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Heritabilities and genetic correlations of fatty acid compositions in longissimus muscle lipid with carcass traits in Japanese Black cattle

T. Nogi,* T. Honda,† F. Mukai,‡ T. Okagaki,* and K. Oyama†[1]

*Tottori Prefectural Agriculture and Forest Research Institute Livestock Research Center, Tohaku-gun, Tottori 689-2503, Japan; †Food Resources Education and Research Center, Graduate School of Agricultural Science, Kobe University, Kasai, Hyogo 675-2103, Japan; and ‡Graduate School of Agricultural Science, Kobe University, Kobe, Hyogo 657-8501, Japan

ABSTRACT: Fatty acid composition and carcass traits of 2,275 Japanese Black steers and heifers were analyzed to estimate the heritabilities and genetic correlations using the REML procedure. Slices of LM at the 6th to 7th rib section were minced and homogenized, and total lipids were extracted for the analysis by a gas chromatograph. Oleic acid accounted for the majority (51.3%), followed by palmitic (26.4%) and stearic (10.8%) acids. Heritabilities of carcass traits were moderate to high, ranging from 0.34 to 0.61, and heritabilities of individual fatty acids varied largely from 0.00 to 0.78. Those of MUFA, SFA, and PUFA were estimated to be 0.68, 0.66, and 0.47, respectively. Predicted breeding values for MUFA in 99 sires ranged from −3.0 to 5.4%. Genetic correlations of fatty acid compositions with carcass traits were generally weak (−0.28 to 0.39). Low but positive genetic correlations were obtained between beef marbling, on which emphasis of selection has been placed, and oleic acid (0.19) or MUFA (0.23). The results indicated the possibility not only for genetic improvement in fat quality traits but also simultaneous improvements with carcass traits by appropriate selection program.

Key words: beef cattle, carcass trait, fatty acid composition, genetic correlation, heritability

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INTRODUCTION

Carcass traits of Japanese Black cattle, especially beef marbling, have improved rapidly due to genetic evaluation under animal model BLUP (Henderson, 1973). Producers are now seeking other economic traits to give additional value to the breed. Among them, fatty acid composition is receiving increased attention because it can influence the palatability of beef (Dryden and Marchello, 1970; Westerling and Hedrick, 1979).

Fatty acid composition is reported to be affected by various nongenetic factors, such as maturity (Zembayashi and Nishimura, 1996), feed (Mandell et al., 1998), depot site (Sturdivant et al., 1992), or season (Link et al., 1970). At the same time, many studies suggested the existence of genetic factors (Yoshimura and Namikawa, 1983; Perry et al., 1998; Oka et al., 2002). Although genetic parameters, which are essential to identify the possibility of genetic improvement, can be found in Pitchford et al. (2002), Tait et al. (2007), and Inoue et al. (2008), the results from an extensive data set are still limited. Therefore, the aim of this study was to estimate the heritabilities and genetic correlations of fatty acids in the LM of Japanese Black beef cattle.

MATERIALS AND METHODS

Data and meat samples used in this study were obtained from carcasses. Therefore, Animal Care and Use Committee approval was not necessary.

Carcass and fatty acid composition traits of 2,275 Japanese Black steers and heifers in Tottori prefecture, Japan, were analyzed in this study. The animals were fed at 19 private farms under their fattening protocols. All animals were slaughtered at Tottori Meat Center between September, 2005, and May, 2008, at an average age of 29.0 ± 1.4 mo (minimum of 21.8 mo to maximum of 35.2 mo). A brief description of Wagyu production in Japan can be found in Oyama et al. (2004).

Traits analyzed were carcass weight (**CW**), LM area (**LMA**), rib thickness (**RT**), subcutaneous fat thickness (**SFT**), yield estimate (**YE**), and beef marbling score (**BMS**). These carcass traits were measured by official graders of the Japan Meat Grading Association accord-

[1]Corresponding author: oyama@kobe-u.ac.jp
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Table 1. Summary statistics of carcass traits and fatty acid compositions in LM lipid (n = 2,275)

Trait[1]	Mean	SD	Minimum	Maximum
CW, kg	450.1	55.2	246.3	632.8
LMA, cm^2	55.0	8.4	28.0	95.0
RT, cm	7.9	1.0	4.3	11.6
SFT, cm	2.5	0.8	0.6	5.7
YE, %	74.0	1.4	68.7	79.0
BMS	1.41	0.68	0.33	5.00
C14:0, %	2.47	0.67	0.08	5.25
C14:1, %	0.87	0.29	0.16	2.18
C16:0, %	26.35	2.28	14.56	33.99
C16:1, %	4.00	0.87	1.50	7.39
C17:0, %	0.79	0.23	0.13	2.33
C17:1, %	0.98	0.27	0.03	3.68
C18:0, %	10.76	1.63	6.70	22.39
C18:1, %	51.27	3.16	40.05	63.09
C18:2, %	2.26	0.60	0.64	5.23
C18:3, %	0.13	0.16	0.00	2.65
C20:0, %	0.12	0.14	0.00	2.61
MUFA, %	57.1	3.3	43.4	69.4
SFA, %	40.5	3.3	28.1	53.3
PUFA, %	2.4	0.7	0.6	7.4
MUFA/SFA	1.43	0.20	0.81	2.47
PUFA/SFA	0.06	0.02	0.02	0.18
DI, %	59.8	3.3	46.3	72.8
EI, %	67.1	2.8	58.7	78.5

