed type etc. Moreover, the quality of IMF in carcasses determines the quality of the meat and is a primary purchasing factor for consumers (Cho et al., 2010). Korean consumers are willing to pay for higher-quality Hanwoo meat which the IMF score influences (Gotoh and Joo, 2016; Motoyama et al., 2016). Hanwoo meat ranks second highest when it comes to its IMF content, second to Wagyu (Nguyen et al., 2021). Consequently, the overall increase of fatty tissue in the carcass would be a waste, which is why there is a need to discover strategies that will improve the quality of IMF.

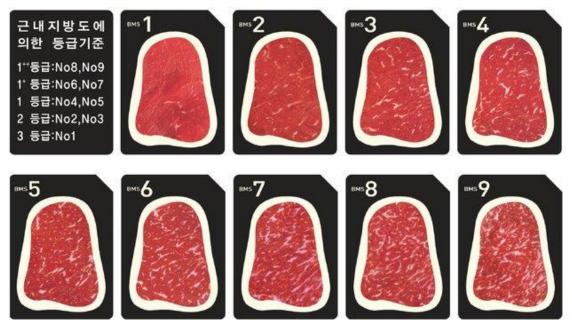


Fig 2. The scores of Hanwoo marbled meat (Jo et al, 2012; Chung et al, 2018)

Processes like adipogenesis which enhances the deposition of IMF are important in improving beef carcass marbling. In the process of adipogenesis, it is unlikely possible to develop IMF tissue during the fetal stage since brown adipose tissue development happens. Instead, IMF multiplies during the mature stage of the cattle (Peng et al., 2021). The nutrigenomic regulation study made by Wang et al., (2016) suggested that during the prenatal stage or late pregnancy and postnatal stage (about 250 days), hyperplasia occurs among the preadipocytes. Maximizing the ability of adipogenesis in improving carcass quality through different methods is important. However, among all the methods of enhancing the IMF deposition through the help of adipogenesis, the use of vitamins in feeding trials in vivo & in vitro (Nguyen et al., 2021) is the easiest to manipulate.

In this review article, the author would like to discuss the use of vitamins A, C, and D, and their potential in improving the carcass quality of the Hanwoo beef through the increase in IMF. Some of these vitamins naturally occur inside the body of the animal or can be found in the feed that it consumes. Improvement in the quality and quantity of IMF through restriction or supplementation of vitamins and the possible risks involved will be discussed in this review article. Furthermore, the challenges that the Hanwoo beef cattle face in the market, and how they could be surpassed will also be tackled. Overall, the author would like to know which methods are advantageous and safe, and further suggestions regarding the betterment of Hanwoo beef cattle will be made.

# **Effect of Vitamin A**

Vitamin A (retinol) is a fat-soluble vitamin that belongs to the carotenoid family, and cannot be synthesized by animals. The supplementation of vitamin A (retinol) is required in the diets of ruminants (NRC, 2016) since they cannot synthesize enough vitamin A for their bodies. However, they can get it through their diet (plant source) and feed additives (retinol or preformed vitamin A) (Chen and Chen, 2014). Primary physiological factors of the animal (Wang et al., 2016; Peng et al., 2021) such as growth, vision, and metabolism (glucose synthesis and adipogenesis) are enhanced through the supplementation of vitamin A. Among these necessities, many researchers found how it can influence IMF deposition through the help of adipogenesis. On the other hand, deficiencies may lead to blindness, skeletal deformation, and reproductive failures (Freking and Lalman, 2018). Retinoic acid, which is a metabolite of vitamin A, plays a significant role in adipogenesis wherein it plays a part in preadipocyte commitment and differentiation of adipocytes (Wang et al., 2016). In addition, the use of vitamin A is one of the most studied when it comes to supplementation for the enhancement of IMF in beef cattle. However, it is also known in the countries of Japan and Korea that restriction or lowering of the retinoic acid content on the early stages may help in the marbling of beef cattle when administered during the fattening stage.

### Supplementation of Vitamin A

Adipogenic commitment can commence when vitamin A supplementation is done on dams, and this is important for the increase in adipogenesis during the early development of the offspring (Ladeira et al., 2018). This is supported by the study conducted by Jo et al. (2020) which in vivo administration of vitamin A orally with a dosage of 78,000 IU/d during the late stage of the pregnancy suggested that it can help in the development of the mRNA expression in relation to preadipocyte (Krüppel-like factor 2 or KLF2) development. According to Wei (2012), epigenetic changes in adipogenic genes and regulation of adipocyte formation can be a result of retinoic supplementation. On the other hand, retinoic acid plays a part in the development of preadipocyte hyperplasia through gene activation (Peng et al., 2021). However, during adipogenic differentiation, it inhibits adipocyte accumulation and restricts hyperplasia (Berry et al., 2012), and this is similar to the study made by Hocquette et al. (2010). It should be noted that hypertrophy and preadipocyte proliferation are found to be more active during the early fetal stage and early growth stages in calves (Yang et al., 2013). In addition, hyperplasia instead of hypertrophy occurs when there is supplementation of vitamin A since the number of flecks increases as the number of adipocytes per fleck also increases (Kruk et al., 2018). Thus, supplementation of vitamin A during the early stages of gestation can promote hyperplasia of preadipocytes. There is a huge impact on the preadipocytes rather than the mature IMF adipocytes when it comes to vitamin A supplementation (Kruk et al., 2018). However, the varying results in the supplementation of retinoic acid will be resolved later when compared to restricting it.

In the studies conducted by Harris et al. (2018), Nguyen et al. (2018), and Peng et al. (2020), the supplementation of 45,000 IU/day of vitamin A was used for growth performance and serum vitamin A which was administered from its birth up to two months of age. When cattle are supplemented with vitamin A from birth until weaning, there could be intramuscular pre-adipocytes for lipid storage until the fattening stage due to the accumulation of intramuscular adipocytes during its early years. Therefore, this can increase the IMF without increasing the fat of other parts of the beef which then increases meat quality (Knutson et al., 2017). This result was supported by the review made by Wang et al. (2016) wherein that supplementation during the neonatal stage promotes preadipocyte hyperplasia in the early stages of development. Interestingly, the results of Peng et al. (2021) are similar to the ones conducted by Berry et al. (2012) and Harris et al. (2018) wherein an increase in the gene Zfp423 (Zinc finger protein 43) by 70%, which is responsible for maintaining the preadipocyte differentiation in the early stages, was found after administration of oral vitamin A. Thus, supplementation of vitamin A in the early stages of the cattle could help genes responsible for preadipocyte differentiation to proliferate which could help in the latter years of the beef (Ladeira et al., 2018).

