

Development of nutrigenomic based precision management model for Hanwoo steers

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Abstract

Focusing high marble deposition, Hanwoo feedlot system uses high-energy diet over the prolonged fattening period. However, due to the individual genetic variation, around 40% of them are graded into inferior quality grades (QG), despite they utilized the same resources. Therefore, focusing on development of a nutrigenomic based precision management model, this study was to evaluate the response to the divergent selection on genetic merit for marbling score (MS), under different dietary total digestible nutrient (TDN) levels. Total of 111 calves were genotyped and initially grouped according to estimated breeding value (high and low) for marbling score (MS-EBV). Subsequently, managed under two levels of feed TDN%, over the calf period, early, middle, and final fattening periods following 2 × 2 factorial arrangement. Carcasses were evaluated for MS, Back fat thickness (BFT) and Korean beef quality grading standard. As the direct response to the selection was significant, the results confirmed the importance of initial genetic grouping of Hanwoo steers for MS-EBV. However, dietary TDN level did not show an effect ($p > 0.05$) on the MS. Furthermore, no genetic-by-nutrition interaction for MS ($p > 0.05$) was also observed. The present results showed no correlation response on BFT ($p > 0.05$), which indicates that the selection based on MS-EBV can be used to enhance the MS without undesirable effect on BFT. Ultimate turnover of the Hanwoo feedlot operation is primarily determined by the QGs. The present model shows that the initial grouping for MS-EBV increased the proportion of carcasses graded for higher QGs (QG1⁺⁺ and QG1⁺) by approximately 20%. Moreover, there appear to be a potential to increase the proportion of QG 1⁺⁺ animals among the high-genetic group by further increasing the dietary energy content. Overall, this precision management strategy suggests the importance of adopting an MS based initial genetic grouping system for Hanwoo steers with a subsequent divergent management based on dietary energy level.

Keywords: Feed energy level, Genetic merit for marbling, Hanwoo

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Competing interests

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Availability of data and material

Upon reasonable request, the datasets of this study can be available from the corresponding author.

Authors' contributions

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Ethics approval and consent to participate

This research was conducted following the animal health and welfare guidelines of Institutional Animal Care and Use Committee of the National Institute of Animal Science, Rural Development Administration, Korea (Approve No: NIAS 2015-112).

INTRODUCTION

Selection focusing the economically important quantitative traits have made a great impact on the genetic improvement of farm animals over recent decades. Recent developments in genomic technologies have also being significantly contributed to the genetic progress as which enhanced accuracy and intensity of the selection and shortening the generation intervals [1–4]. However, many researchers believe that the rate of further genetic improvement will not be much as previous [2,5]. Therefore, they focus alternative strategies for enhancement of livestock production since which critical to fulfilling the ever increasing demand with the population growth.

Production and performance of the farm animals are primarily determined by the genotype (heritable) and environmental (non-heritable) factors, where nutrition plays a major role as an environmental determinant [6]. In term of nutritional aspects, feed efficiency has a major influence on farm profitability since feed cost is the single most significant cost component in the total livestock production cost. Furthermore, feed cost for beef cattle has increased by 70%–80% over the last decade [7,8]. Feed efficiency of cattle has greatly enhanced over the past few decades, mostly as a byproduct of the selection over the other quantitative production traits [5]. However, it will be harder to improve the feed efficiency further by just focusing the selection for production traits. Therefore, emphasis has been laid on the importance of dietary management in the context of individual genetic background focusing on the enhancement of the production, profit as well as environmental sustainability [9].

Historically, Hanwoo (Korean native cattle) was extensively a draft animal used for agriculture but it has been systematically and intensively bred over the last 30 years to improve as a meat breed for production of high marbled meat [10–12]. Hanwoo selection index basically uses three carcass traits, eye muscle area (EMA), backfat thickness (BFT) and marbling score (MS) with a weight ratio of standardized breeding values of 1: -1: 6, respectively [10,13]. On the other hand, marbling the accumulation and distribution of intramuscular fat [IMF] is the most important factor determining the quality and the market value of beef [14–17]. In this study, since MS is the crucial trait for genetic selection, we firstly focused on grouping animals based on their genetic merits for MS.