However, Bryant et al. (2010) contradicted that there was no carcass improvement observed and showed negative effects such as vitamin A deficiency (Pickworth et al., 2012a; Ward et al., 2012) even after feeding the finishing steers four times the National Research Council (NRC) recommended vitamin A ration requirement. In addition, vitamin A supplementation does not affect the increase of the marbling score of the longissimus thoracis (Krone et al., 2015). This is contraindicated by the studies made by Ward et al. (2012) as there was an increase in the marbling score. In addition, vitamin A supplementation in another study did not cause an increase in the marbling score of the longissimus thoracis (Krone et al., 2015).

However, vitamin A supplementation may not be commercially logical to do since it needs strict monitoring of individual animals to prevent deficiency. However, its effectivity towards marbling is positive (Kruk et al., 2018). Moreover, if the consumers are willing to pay for higher quality, doing so may still be suggested. Since the dosage of vitamin A varies per study, further studies regarding its supplementation need careful evaluation.

#### **Restrictions of Vitamin A**

Retinol restricts hyperplasia of adipocytes which occurs during IMF deposition (Kruk et al., 2018). Its restriction can increase IMF instead of subcutaneous fat deposition. The decrease in retinoic acid concentration upregulates adipogenic differentiation of 3T3-L1 cells, a preadipocyte from a mouse that can be used for in vitro studies, for adipocyte cells and adipogenic genes (Dela Cruz et al., 2017). In the earlier studies made by Dela Cruz et al. (2015), the decrease in the level of retinoic acid promoted the increase of triglyceride in the adipose tissue of stromal vascular cells when done in vitro.

Oral supplementation of vitamin A in Korean native (Hanwoo) calves increased their growth performance and preadipocyte factor 1(Pref-1) according to Peng et al. (2020). The Pref-1 gene is responsible for the inhibition of adipogenesis and prevents the excessive deposition of fat inside the body which could lead to obesity (Hudak and Sul, 2013). When cattle reach their fattening stages, the restriction

of vitamin A increases the accumulation of lipids through hypertrophy. On the other hand, Pickworth et al. (2012a) found that restriction of vitamin A can increase hyperplasia of IMF although IMF adipocytes per gram did not change in terms of size and density after the restriction of Vitamin A. The restriction of vitamin A supplementation has a great effect on IMF without manipulating muscle size (Kruk et al., 2018). It should be noted that fat hyperplasia is more significant in the development of cattle IMF (Yang et al., 2006; Kern et al., 2014).

According to the NRC, restriction or inhibition of vitamin A treatments during the fattening period increased the marbling of carcasses which was similar to the reports made by Pickworth et al. (2012a), Knutson et al. (2017), and Peng et al. (2019). This was attributed to the reduction of adipogenesis in mature adipocytes therefore lipid accumulation and adipocyte hypertrophy decreases (Amengual et al., 2012). The increase in the marbling of the carcass through restriction of vitamin A during the finishing stage can only be seen among breeds with high-marbling potential (Siebert et al., 2006; Gorocica-Buenfil et al., 2007b; Ward et al., 2012; Knutson et al., 2020). Since Hanwoo beef has high marbling ability, this restriction technique can be used to increase marbling scores.

There are studies suggesting that vitamin A restriction does not affect marbling and lipid metabolism (Pickworth et al., 2012a, 2012b). The restriction process decreases glycerol-3-phosphate dehydrogenase which is an important metabolite during adipogenesis (Oh et al., 2005). Restriction can affect the later stages of the growth rate of the animal which can lead to blindness, arthritis, edema, and muscular edema. On the other hand, continuous supplementation of the normal level of vitamin A during the later stages of life may still result in poor marbling and IMF deposition. However, it is suggested that supplementation of 30 IU/dL of vitamin A would be sufficient, and this should not go lower so that the enhancement of carcass marbling and the overall health of the animal will be maintained (Park et al, 2018). Adipogenesis can still commence when there are low levels of vitamin A. The extracellular use of calcium and retinoic acid in low concentrations can increase adipogenic differentiation. In the study conducted by Peng et al. (2021), most of the vitamin restriction studies made before did not realize that pro-vitamin A or carotenoids might have a large amount of vitamin A which should be noted when conducting further vitamin A restriction.

# **Effect of Vitamin C**

Ascorbic acid is naturally synthesized in bodies of ruminants particularly in the liver or kidneys (Matsui, 2012). Forms of vitamin C such as ascorbate which is the active form of vitamin C will be discussed in this section. Vitamin C or L-ascorbic acid may not be given to cattle since they can synthesize it, but supplementing them is essential since it is easily degraded in the rumen. Hence, ruminants have a hard time synthesizing it alone which results in low plasma vitamin C and/or deficiencies such as scurvy (hemorrhage and teeth loss are one of the clinical signs of scurvy) in calves (Matsui, 2012). The administration of vitamin C should be rumen-protected such as the use of fat-coated vitamin C, since it can be degraded easily (Matsui, 2012; Mwangi et al., 2018; Park et al., 2018; Mwangi et al., 2019).

#### Modes of administration of Vitamin C

The levels of plasma vitamin C drop below its normal range (2.4-4.7 mg/ml) during its fattening period. This was explained by Matsui (2012) where cattle fattening can cause oxidative stress and it decreases the plasma vitamin C concentration. The plasma vitamin C in the body is a biomarker of vitamin C obtained from the ration hence, it is important to supply this in fattener cattle. Administration of vitamin C helps in IMF deposition by promoting adipocyte differentiation (Mwangi et al., 2019), and it is necessary during the fattening stage to ensure adipogenesis (Kawachi, 2006). The Hanwoo steers used by Pogge et al. (2015) showed an improvement in carcass quality in terms of marbling score, texture, and quality grade after supplementation of vitamin C. However, vitamin C is easily degraded by the rumen due to its highly acidic environment, which is why in the study conducted by Jang et al. (2016), a palm oil-coated vitamin C supplement was administered to Hanwoo steers which showed an increase in marbling. Other preparations for vitamin C such as powdered, silicone-coated ethyl cellulose-coated, and hydrogenated oilcoated were also evaluated. The use of silicone and the use of hydrogenated oil showed better efficacy (Matsui, 2012). However, supplementation of it may not be useful especially when the plasma concentration of vitamin C is high in fattening cattle. It was suggested that the use of vitamin C for the enhancement of marbling may be conditional (Matsui, 2012) since environmental factors may play along when it is administered to calves, as well as the levels of plasma vitamin C in cattle. Further studies regarding the use of different preparations of a rumen-protected vitamin C should be explored to determine the best practice to increase the marbling of the carcasses with inconsideration of different growth stages and vitamin dosages.