On the other hand, dietary energy level also plays a key role in production of high quality beef. Thus, Hanwoo feedlot system typically uses high-energy corn based diet over a long fattening period [18]. Recently, Chung *et al.* [19] showed the influence of high energy diet (+2% total digestible nutrient [TDN]) on enhancing the quality grades (QG) of Hanwoo carcass. Accordingly, we observed some farmers tend to use more than the recommended TDN level to enhance the deposition of marbling, especially toward the final fattening period. To cater to farmer's demand, some feed companies also add extra energy in their fattening feed. Therefore, in this study, we investigate the effect of divergent selection for estimated breeding value of MS (MS-EBV) and the level of energy in the feed (+2% TDN) on the carcass MS of Hanwoo steers. Moreover, since farmer's perspectives and market aspects, QG is important in Hanwoo feedlot system, we appraised the effect of our nutrigenomic based management model on Korean beef quality grading stands.

MATERIALS AND METHODS

Animal

Total of 111 calves of the progeny of Korean proven bulls from Pyeongchang commercial Hanwoo feedlot were used for this study. Research was started when calves were introduced to feedlot system from the cow-calf operation at average age of six months and had attained average live weight

196.97 ± 18.5 kg. This research was conducted following the animal health and welfare guidelines of Institutional Animal Care and Use Committee of the National Institute of Animal Science, Rural Development Administration, Korea (Approve No: NIAS 2015-112).

Management

Present nutrigenomics based precision management model suggesting two key steps as; initial genetic grouping and subsequent management grouping.

Initial grouping based on genetic merit for marbling score

Genomic DNA from all the selected steers were extracted from blood samples using the standard methods. Samples were genotyped with the Illumina Bovine single nucleotide polymorphism (SNP)50 BeadChip (50K, Illumina, SanDiego, CA, USA). Reference population of 2,394 animals of the progeny of Korean proven bulls that are both genotyped and phenotyped by National Institute of Animal Science, RDA, Korea were used to estimate the breeding value of MS. Genotype quality control performed based on the following exclusion criteria: Hardy–Weinberg equilibrium < 0.0001(768 SNP were removed), missing genotype < 0.1 (12,317 SNP were removed) and minor allele frequencies < 0.01(6848 SNP were removed), using PLINK 1.9 software [20]. Non-autosomal SNPs were also removed from analyses. Out of 54,609 SNPs a total of 34,676 SNPs were retained after the quality control for further analyses. To estimate the genomic breeding value (EBV), genomic best linear unbiased prediction (GBLUP) approach [21,22] was applied with the following model using ASReml 4.1 software [23]. Genomic relationship matrix was derived by GCTA software [24].

The mixed model equation used was; $Y = X\beta + Zu + e$

Where Y is a vector of phenotypic observation for MS, β is a vector of fixed effects, u is a vector for random effect and e is a vector of random residual terms, and X and Z the corresponding design matrices.

Steers were ranked based on the MS-EBV and drafted into two groups; steers with MS-EBV greater than the mean (0.2) were assigned into high EBV group and less than mean allocated to low EBV group. Among the 111 steers, 54 steers were assigned to the low EBV group while the rest of the 57 steers were drafted into the high EBV group (Fig. 1).

Management of dietary energy level and measurement of body weight

All animals used in this experiment were raised in a pen with group feeding procedure using the standard Korean feedlot management system. Animals were assigned to the pens following the randomized 2 × 2 factorial arrangement, including four heads per each pen. An equal number of pens of each genetic groups were again randomly designated to the nutrition treatments according to the Table 1 and Fig. 1. All the rations used in the experiment were prepared by commercial feed manufacturer following the Table 1. Nutritional composition of the control feed is comparable with the existing feeds which followed the current recommendations and the treatment contained approximately 2% higher TDN than the control. Accordingly, all the experimental steers were managed under two levels of feed TDN%, over the growing period, early and final fattening periods. Growing period; First 6 months of the experiment (6–11 months) steers were fed by growing ration according to Table 1 along with the ad-libitum supply of high quality hay. Whereas, the ration was gradually increased from 3–4.2 kg/day/ animal. Early fattening period; During the 12 to 20 months they were fed with the early fattening ration which increased steadily from 4.5 to 9.2 kg while hay was gradually substituted by rice straw. At the final fattening period (21–30 months) the rate of the concentrate was raised to 90% while providing only 10% rice straw. Final