Addition of a high sulfur diet was added in the experiment conducted by Pogge and Hansen (2013) to 21 maximize the ability of starch to contribute to the marbling of the carcass along with vitamin C. The addition of vitamin C in high sulfur diet given in the first 90 days of the study improved the marbling score due to the sufficient amount of ascorbate concentrations utilized during lipid metabolism. Nguyen et al. (2019) suggested that more research should be made on the supplementation of vitamin C along with other minerals found in food for better utilization.

On the other hand, an increase in polyunsaturated fatty acid (PUFA) in the muscle is evident when vitamin C was administered in the diet and was hypothesized that this is due to an increase in the proportion of cell membrane lipids in the samples used in the study (Pogge et al., 2014). The tenderness of the final meat products and their quality is said to be improved by 1.25% to 2.25% when vitamin C is supplied (Pogge et al., 2013). This indicates that supplementation may be used to improve the lipid profile of beef. Furthermore, it decreased the amount of C16:0 (Palmitic acid) and C18:0 (Stearic acid) which are saturated fatty acids (SFAs) (Chiu et al., 2017). Saturated fatty acid (SFAs), which is associated with coronary heart disease, is abundant in ruminant meat (French et al., 2000; Scollan et al., 2006). However, its association with coronary heart disease is still controversial (Dehghan et al., 2017; Astrup et al., 2019). Lessening the amount of saturated fatty acid in the intramuscular fat of the carcass is gaining more focus in various studies (Scollan et al., 2006; Troy et al., 2016).

Further studies regarding the effect of vitamin C in the improvement of the fatty acid profile should be conducted since this can be potential in the market. This is supported by Troy et al. (2016) in which consumption of healthy fats, such as those found in the carcass of Hanwoo beef, can benefit the well-being of humans (Troy et al., 2016). Purchasing a highly marbled Hanwoo beef product while ensuring its healthiness through a better fatty acid profile may gain the trust of the consumers (Półtorak et al., 2017). Moreover, the addition of vitamin C in diets and meat processing can stabilize the lipid in the carcass since it can prevent reactive oxygen from damaging the cellular components such as lipids (Harris et al., 2001; Pogge et al., 2014).

# **Effect of Vitamin D**

Vitamin D or known as 1,25-dihydroxy vitamin D3 is an active form of vitamin D which is known for its calcium homeostasis and bone metabolism role inside the body. It is normally synthesized inside the body through activation from the sun's ultraviolet rays. Cattle in general can also get vitamin D from plants, called ergosterol, which is converted to vitamin D2 once the plant is exposed (cured) to sunlight. Rickets is the weakening of bones to prolonged deficiency of vitamin D, while osteomalacia is the inefficiency to absorb calcium in the diet in which vitamin D aids in homeostasis (Uhl, 2018). Supplementation can also manage obesity which is associated with the lack of vitamin D (Ladeira et al., 2018). On the other hand, excessive supplementation of vitamin D could lead to toxicity which could result in anorexia, acetonemia, and even death (Grünberg, 2022). Moreover, different stages in the life of cattle require different levels of vitamin D, and these risks should be noted when supplementing or restricting vitamin D.

#### Supplementation of Vitamin D

Young cattle have a higher demand for the supplementation of vitamin D. They obtain a proper amount of vitamin D if administered or fed approximately 300 IU of vitamin D per 100 pounds of its body weight 25 (Bailey, 2017). According to Park et al. (2018), the 1,25- dihydroxy vitamin D3 produced in calcium homeostasis downregulates preadipocyte differentiation. Thus, a low dosage of calcium increases the level of 1,25- dihydroxy vitamin D3. This action reduces the marbling in the carcass of the beef since it inhibits the differentiation of preadipocytes (Hida et al., 1998). The downregulation of preadipocyte differentiation results in a poor intramuscular fat deposition which is associated with the supplementation of Vitamin D as an important regulator for adipogenesis (Berry et al., 2012). Thus, vitamin D3 supplementation is used to increase the tenderness of meat through the help of 1,25-dihydroxy-vitamin-D3 by increasing IMF deposition. Additionally, enhancement of the visual aspects of the meat such as marbling can be done with the use of vitamin D3. During calcium homeostasis, the mobilization of calcium which is important for the content of connective tissue and the mechanism of muscle contraction is due to vitamin D (Półtorak et al., 2017).

The stimulation of calcium by vitamin D3 increases the calcium content and this can affect the muscles, specifically skeletal muscles. According to Carnagey et al., (2008), the administration of high doses of vitamin D3 in vivo during the last phase of the fattening period can improve the tenderness of the

carcass. There is an improvement in the tenderness, juiciness, and flavor of the carcass when cattle underwent high supplementation of Vitamin D3 before slaughter (Rafalska, 2016). This is similar to the ones conducted by Karges et al. (2001) and Montgomery et al. (2004) in which high supplementation of vitamin D with a rate of more than or equal to 1 million IU/d for the finishing cattle in the last week is suggested to improve the tenderness. The latissimus dorsi improved its tenderness when cattle were supplemented with high doses of vitamin D3 at pre-slaughter (Swanek et al., 1999).

The minimum requirement given by the NRC for vitamin D is 300 IU/kg to avoid any risks involving vitamin D deficiency. Furthermore, Półtorak et al. (2017) observed an increase in calcium concentration in the muscle when vitamin D3 was supplemented in the last stages of its fattening stage. However, the supplementation of vitamin D and improvement of tenderness is not the same in the studies conducted by Scanga et al. (2001) and Reiling and Johnson (2003) wherein no improvement in the tenderness of the carcass was observed. In colder climates, supplementation of vitamin D in cattle is important due to the limited source of sunlight (Cashman, 2020; Kiely and Black, 2012). The use of high doses of vitamin D3 in the improvement of its quality through intramuscular fat deposition can be economically helpful in way that it can reduce the amount of unsold meat being returned from retailers to meat processing facilities (Półtorak et al., 2017).

#### **Restriction of Vitamin D**

Restriction of the 1,25-dihydroxy vitamin D receptor, which activates 1,25-dihydroxy vitamin D, regulates adipogenesis by suppressing it (Lu et al., 2018; Miao et al., 2020). Additionally, restriction before slaughter positively affects the calcium levels in meat, particularly in the post-mortem proteolysis and tenderization process. In the study conducted by Lee et al. (2003) in which Hanwoo steers received low calcium in the ratio, led to high levels of plasma 1,25-dihydroxy vitamin D3 and resulted in high marbling scores during the finishing stage of rearing. Feeds can be used as an alternative tool in supplementing the cattle vitamin D ration to improve the fatty acid profile or lipid stability (Castillo et al., 2013; Półtorak et al., 2021). The restriction of adipocyte differentiation and promotion of fat accumulation in adipocytes will depend on the cattle's stage of life (Kawachi, 2006).

Unfortunately, there are only a few studies regarding the effects of vitamin D on bovines. Contradicting results regarding supplementation and restrictions of vitamin D resulted in different farm practices regarding the use of vitamin D restriction. Some farmers are following full vitamin D restriction during the fattening stage, while others practice partial or intermittent restriction. Thus, further studies regarding the effects of Vitamin D should be done in order to fully understand its effects on bovine and marbling.

# General Acceptance of Hanwoo Beef

# Marketability

Beef is the third most consumed meat around the world at 6.4 kg. per capita (OECD, 2022). It is expected that beef consumption will rise by 8-12% higher than the current status for developing countries and developed countries, such as Korea (OECD, 2022). Generally, consumers base the quality of the carcass on the quality of the product which satisfies them, and tenderness is one of these factors for quality. Healthy nutritional attributes and overall sensory characteristics are the other factors for consumers to act on their willingness-to-pay decision (Mwangi et al., 2019; Khamikoeva et al., 2021).

#### Fatty acid profile of Hanwoo beef

Fat is classified as both substrate and reservoir of flavor compounds which contributes to the marbling of the carcass (Frank et al., 2016). The fatty acid profile manipulation in beef carcasses and human health has been an issue over the years. The fatty acid profile of Hanwoo beef is different from the meat from the USA or Australia (Kwon and Choi, 2015; Hwang and Joo, 2017) in a way that it has higher monounsaturated fatty acids (MUFAs), particularly oleic acid (Kwon and Choi, 2015). According to (Guasch-Ferré et al., 2019), MUFAs can lower mortality rates. However, the association between MUFAs and mortality does not match the report of Dehghan et al. (2017). Higher IMF in Hanwoo carcasses shows a higher amount of oleic acid which defines the meat flavor component of the carcass, and it is genetically innate among Hanwoo cattle to predispose oleic acid inside their bodies (Smith, 2016).

A study made by Bhuiyan et al. (2017) showed that fatty acids, carcass, and meat quality traits may be improved simultaneously which can lead to an increase in fatty acid meat profile. In the study conducted by Smith et al. (2018), the current production population of Hanwoo cattle is around 2.6 million head, and the per capita consumption increased by 11.6 kg in 2015. However, the decline in demand for

Hanwoo beef is due to animal and saturated fat phobia. Korean consumers are leaning toward a leaner type of beef, which the Korean government took initiative through a traceability system. The system aims to provide the consumers with the beef's information such as its breed, herd, etc. The encouragement of public health authorities regarding the reduction of saturated fat and red meat consumption also contributes to the decline in demand. Evidence regarding mortality linked to CVD and obesity due to the consumption of red meat is found in the study conducted by Pan et al. (2012). However, a contradicting study was made by Oostindjer et al. (2014) in which no strong relationship was observed between the consumption of red meat and CVD and obesity.

The association between saturated fat and beef carcass, and negative effects on health of humans, particularly cardiovascular health created the fear of fat in foods. The real culprit for the development of cardiovascular disorder (CVD) and obesity is linked to the consumption of processed meat. It is important to make further studies regarding the effects of consumption of processed meat, and to what degree it is already harmful to the overall health of humans. Thus, improvement and regulation of lipid metabolism which can be affected by MUFAs, as well as maintaining the balance of cardiac muscle (Lahey et al., 2014) with improvement of fatty acid profile in Hanwoo beef.

According to Webb and O'Neill (2008), consuming beef fat will aid in transporting fat-soluble vitamins and enhance immune response. Consumption of healthy fats, such as those found in the carcass of Hanwoo beef, can benefit the well-being of humans (Troy et al., 2016). A 33 lower risk of heart failure can be attributed to the APOA1 gene which is related to the high-density lipoprotein (HDL) found in the liver and intestine (Sacks and Jensen, 2018). High-density lipoprotein (HDL) is known as the "good cholesterol" which is good for human health in a way that it lowers the risk of cardiovascular disease and obesity (Centers for Disease Control and Prevention, 2022). Hanwoo beef carcasses have lower cholesterol levels compared to other beef carcasses in the market and have higher omega-3 fatty acids (Cho et al., 2010). Demand for Higher Quality Hanwoo Beef Consumers are shifting from high marbling quantity to high marbling quality. Specifically, consumers in Japan and Korea prefer evenly distributed marbling in beef which is priced much higher than coarsely marbled beef and these countries are willing to purchase high-quality beef (Lee et al., 2019).

Furthermore, increasing the quality of the product with the concept of its origin must be guaranteed by the producers to attract the public to consume the product. Chung et al. (2018) suggested that farmers need to be smart in solving the current challenges in imported feed costs, increasing calf prices, increasing land costs, and cheaper imported beef. Another challenge that the Hanwoo beef industry faces is false labeling, and this poses a threat to the Hanwoo meat market. Some carcasses are intentionally mislabeled as Hanwoo due to their higher price in the market which they take advantage of.

#### Conclusion

The implementation of only a single procedure may not be efficient when it comes to increasing the IMF but it is already a leap. Further studies regarding the IMF promoting effects of vitamins A, C, and D may be conducted in relation with different feeding strategies to further clarify their mechanism of action. Other vitamins may also be considered in conducting further studies with regards to marbling. Despite personal preferences, and culture, beef is one of the popular meats consumed globally. Further studies with these vitamins and fusing them with other procedures may bring out the hidden potentials of Hanwoo beef that are yet to be discovered.