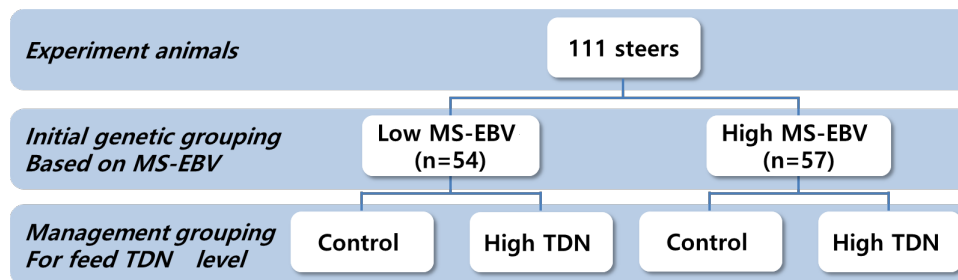


Fig. 1. Graphical illustration of research design. Control, existing feed recommendations; High TDN, control +2% TDN; MS-EBV, genomic estimated breeding value for marbling score; TDN, total digestible nutrition.

fattening ration offered freely up to 9.5–10 kg/day/ animal whereas, rice straw supply was regularly reduced up to 1–0.5 kg/ day/ animal. Growth performance analysis for the fattening period was conducted at the following intervals: growing, fattening period of feeding. Steers were weighed three times (6, 13, and 30 months) during the experiment period on a scale (CAS, Yangju, Korea) in the early morning before being fed. Animals had ad libitum access to fresh water and mineral salts blocks throughout the period.

Evaluation marbling score, backfat thickness and Korean quality grading standard

The animals were fasted off feed for around 12 hours after transported them to the local abattoir, while they had free access to water. On the following day, animals were slaughtered according to the Korean standard procedures [25]. After 24 hours chilling, the left side of the carcasses were ribbed between the 13th rib and the 1st lumber vertebra and evaluated for MS and BFT (mm) [26].

According to the Korean carcass grading Procedure, Carcasses were evaluated for the QG by experienced official grader. Carcasses were categorized in to five QGs (grade 1⁺, 1⁺, 1, 2, 3) based on the MS (1 = devoid, 9=abundant), lean meat color (1 = very bright red, 7 = very dark red), fat color (1=creamy white, 7=yellowish), firmness and texture of lean (1 = firm, 3 = soft) and maturity (1 = youthful, 3 = mature) of the longissimus dorsi (LD) muscle [25].

Statistical analysis

Carcass traits were analyzed using the following linear mixed models to identify the effect of genetic selection for MS-EBV and dietary energy levels. A divergent group for genetic merit, different feeding plan, slaughter year, slaughter month and birth month were served as a fixed effect and animal effect was included as a random effects. Age at slaughter was included as a covariate:

$$Y_{ijklnopq} = \mu + G_i + N_j + (G * N)_k + Ag_m + SY_n + SM_o + BM_p + A_q + e_{ijklnopq}$$

Where $Y_{ijklnopq}$ indicates the carcass traits, μ is overall mean, G_i is divergent group according to the MS-EBV high or low, N_j is feeding plan; control or high TDN, $(G * N)_k$ is the interaction of the genetic group and feeding plan, Ag_m is Age at slaughtering, SY_n is slaughter year, SM_o is slaughter months, BM_p is birth month, A_q is Animal effect, $e_{ijklnopq}$ is the random residual effect.

The statistical significant differences between data were analyzed with ANOVA, followed by Fisher's Least Significant Difference (LSD) test at a significance level of 0.05. All data were analyzed using the statistical software package R [27].

Table 1. Feed ingredients and nutrients composition of the treatment rations (DM basis, %)