#### **Conflict of interest**

We certify that there is no conflict of interest with any financial, personal, or other relationships with other people or organizations related to the material discussed in the manuscript.

# Author Contributions

M.A.E.I., J.F.C. conceptualization, formal analysis, investigation, M.A.E.I., LP, S.G.H., and J.F.C. writing the manuscript.

# References

- Amengual J, Ribot J, Bonet ML, Palou A, 2008 Retinoic acid treatment increases lipid oxidation capacity in skeletal muscle of mice. Obesity (Silver Spring). 16(3):585–591. https://doi.org/10.1038/oby.2007.104
- 2) Astrup A, Bertram HCS, Bonjour JP, De Groot LCP, De Oliveira Otto MC, Feeney EL, Garg ML, Givens I, Kok FJ, Krauss RM, 2019. WHO draft guidelines on dietary saturated and trans fatty acids: Time for a new approach? BMJ. 366:14137. doi: 10.1136/bmj.l4137.

- 3) Bailey E, 2017. Vitamins for beef cattle. The University of Missouri Extension. Retrieved October 25, 2022, from https://extension.missouri.edu/publications/g2058
- 4) Berry DC, DeSantis D, Soltanian H, Croniger CM, Noy N. 2012. Retinoic acid upregulates preadipocyte genes to block adipogenesis and suppress diet-induced obesity. Diabetes.; 61(5):1112–1121.
- 5) Bhuiyan MSA, Lee DH, Kim HJ, Lee SH, Cho SH, Yang BS, Kim SD, Lee SH, 2018. Estimates of genetic parameters for fatty acid compositions in the longissimus dorsi muscle of Hanwoo cattle. Animal, 12(4): 675-683 https://doi.org/10.1017/S1751731117001872
- 6) Bryant TC, Wagner JJ, Tatum JD, Galyean ML, Anthony RV, Engle. TE, 2010. Effect of dietary supplemental vitamin A concentration on performance, carcass merit, serum metabolites, and lipogenic enzyme activity in yearling beef steers. Journal of Animal Science. 88:1463–1478
- 7) Castillo C, Pereira V, Abuelo Á, Hernández J, 2013. Effect of supplementation with antioxidants on the quality of bovine milk and meat production. The Science World Journal, 2013: 1–8
- 8) Chen W, Chen G. The roles of vitamin A in the regulation of carbohydrate, lipid, and protein metabolism. Journal of Clinical Medicine. 2014;3:453–79.
- 9) Chen D, Li W, Du M, Cao B, 2019. Adipogenesis, fibrogenesis and myogenesis related gene expression in longissimus muscle of high and low marbling beef cattle. Livestock Science, 229, 188–193. https://doi.org/10.1016/j.livsci.2019.09.032
- 10) Cheng W, Cheng JH, Sun DW, Pu H, 2015. Marbling analysis for evaluating meat quality: Methods and Techniques. Comprehensive Reviews in Food Science and Food Safety, 14(5), 523–535. https://doi.org/10.1111/1541-4337.12149
- Chung KY, Lee SH, Cho SH, Kwon EG, Lee JH, 2018. Current situation and future prospects for beef production in South Korea — a review. Asian- Australasian Journal of Animal Sciences, 31(7), 951– 960. https://doi.org/10.5713/ajas.18.0187
- 12) Cho SB, Kim J, Park BY, Seong PN, Kang Gh, Jung SG, Im SK, Kim DH, 2010. Assessment of meat quality properties and development of a palatability prediction model for Korean Hanwoo steer beef. Meat Science 86(1):236-42. DOI: 10.1016/j.meatsci.2010.05.011
- 13) Dela Cruz JF, Oh YK, Hwang SG, 2015. The control of stromal vascular cell differentiation by retinoic acid and calcium in Hanwoo beef cattle adipose tissue. Journal of Animal Production Advances, 5(11), 835. https://doi.org/10.5455/japa.20151118020233
- 14) Dela Cruz J, Hwang SG, 2016. Increased adipocyte differentiation may be mediated by extracellular calcium levels through effects on calreticulin and peroxisome proliferator activated receptor gamma expression in intramuscular stromal vascular cells isolated from Hanwoo beef cattle. Italian Journal of Animal Science. 15. 256-263. 10.1080/1828051X.2016.1186503.
- Dela Cruz J. 2017. Low extracellular calcium and retinoic acid concentration promotes adipocyte differentiation in 3T3-L1 preadipocytes. Philippine Science Letters. 10. 8-13.
- 16) Dehghan M, Mente A, Zhang X, Swaminathan S, Li W, Mohan V, Iqbal R, Kumar R, Wentzel-Viljoen E, Rosengren A, Amma LI, Avezum A, Chifamba J, Diaz R, Khatib R, Lear S, Lopez-Jaramillo P, Liu X, Gupta R, Mohammadifard N, Gao N, Oguz A, Ramli AS, Seron P, Sun Y, Szuba A, Tsolekile L, Wielgosz A, Yusuf R, Hussein Yusufali A, Teo KK, Rangarajan S, Dagenais G, Bangdiwala SI, Islam S, Anand SS, Yusuf S, 2017. Prospective Urban Rural Epidemiology (PURE) study investigators. Associations of fats and carbohydrate intake with cardiovascular disease and mortality in 18 countries from five continents (PURE): a prospective cohort study. Lancet. 2017 Nov 4;390(10107):2050-2062. doi: 10.1016/S0140-6736(17)32252-3. Epub 2017 Aug 29. PMID: 28864332.
- 17) Frank D, Ball A, Hughes J, Krishnamurthy R, Piyasiri U, Stark J, Watkins P, Warner R, 2016. Sensory and flavor chemistry characteristics of Australian beef: Influence of intramuscular fat, feed, and breed. Journal of Agricultural and Food Chemistry, 64(21), 4299–4311. https://doi.org/10.1021/acs.jafc.6b00160
- 18) Gajaweera C, Chung KY, Lee SH, Wijayananda HI, Kwon EG, Kim HJ, Cho SH, Lee SH, 2019. Assessment of carcass and meat quality of longissimus thoracis and semimembranosus muscles of Hanwoo with Korean beef grading standards. Meat Science, 160, 107944. https://doi.org/10.1016/j.meatsci.2019.107944 41
- 19) Gorocica-Buenfil M, Fluharty F, Bohn T, Schwartz S, Loerch SC, 2007. Effect of low vitamin A diets with high- moisture or dry corn on marbling and adipose tissue fatty acid composition of beef steers. Journal of Animal Science 85, 3355–3366.
- Freking B and lalman D, 2018. Supplementing vitamin a to beef cattle. Oklahoma Cooperative Extension Service. ANSI-3036

- 21) Gotoh T, Joo ST, 2016. Characteristics and health benefit of highly marbled Wagyu and Hanwoo Beef. Korean Journal for Food Science of Animal Resources, 36(6), 709–718. https://doi.org/10.5851/kosfa.2016.36.6.709
- 22) Hansen S, Frylinck L, Strydom PE, 2012. The effect of vitamin D3 supplementation on texture and oxidative stability of beef loins from steers treated with zilpaterol hydrochloride. Meat Science, 90, 145–151.
- 23) Harris SE, Huff-Lonergan E, Lonergan SM, Jones WR, Rankins D, 2001. Antioxidant status affects color stability and tenderness of calcium chloride-injected beef. Journal of Animal Science, 79, 666– 677
- 24) Harris CL, Wang B, Deavila JM. 2018. Vitamin A administration at birth promotes calf growth and intramuscular fat development in Angus beef cattle. Journal of Animal Science and Biotechnology 9, 55. https://doi.org/10.1186/s40104-018-0268-7
- 25) Herault F, Vincent A, Dameron O. Le Roy P, Cherel P, Damon M, 2014. The Longissimus and Semimembranosus Muscles Display Marked Differences in Their Gene Expression Profiles in Pig. PLoS ONE, 9(5), e96491. http://doi.org/10.1371/journal.pone.0096491
- 26) Hocquette JF, Gondret F, Baza E, Mdale F, Jurie C, Pethick DW, 2010. Intramuscular fat content in meat-producing animals: Development, genetic and nutritional 42 control, and identification of putative markers. Animal, 4: 303–319
- 27) Hudak CS and Sul HS, 2013. Pref-1, a Gatekeeper of Adipogenesis. Frontiers in Endocrinology 4:79. https://doi.org/10.3389%2Ffendo.2013.00079
- 28) Jang SC, Chung KY, Lee EM, Yang SH, Kwon EG, 2016. Vitamin C supplement increased intramuscular adipose tissues but not affect myogenic development of Hanwoo Steers. Journal of Animal Science, 94(suppl\_5), 369–369. https://doi.org/10.2527/jam2016-0767
- 29) Jo C, Cho SH, Chang J, Nam KC, 2012. Keys to production and processing of Hanwoo Beef: A perspective of tradition and science. Animal Frontiers, 2(4), 32–38. https://doi.org/10.2527/af.2012-0060
- 30) Jo YH, Peng DQ, Kim WS, Kim SJ, Kim NY, Kim SH, Nejad JG, Lee JS, Lee HG, 2020. The effects of vitamin A supplementation during late-stage pregnancy on longissimus dorsi muscle tissue development, birth traits, and growth performance in postnatal Korean native calves. Asian-Australasian Journal of Animal Science. 33:742–52. https://doi.org/10.5713/ajas.19.0413
- 31) Joo ST, Hwang YH, Frank D, 2017. Characteristics of hanwoo cattle and health implications of consuming highly marbled Hanwoo Beef. Meat Science, 132, 45–51. https://doi.org/10.1016/j.meatsci.2017.04.262
- 32) Karges K, Brooks JC, Gill DR, Breazile JE, Owens FN, Morgan JB, 2001. Effects of supplemental vitamin D3 on feed intake, carcass characteristics, tenderness, and muscle properties of beef steers. Journal of Animal Science. 79:2844–2850.
- Kawachi, H. 2006. Micronutrients affecting adipogenesis in beef cattle. Animal Science Journal, 77, 463–471.
- 34) Kern SA, Pritchard RH, Blair AD, Scramlin SM, Underwood KR, 2014. The influence of growth stage on carcass composition and factors associated with marbling development in beef cattle1. Journal of Animal Science, 92(11), 5275–5284. https://doi.org/10.2527/jas.2014-7891
- 35) Khamikoeva S.R., Bosieva O.I., Temiraev V.Kh., Temiraev R.B., Pshikova O.V., Bobyleva L.A., Cis E.Yu. 2021. Effect of feeding sorbent and enzymes on heavy metal toxicity in young steers. Journal of Livestock Science 12: 341-345 doi. 10.33259/JLivestSci.2021.341-345
- 36) Kiely M, Black LJ. 2012. Dietary strategies to maintain the adequacy of circulating 25-hydroxyvitamin D concentrations. Scandinavian Journal of Clinical and Laboratory Investigation, 243:14–23
- 37) Knutson E, Sun X, Fontoura A, Gaspers J, Liu J, Carlin K, 2017. Effect of a low vitamin A diet on marbling and carcass characteristics of Angus cross and Simmental steers. In: Proceedings, Western Section, American Society of Animal Science. p. 96–100.
- 38) Knutson EE, Menezes ACB, Sun X, Fontoura ABP, Liu JH, Bauer ML, Maddock-Carlin KR, Swanson KC, Ward AK, 2020. Effect of feeding a low-vitamin A diet on carcass and production characteristics of steers with a high or low propensity for marbling. Animal, 14 (11), 2308–2314. https://doi.org/10.1017/s1751731120001135
- 39) Krone KG, Ward AK, Madder KM, Hendrick S, McKinnon JJ, Buchanan FC, 2015. Interaction of vitamin A supplementation level with ADH1C genotype on intramuscular fat in beef steers. Animal, 10 (3), 403–409. https://doi.org/10.1017/s1751731115002153