| Ingredient (% DM) | Growing | | Early fattening | | Final fattening | | Hay | Rice straw |
|----------------------------|-------------|----------|-----------------|----------|-----------------|----------|-------|------------|
| | 6–11 months | | 12–20 months | | 21–30 months | | | |
| | Control | High TDN | Control | High TDN | Control | High TDN | | |
| Corn | 20.00 | 22.00 | 25.00 | 26.00 | 13.56 | 11.72 | | |
| Steamed flaked corn | - | - | - | - | 25.00 | 25.00 | | |
| Wheat | 18.00 | 18.00 | 19.00 | 19.00 | 18.00 | 20.00 | | |
| Wheat bran | 14.00 | 12.00 | 13.00 | 10.00 | - | - | | |
| Rice bran | 2.00 | 2.00 | 5.00 | 5.00 | - | - | | |
| Cotton seed whole | - | - | - | - | - | 4.00 | | |
| Soybean | 3.00 | 5.00 | - | - | - | - | | |
| Soy hull | - | - | 1.00 | - | 0.40 | 4.00 | | |
| Corn gluten feed | 7.00 | 7.00 | 9.00 | 11.00 | 19.89 | 20.09 | | |
| Coconut oil | 8.00 | 6.00 | 7.00 | 7.00 | - | - | | |
| Copra meal | - | - | - | - | 3.60 | 1.82 | | |
| Palm kernal meal | 8.00 | 8.00 | 7.00 | 7.00 | 11.24 | 5.00 | | |
| Rapeseed meal | 5.00 | 5.00 | 2.00 | 3.00 | - | - | | |
| Palm olein oil | - | - | - | - | 0.30 | 1.05 | | |
| DDGS | 4.00 | 4.00 | 2.00 | 2.00 | - | - | | |
| Molasses cane | 3.00 | 3.00 | 3.00 | 3.00 | 3.00 | 2.7 | | |
| Condensed molasses soluble | - | - | - | - | 0.85 | 0.84 | | |
| Limestone | 3.00 | 3.00 | 3.00 | 3.00 | 2.33 | 1.94 | | |
| Salt | 0.80 | 0.80 | 0.80 | 0.80 | 0.16 | 0.16 | | |
| Sodium bicarbonate | 0.40 | 0.40 | 0.50 | 0.50 | 0.91 | 0.92 | | |
| Magnesium oxide | 0.30 | 0.30 | 0.30 | 0.30 | - | - | | |
| Mineral PX | 0.20 | 0.20 | 0.22 | 0.22 | - | - | | |
| Vitamin PX | 0.18 | 0.18 | 0.05 | 0.05 | - | - | | |
| Mineral-vitamin premix | - | - | - | - | 0.20 | 0.20 | | |
| Others ¹⁾ | 3.12 | 3.12 | 2.13 | 2.13 | 0.56 | 0.56 | | |
| SUM | 100 | 100 | 100 | 100 | 100 | 100 | | |
| Nutrient level (% DM) | | | | | | | | |
| Dry matter | 87.83 | 87.69 | 87.79 | 87.94 | 88.16 | 88.14 | 90.13 | 91.43 |
| Crude protein | 16.00 | 16.48 | 13.00 | 13.39 | 12.95 | 12.95 | 15.87 | 4.39 |
| Ether extract | 3.42 | 3.76 | 3.74 | 4.57 | 3.33 | 4.90 | 2.78 | 2.36 |
| Crude fiber | 6.74 | 6.5 | 6.76 | 6.36 | 6.24 | 6.35 | - | - |
| Crude ash | 9.12 | 8.48 | 9.04 | 8.62 | 6.99 | 6.00 | 7.15 | 13.07 |
| Ca | 1.25 | 1.2 | 1.25 | 1.23 | 1.23 | 1.08 | - | - |
| P | 0.57 | 0.56 | 0.57 | 0.56 | 0.46 | 0.46 | - | - |
| ADF | 11.36 | 10.84 | 10.84 | 10.35 | 8.70 | 9.21 | 40.15 | 38.13 |
| NDF | 28.25 | 27.1 | 27.61 | 26.85 | 22.01 | 22.33 | 76.29 | 70.21 |
| TDN | 70.53 | 72.65 | 71.00 | 73.13 | 73.01 | 75.99 | 53.00 | 44.00 |

¹⁾Specials: Pre-/Probiotics, organic minerals, buffers, taster & flavors etc.

DM, dry matter; TDN, total digestible nutrients; DDGS, dried distiller's grains with solubles; PX, premix; ADF, acid detergent fiber; NDF, neutral detergent fiber.

RESULTS

The initial body weight did not differ ($p > 0.05$) between the two dietary treatments. However, the initial body weight was greater in the high MS-EBV group compared to the low MS-EBV group. The average daily gain was not influenced ($p > 0.05$) by either MS-EBV or dietary treatment (Table 2). Summary statistics for the number of steers for each carcass trait, mean, standard deviation, range, and breeding value for MS are shown in Table 3. The number of animals accounting for each QG is shown in Table 3. The mean value of the MS-EBV was 0.2 with the range between -0.86 to 0.99 . Steers that were selected for divergence in genetic merit for MS showed difference ($p < 0.05$) in phenotypic MS at the end of fattening period (Table 4). Thus, the results clearly indicate that direct response to the divergent selection on MS-EBV ($p < 0.05$). However, MS did not differ ($p > 0.05$) between the control and the high TDN nutrition groups. Even though, this study primarily focused on interaction between the genetic and nutrition, the results did not show an interaction ($p > 0.05$) between the MS-EBV and the dietary TDN level on carcass MS.