- 40) Kruk ZA, Bottema MJ, Reyes-Veliz L, Forder REA, Pitchford WS, Bottema, CDK, 2018. Vitamin A and marbling attributes: Intramuscular fat hyperplasia effects in cattle. Meat Science, 137, 139–146. https://doi.org/10.1016/j.meatsci.2017.11.024
- 41) Kwon HN, Choi CB, 2015. Comparison of Lipid Content and Monounsaturated Fatty Acid Composition of Beef by Country of Origin and Marbling Score. Journal of the Korean Society of Food Science and Nutrition, 44(12),1806-1812.
- 42) Lahey R, Wang X, Carley AN, Lewandowski ED, 2014. Dietary fat supply to failing hearts determines dynamic lipid signaling for nuclear receptor activation and oxidation of stored triglyceride. Circulation, 130(20), 1790–1799. https://doi.org/10.1161/circulationaha.114.011687
- 43) Ladeira M, Schoonmaker J, Swanson K, Duckett S, Gionbelli M, Rodrigues L, & Teixeira, P, 2018. Review: Nutrigenomics of marbling and fatty acid profile in ruminant meat. Animal, 12(S2), S282-S294. doi:10.1017/S1751731118001933
- 44) Lee CE, Park NK, Seong PN, Jin SH, Park BY, Kim KI, 2003. Effects of deletion of Ca Supplement (limestone) on growth and beef quality in Hanwoo finishing steers. Journal of Animal Science and Technology. 45, 455–462.
- 45) Lee SH, Park BH, Sharma A, Dang CG, Lee SS, Choi TJ, Choy YH, Kim HC, Jeon KJ, Kim SD, Yeon SH, Park SB, Kang HS, 2014. Hanwoo Cattle: Origin, domestication, breeding strategies and genomic selection. Journal of Animal Science and Technology, 56(1), 2. https://doi.org/10.1186/2055-0391-56-2
- 46) Listrat A, Lebret B, Louveau I, Astruc T, Bonnet M, Lefaucheur L, Picard B, Bugeon J, 2016. How Muscle Structure and Composition Influence Meat and Flesh Quality. The Scientific World Journal, 2016, 1–14. http://doi.org/10.1155/2016/3182746
- 47) Lu M, Taylor BV, Korner H, 2018. Genomic effects of the vitamin D receptor: Potentially the link between vitamin D, immune cells, and multiple sclerosis. Frontiers in immunology, 9, 477. 45
- 48) Matsui T, 2012. Vitamin C nutrition in cattle. Asian- Australasian Journal of Animal Sciences, 25(5), 597–605. https://doi.org/10.5713/ajas.2012.r.01
- 49) Miao Z, Wang S, Wang Y, Guo L, Zhang J, Liu Y, 2020. A potential link between vitamin D and adipose metabolic disorders. Canadian Journal of Gastroenterology and Hepatology, 2020
- 50) Montgomery JL, King MB, Gentry JG, Barham AR, Barham BL, Hilton GG, Blanton JR, Horst RL, Galyean ML, Morrow KJ, Wester DB, Miller MF, 2004. Supplemental vitamin D3 concentration and biological type of steers. II. Tenderness, quality, and residues of beef. Journal of Animal Science. 82:2092–2104.
- 51) Motoyama M, Sasaki K, Watanabe A, 2016. Wagyu and the factors contributing to its beef quality: A Japanese industry overview. Meat Science, 120, 10–18. https://doi.org/10.1016/j.meatsci.2016.04.026
- 52) McTavish EJ, Decker JE, Schnabel RD, Taylor JF, Hillis DM, 2013. New World Cattle Show Ancestry From Multiple Independent Domestication Events. PNAS Early Edition
- 53) Mwangi FW, Charmley E, Gardiner CP, Malau-Aduli BS, Kinobe RT, Malau-Aduli AE, 2019. Diet and genetics influence beef cattle performance and meat quality characteristics. Foods, 8(12), 648. https://doi.org/10.3390/foods8120648
- 54) Nguyen, D. V., Nguyen, O. C., & Malau-Aduli, A. E. O. (2021). Main regulatory factors of marbling level in beef cattle. Veterinary and Animal Science, 14, 100219. https://doi.org/10.1016/j.vas.2021.100219
- 55) NRC. 2016. Nutrient requirements of beef cattle. 8th ed. Washington, DC: National Academies Press. 46 OECD (2022), Meat consumption (indicator). doi: 10.1787/fa290fd0-en (Accessed on 18 November 2022)
- 56) Oh YS, Cho SB, Baek KH, Choi CB, 2005. Effects of testosterone, 17β-estradiol, and progesterone on the differentiation of bovine intramuscular adipocytes. Asian-Australasian Journal of Animal Sciences, 18, pp. 1589-1593 https://doi.org/10.5713/ajas.2005.1589
- 57) Oostindjer M, Alexander J, Amdam GV, Andersen G, Bryan NS, Chen D, Corpet DE, De Smet S, Dragsted LO, Haug A, Karlsson AH, Kleter G, de Kok TM, Kulseng B, Milkowski AL, Martin RJ, Pajari AM, Paulsen JE, Pickova J, Egelandsdal B, 2014. The role of red and processed meat in colorectal cancer development: A perspective. Meat Science, 97(4), 583–596. https://doi.org/10.1016/j.meatsci.2014.02.011
- 58) Pan A, Sun Q, Bernstein M, Schulze MB, Manson JE, Stampfer MJ, Willet WC, and Hu FB, 2012. Red Meat Consumption and Mortality. Archives of Internal Medicine, 172(7), 555–. doi:10.1001/archinternmed.2011.2287
- 59) Park SJ, Beak SH, Jung DJ, Kim SY, Jeong IH, Piao MY, Kang HJ, Fassah DM, Na SW, Yoo SP, Baik M, 2018. Genetic, management, and nutritional factors affecting intramuscular fat deposition in

beef cattle — a review. Asian-Australasian Journal of Animal Sciences, 31(7), 1043–1061. https://doi.org/10.5713/ajas.18.0310