The other important feature of this model was the selection based on genetic merit for MS or the level of TDN in feed did not affect ($p > 0.05$) on the carcass BFT deposition. Moreover, MS was greatly increased ($p < 0.05$) when High TDN nutrition plan applied on the high genetic (MS-EBV) steers compared to low genetic steers managed under low nutrition plan.

Ultimate turnover of the Hanwoo feedlot operation is mainly determined based on the QG [28]. Fig. 2 illustrates the proportion of carcasses assigned to QG according to the main effects and the combinations. As a direct consequence of the divergent selection for MS, the proportion of QG1⁺⁺ and QG1⁺ carcasses were greatly increased in high MS-EBV group (81.82%) compared to the low MS-EBV group (64.29%). However, the cumulative proportion of higher QG carcasses (QG1⁺⁺ and QG1⁺) almost similar between the nutrition treatments. The results showed approximately 10% increase in QG1⁺⁺ by both main effects; genetic merit for MS and dietary TDN level. Furthermore, initial grouping for high MS-EBV and feed them high TDN plan increased the ratio of animals graded to QG1⁺⁺ by 15.1% compared to the steers with the same genetic merit but managed under control ration. However, no difference in the number of carcasses belongs to QG1⁺⁺ and QG1⁺ in both genetic groups regardless the feed TDN level. Moreover, carcasses graded for lowest QG (QG 3) were found only from the low MS-EBV steers when they manage under control ration.

DISCUSSION

The intention of the breeding is to improve the desirable genetic traits in future generations. Most of the economically important traits are environmentally dependent biological traits. Variation in

Table 2. Effect of divergent selection for genetic merits for MS and nutritional treatment (different TDN level) on growth performance of the Hanwoo steers

| | MS-EBV | | SEM | Diet | | SEM | p-value | | |
|-----------|---------------------|--------------------|------|---------|------------------------|------|---------|------|---------------------|
| | Low | High | | Control | High TDN ¹⁾ | | EBV | Diet | E × D ²⁾ |
| IBW (kg) | 189.27 ^b | 201.6 ^a | 6.17 | 193.89 | 199.76 | 2.93 | 0.04 | 0.28 | 0.12 |
| ADG (kg) | | | | | | | | | |
| Growing | 1.00 | 0.94 | 0.03 | 0.94 | 0.98 | 0.02 | 0.07 | 0.11 | 0.60 |
| Fattening | 0.82 | 0.80 | 0.01 | 0.80 | 0.82 | 0.01 | 0.38 | 0.32 | 0.84 |

¹⁾High TDN, control +2% TDN.

²⁾E × D, interaction between MS-EBV and dietary TDN level.

MS, marbling score; TDN, total digestible nutrient; EBV, genomic estimated breeding value for marling score; IBW, initial body weight; ADG, average daily gain.

Table 3. Description of carcass traits, estimate breeding values for marbling scores and carcass quality grades

| | Number of steers | Mean | Standard deviation | Range |
|-----------------|------------------|-------|--------------------|------------|
| MS | 111 | 6.3 | 1.623386 | 2–9 |
| BFT (mm) | 111 | 13.53 | 3.59247 | 4.0–26.0 |
| MS-EBV | 111 | 0.2 | 0.35 | –0.86–0.99 |
| Quality grade | | | | |
| 1 ⁺⁺ | 23 | | | |
| 1 ⁺ | 58 | | | |
| 1 | 23 | | | |
| 2 | 6 | | | |
| 3 | 1 | | | |

MS, marbling score; BFT, back-fat thickness; MS-EBV, estimated genomic breeding value for marbling score.

Table 4. Effect of divergent selection for genetic merits for MS and nutritional treatment (different TDN level) on carcass traits of the Hanwoo steers

| | MS-EBV | | SEM | Diet | | SEM | p-value | | |
|----------|-------------------|-------------------|------|---------|------------------------|------|---------|------|---------------------|
| | Low | High | | Control | High TDN ¹⁾ | | EBV | Diet | E × D ²⁾ |
| BFT (mm) | 13.07 | 13.91 | 0.42 | 13.15 | 13.86 | 0.36 | 0.22 | 0.28 | 0.83 |
| MS | 5.85 ^b | 6.63 ^a | 0.39 | 6.22 | 6.29 | 0.03 | 0.01 | 0.77 | 0.99 |

¹⁾High TDN, control +2% TDN

²⁾E × D, interaction between MS-EBV and dietary TDN level.

MS, marbling score; TDN, total digestible nutrient; EBV, genomic estimated breeding value for marling score; BFT, backfat thickness.

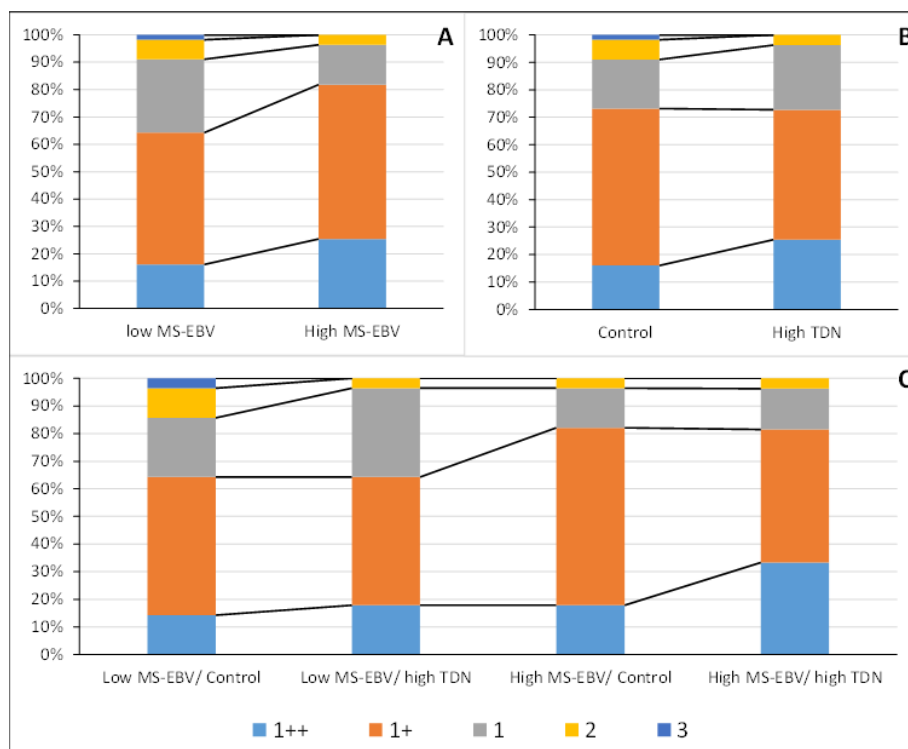


Fig. 2. Effect of divergent selection for MS-EBV and nutritional treatment (different TDN level) on carcass quality grades. Control, existing feed recommendations; High TDN, control +2% TDN; MS, marbling score; EBV, genomic estimated breeding value; TDN, total digestible nutrition.

those traits is primarily caused by genetic, environmental and genotype by environment interactions [29,30]. Therefore, even though the animals select for genetic merits do not necessarily have the best phenotype across the different environmental conditions [29,31,32]. On the other hand, variation exist among the individuals throughout the livestock supply chains make an unwanted nuisance, which affects the productivity of the farm operation [9]. Therefore, the illustrated the importance of initial grouping of the animals based on their genetic merits before entering the supply chains that help to reduce the genetic variation within the groups. Subsequently, the formation of management subgroups with minimal variation among the animals that are already in the supply chain will lead to achieving the maximum productivity and efficiency of the system than the sole management regime. This experiment provides compelling evidence for importance of the initial grouping based on the genetic merits before entering to the feedlot system and the subsequent management grouping for Hanwoo steers.

Marbling is the most important value-determinant in the Korean beef market. The present genomic based precision management model imply the advantage of divergent selection based on genetic merit for MS since which directly influence on enhancing the phenotypic MS. Intrinsic (genetic) and extrinsic (nutrition and management) factors exert the most impact on the complex process of formation and composition of IMF in cattle [17,33,34]. In genetic terms, marbling is a complex and highly polygenetic trait controlled by many genes with a small effect [15,35,36]. Numerous studies screened the diverse expression pattern of several genes with the level of marbling, especially for high marbling breeds like Hanwoo [37–49]. Accordingly, divergent expression pattern of the gene responsible for MS enables the genotype-based selection approach. On the other hand, heritability variation of the traits determines the potential for responding to the selection, where moderate or high heritable traits responding well to genetic selection [50,51]. Previous studies of Lee et al. [10], Hwang et al. [52], Yoon et al. [53] found moderate to high estimated heritability of MS of Hanwoo was 0.4, 0.56 and 0.57 respectively. Which reflect the potential of responding to the selection for MS of Hanwoo cattle.