- 60) Peng DQ, Lee JS, Kim WS, Kim YS, Bae MH, Jo YH, Oh YK, Baek YC, Hwang SG, Lee HG, 2019. Effect of vitamin A restriction on carcass traits and blood metabolites in Korean native steers. Animal Production Science, 59(12), 2138. https://doi.org/10.1071/an17733
- 61) Peng DQ, Jo YH, Kim SJ, Kim NY, Nejad JG, Lee HG, 2020. Oral vitamin A supplementation during neonatal stage enhances growth, pre-adipocyte and muscle development in Korean native calves. Animal Feed Science and Technology. 268:114609. 47
- 62) Peng DQ, Smith SB, Lee HG, 2021. Vitamin A regulates intramuscular adipose tissue and muscle development: Promoting high-quality beef production. Journal of Animal Science and Biotechnology, 12(1). https://doi.org/10.1186/s40104-021-00558-2
- 63) Pickworth CL, Loerch SC, Fluharty FL. Effects of timing and duration of dietary vitamin A reduction on carcass quality of finishing beef cattle. Journal of Animal Science. 2012a; 90(8):2677–2691.
- 64) Pickworth CL, Loerch SC, Fluharty FL, 2012b. Restriction of vitamin A and D in beef cattle finishing diets on feedlot performance and adipose accretion. Journal of Animal Science. 90(6):1866–1878. [PubMed: 22178850]
- 65) Qi W, Chan H, Teng Pogge, Danielle J.; Lonergan, Steven M.; Hansen, Stephanie L. 2013. Influence of supplemental vitamin C on postmortem protein degradation and fatty acid profiles of the longissimus thoracis of steers fed varying concentrations of dietary sulfur. Meat Science, 96(2), 956–963. doi:10.1016/j.meatsci.2013.08.031.
- 66) Pogge DJ, Hansen SL, 2013. Supplemental vitamin C improves marbling in feedlot cattle consuming high sulfur diets. Journal of Animal Science, 91(9), 4303–4314. doi:10.2527/jas.2012-5638
- 67) Pogge DJ, Lonergan SM, Hansen SL, 2014. Influence of supplementing vitamin C to yearling steers fed a high sulfur diet during the finishing period on meat color, tenderness and protein degradation, and fatty acid profile of the longissimus muscle. Meat Science, 97(4), 419–427. https://doi.org/10.1016/j.meatsci.2014.02.016
- 68) Pogge, D. J., Lonergan, S. M., & Hansen, S. L. (2015). Impact of supplementing vitamin C for 56, 90, or 127 days on growth performance and carcass characteristics of steers fed a 0.31 or 0.59% sulfur diet. Journal of Animal Science, 93(5), 2297–2308. https://doi.org/10.2527/jas.2014-7913
- 69) Półtorak A, Moczkowska M, Wyrwisz J, Wierzbicka A, 2017. Beef tenderness improvement by dietary vitamin D3 supplementation in the last stage of fattening of cattle. Journal of Veterinary Research, 61(1), 59–67. https://doi.org/10.1515/jvetres-2017-0008
- 70) Rafalska UK, 2016. Influence of dietary vitamin D3 supplementation on the sarcomere length, Warner-Bratzler shear force, shortening of aging time, and sensory acceptance of culinary beef muscles. Turkish Journal of Veterinary & Animal Sciences, 40, 514–520.
- 71) Reiling BA, Johnson DD, 2003. Effects of implant regimens (trenbolone acetate-estradiol administered alone or in combination with zeranol) and vitamin D3 on fresh beef color and quality. Journal of Animal Science. 81:135–142.
- 72) Sacks FM, Jensen MK. 2018. From high-density lipoprotein cholesterol to measurements of function. Arteriosclerosis, Thrombosis, and Vascular Biology, 38(3), 487–499. https://doi.org/10.1161/atvbaha.117.307025
- 73) Scanga JA, Belk KE, Tatum JD, and Smith GC. 2001. Supranutritional oral supplementation with vitamin D3 and calcium and the effects on beef tenderness. Journal of Animal Science. 79:912–918.
- 74) Scollan N, Hocquette JF, Nuernberg K, Dannenberger D, Richardson I, Moloney A, 2006. Innovations in beef production systems that enhance the nutritional and health value of beef lipids and their relationship with meat quality. Meat Science. 74, 17–33.
- 75) Siebert B, Kruk Z, Davis J, Pitchford W, Harper G and Bottema C, 2006. Effect of low vitamin A status on fat deposition and fatty acid desaturation in beef cattle. Lipids 41, 365–370 49
- 76) Smith SB, 2016. Marbling and its nutritional impact on risk factors for cardiovascular disease. Korean Journal for Food Science of Animal Resources, 36(4), 435–444. https://doi.org/10.5851/kosfa.2016.36.4.435
- 77) Swanek SS, Morgan JB, Owens FN, Gill DR, Strasia CA, Dolezal HG, Ray FK, 1999. Vitamin D3 supplementation of beef steers increases longissimus tenderness. Journal of Animal Science 1999, 77, 874–881.
- 78) Troy DJ, Tiwari BK, Joo ST, 2016. Health implications of beef intramuscular fat consumption. Korean Journal for Food Science of Animal Resources,

- 79) Uhl, EW. 2018. The pathology of vitamin D deficiency in domesticated animals: An evolutionary and comparative overview. International Journal of Paleopathology, S1879981717301213–. doi:10.1016/j.ijpp.2018.03.001 36(5), 577.
- 80) Wang B, Yang Q, Harris CL, Nelson ML, Busboom JR, Zhu MJ. Du M, 2016. Nutrigenomic regulation of adipose tissue development — role of retinoic acid: A review. Meat Science, 120, 100–106. doi:10.1016/j.meatsci.2016.04.
- 81) Wang B, Fu X, Liang X, Wang Z, Yang Q, Zou T, Nie W, Zhao J, Gao P, Zhu M-J, de Avila JM, Maricelli J, Rodgers BD, Du M, 2017. Maternal retinoids increase PDGFRα(+) progenitor population and beige adipogenesis in progeny by stimulating vascular development. EBioMedicine 18, 288
- 82) Ward AK, McKinnon JJ, Hendrick S, Buchanan FC, 2012. The impact of vitamin A restriction and ADH1C genotype on marbling in feedlot steers. Journal of Animal Science 90, 1–8.
- 83) Webb EC, O'Neill HA., 2008. The animal fat paradox and meat quality. Meat Science. 80, 28–36.
- 84) Wei LN, 2012. Chromatin remodeling and epigenetic regulation of the CrabpI gene in adipocyte differentiation. Biochimica et Biophysica Acta. 1821(1):206–212. [PubMed: 21435396]
- 85) Yang XJ, Albrecht E, Ender K, Zhao RQ, Wegner J, 2006. Computer image analysis of intramuscular adipocytes and marbling in the longissimus muscle of Cattle1. Journal of Animal Science, 84(12), 3251–3258. https://doi.org/10.2527/jas.2006-187
- 86) Yang QY, Liang JF, Rogers CJ, Zhao JX, Zhu MJ, Du M, 2013. Maternal obesity induces epigenetic modifications to facilitate Zfp423 expression and enhance adipogenic differentiation in fetal mice. Diabetes 62, 3727-3735.