One of the major concerns of the sustainable beef production system is to increase marbling without increasing the overall fatness. All the excess fat produced by subcutaneous adipocytes are trimmed off before consumption and which adversely affect feed efficiency. Especially, this topic is much important in East Asian beef market since they preferred high marble beef compared the rest of the world. Even though both are fat related traits, present results confirmed that the genetic selection for marbling could increase the carcass MS without increasing the BFT of Hanwoo steers. Correspondingly, few previous studies such as Vieselmeyer et al. [54] and Gwartney et al. [55] also revealed that selection based on expected progeny difference (EPD) for marbling can be utilized to increase marbling ability without increasing the external fat. Moreover, it has shown a very low genetic ($-0.2 - 0.17$) and phenotypic ($-0.02 - 0.19$) correlation between the MS and BFT for Hanwoo steers [10,52,53,56,57], which confirm the less or no correlation response to the selection for MS on BFT of Hanwoo. Likewise, Rincker et al. [58] also revealed that estimated progeny difference for MS was correlated ($p < 0.05$) with MS ($r = 0.44$) and IMF percentage ($r = 0.27$) while no correlation was found with the BFT ($r = -0.04$). In addition, Martínez-Álvaro et al. [59] showed that divergent selection of IMF lead to the genetic progress in rabbit followed a symmetrical trend for phenotypic difference between the high-IMF and low-IMF lines.

An animal needs energy for its maintenance, growth, reproduction, and production. Beyond that requirement, ultimately excess energy will be accumulated as a carcass fat [60] However, fat accretion throughout the body is not homogeneous. There is a specific order to the process, with abdominal fat being formed first, followed by intermuscular, subcutaneous, and finally, deposited as an IMF [61]. The morphology, cellular and biochemical characteristics of the adipose tissues are

varied at a different site of the body [62] such as the diameter of the adipocyte are much smaller in intermuscular depot than the subcutaneous fat [63,64]. On the other hand, the source of energy used to synthesize fat is diverse in the different site of the body fat depot. Subcutaneous adipose tissue primarily uses acetate for lipid synthesis, which is a volatile fatty acid produced by rumen fermentation. Whereas, intramuscular adipose tissue utilize glucose as an energy source for fatty acid synthesis [65,66]. Therefore, it is possible to use nutritional strategies such as a manipulation of diets to enhance IMF deposition by increasing the glucose supply [34]. Likewise, several studies showed that IMF content of beef cattle can be promoted by high-energy grain rations compared to the forage-based feeding systems [61,67–69]. Accordingly, Hanwoo cattle are typically fed a high-energy concentrate diet throughout the prolonged feedlot system focusing on the greater marbling deposition [70]. However, the present study did not show an effect of dietary TDN level on the carcass MS. This might be due to that just 2% increase of TDN may not be enough to express significant variation in IMF%, since the control ration already containing a superior energy content (TDN % in growing, early fattening and final fattening control rations were 70.53, 71.00 and 73.01 respectively). Current results are consistent with the previous study of Chung et al. [19] as high energy diet (+2% TDN) did not contribute ($p > 0.05$) to the MS or BFT of Hanwoo carcass. Nevertheless, Li et al. [71] showed 10% different in TDN had a significant effect on IMF% in Angus × Chinese Xiangxi yellow cattle. Ladeira et al. [34] and Ladeira et al. [72] reviewed the nutrigenomics aspects focusing the how nutrient and diet manipulation is influenced on the expression of genes involving lipid metabolism and marbling of beef cattle. However, the present study did not find an interaction between MS-EBV and the dietary TDN level. This also might be due to the limited difference in TDN% among the dietary treatments and the method we used to assign the genetic groups based on their mean MS-EBV. If the animals divided into highest and lowest genetic groups by excluding the intermediate animals as Herd et al. [73] did, the results would be more precious. However, due to the limitation of available animals at the research facility and high experimental budget, we tried to maximize the representing samples.

In general, beef QG reflect the expected eating quality of the carcasses. After introduced the Korean carcass grading system in 1992, a substantial price difference can be seen according to the QGs [57]. Therefore, to obtain a greater value at the auction, Hanwoo farmers usually trying to increase the carcass QGs by enhancing the marbling deposition [74]. Auction price of QG1⁺⁺ is almost double than the QG3, as average QG 1⁺⁺ was 18.10 \$/kg, QG1⁺ was 16.35 \$/kg, QG1 was 15.25 \$/kg, QG2 was 12.97 \$/kg and QG3 was 9.58 \$/kg in the Korean market in 2017 [25]. In economic aspects, if farmers would be able to upgrade the QG of a carcass by one grade, the average income per animal will be increase almost by 1,000 \$ (as the average carcass weight [CWT] of the studied animals was 455.22 kg).

In terms of QG also, the present study revealed the significance of genetic based nutritional management strategy to uplift the Hanwoo production system. There appears to be a potential to increase the proportion of higher QGs, while minimizing the occurrences of lower QGs by initial genetic grouping for MS-EBV. Likewise, application of high TDN nutrition plan on the steers with high genetic merit had shown further enhancement in the proportion of QG1⁺⁺. Interestingly, our results showed even under 2% less dietary TDN plan, both high and low MS-EBV groups produced similar proportion of cumulative highest two QGs. This is important in economic aspects since the feeding cost accounts almost 40% of the total production cost and the largest single cost component of the Hanwoo industry. Corresponding to the present study, Cho et al. [75] and Moon et al. [76] also showed a significant influence of MS on the QG of Hanwoo carcass. Likewise, Piao et al. [74] and Panjono et al. [77] reported high correlation between MS and QG ($r = 0.98$). Vieselmeyer et al. [54] and Gwartney et al. [55] observed similar results to our as substantially more

cattle in high EPD-MS group graded into USDA choice grade than the low EPD-MS group. Rincker *et al.* [58] also showed a noticeable correlation between EPD-MS and QG ($r = 0.40$). In addition, among the 205,070 Hanwoo steers were slaughtered in South Korea in 2017, average 14.3% were graded to QG 1⁺, 48.3% were graded to QG 1, 24.4% were graded to QG 2, and 0.9% were graded to QG 3 [25]. Compared to the prevailing country average, application of present nutrigenomic based management model is prospective to develop the productivity of Hanwoo industry by enhance the superior QGs, while reducing the inferior QGs.

Moreover, our model enables that importance of initial grouping based on the genetic merit and divergent management focusing the different production goals. Hanwoo farmers in Korean peninsula use a common management strategy for all the animals based only on the fattening stages. Especially, they use an ad libitum high-energy concentrate feeds supply for an extended fattening phase up to 30 months in average. However, it could cause to huge economic and environmental loss if animal produced low MS at the end. On the other hand, aiming at high accumulation of IMF, they normally practice castration at 6 months of age. Although it is well known that castration induces the deposition of marbling, it has a detrimental effect on growth rate [78,79]. Therefore, if the animal unable to produce high MS, there is no need to castrate them earlier since it adversely affects on the CWT. Accordingly, the existing management strategy is more appropriate for the animals with high genetic merit for MS. In addition, present results suggest it is possible to further raise the TDN level of the ration, especially toward the end of the fattening period for high MS-EBV steers. Likewise, for the animals prospective for low marble deposition could be focus CWT instead of MS. Therefore, it is possible to consider an alternative management strategy for them; they can be subjected to late castration and reduced the endpoint like other beef breeds while managing under low energy diet. However further researches are needed to confirm and expand the present findings before recommendation.

CONCLUSION

This experiment confirmed the importance of initial genetic selection of Hanwoo steers based on MS-EBV since the results revealed the significant direct response to the selection. However, no correlation response on the carcass BFT, indicating that the selection based on MS-EBV can be used to enhance the MS without undesirable affect on the Back fat deposition. Dietary treatment (+2%TDN) did not show an effect on the carcass marbling deposition. Further, there was no genetic-by-nutrition interaction for MS. The present model shows that the initial grouping for MS-EBV increased the proportion of carcasses graded for higher QGs (QG1⁺ and QG1⁺), which will enhance the ultimate return of the farmers. Moreover, it is potential to increase the proportion of QG 1⁺ animals among the high MS-EBV group by further increasing their dietary energy content. Overall, this nutrigenomic based management approach for Hanwoo steers provides compelling evidence for importance of the initial grouping based on the genetic merits before enter to the feedlot, with a subsequent divergent management based on dietary energy level.

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