[1]CW: carcass weight, LMA: LM area, RT: rib thickness, SFT: subcutaneous fat thickness, YE: yield estimate, BMS: beef marbling score, MUFA = C14:1 + C16:1 + C17:1 + C18:1, SFA = C14:0 + C16:0 + C17:0 + C18:0 + C20:0, PUFA = C18:2 + C18:3, DI: desaturation index = 100 [(C16:1 + C18:1)/(C16:0 + C16:1 + C18:0 + C18:1)], EI: elongation index = 100 [(C18:0 + C18:1)/(C16:0 + C16:1 + C18:0 + C18:1)].

ing to the carcass grading standards (JMGA, 1988). Carcass traits except CW and YE are evaluated at the 6th to 7th rib section, and YE is calculated using CW, LMA, RT, and SFT as an indicator of salable meat proportion. Beef marbling score is a subjective measure of the degree of marbling, especially in the LM, and is categorized into 12 grades (from 0 to 3 with intervals of 0.33, 4, and 5) according to the standards.

When carcass traits were measured, slices of approximately 2 mm thick were sampled from LM at the 6th to 7th rib section of cold carcasses, and immediately frozen and stored at −30°C until extraction of total lipids. Emphasis was placed on intramuscular fat (marbling) because it cannot be removed before consumption and thus has an impact on human health (De Smet et al., 2004).

Total lipids were extracted from approximately 100 mg of minced and homogenized LM samples using 2 mL of chloroform:methanol (2:1, vol/vol) and methylated according to the method of Oka et al. (2002). Methylated fatty acids were analyzed by a gas chromatograph (Shimadzu GC-2014, Kyoto, Japan) using a flame ionization detector equipped with a 30 m × 0.32 mm capillary column. The column was programmed to warm from 150 to 210°C at 3°C/min followed by 2 min at 210°C. The injector and detector temperatures were 250°C. Helium was used as a carrier gas. Chromatograms were recorded with a computing integrator (Shimadzu Chromatopac C-R8A). Individual fatty acids were identified by comparison of retention times with known reference standards, and the relative proportions were determined as percentages of summed peak areas.

Fatty acids analyzed included myristic (C14:0), myristoleic (C14:1), palmitic (C16:0), palmitoleic (C16:1), margaric (C17:0), heptadecenoic (C17:1), stearic (C18:0), oleic (C18:1), linoleic (C18:2), linolenic (C18:3), and arachidic (C20:0) acids. Isomers of the acids were not separated and are included with respective acids. They were combined appropriately to calculate total SFA, MUFA, and PUFA. In addition, desaturation (**DI**) and elongation indices (**EI**) were calculated as per Pitchford et al. (2002):

$$\text{SFA} = \text{C14:0} + \text{C16:0} + \text{C17:0} + \text{C18:0} + \text{C20:0};$$

$$\text{MUFA} = \text{C14:1} + \text{C16:1} + \text{C17:1} + \text{C18:1};$$

$$\text{PUFA} = \text{C18:2} + \text{C18:3};$$

$$\text{DI} = 100\ [(\text{C16:1} + \text{C18:1})/(\text{C16:0} + \text{C16:1} + \text{C18:0} + \text{C18:1})];$$

$$\text{EI} = 100\ [(\text{C18:0} + \text{C18:1})/(\text{C16:0} + \text{C16:1} + \text{C18:0} + \text{C18:1})].$$

Descriptive statistics of these analyzed traits are given in Table 1.

Variance or covariance components were estimated by a uni- or bivariate animal model containing fixed effects of year of slaughter (4 levels), month of slaughter (12 levels), sex (heifer or steer), and fattening farms (19 levels). The model also included covariates of age at slaughter (linear and quadratic) and inbreeding (linear), and random effects of additive genetic and environment. Fattening animals in Japan are usually kept in small pens containing 1 to 10 animals. Because animals in a pen are not often slaughtered at one time and animals from different pens may be combined at slaughter, contemporary group effect was not considered. Slaughter age was considered to account for the change due to aging, whereas the year or month effect was for specific environmental effect. Pedigrees were traced back to animals born in 1975 using information from the Wagyu Registry Association, and as a result 9,584 ancestors were added to calculate the additive relationship matrix.

Variance and covariance components were estimated by our Fortran program with FSPAK (Perez-Enciso et al., 1994). The estimates were iteratively obtained by REML (Patterson and Thompson, 1971) using the EM algorithm (Dempster et al., 1977). Principal components analysis was applied for estimated genetic cor-

relation matrix among individual fatty acids. Factor loadings of the first and second principal components were plotted to clarify the relationship among fatty acid composition traits.

RESULTS AND DISCUSSION

Major fatty acids in LM lipid were C18:1, C16:0, and C18:0 (Table 1). Among them, C18:1, which was regarded as an important component for beef flavor or palatability (Dryden and Marchello, 1970; Westerling and Hedrick, 1979), accounted for a majority (51%). The value was equivalent to the reports of Sturdivant et al. (1992), Zembayashi et al. (1995), and Oka et al. (2002) using the same tissue of Japanese Black. The average of BMS, which has the most influence on carcass price in Japan, was 1.41. This average indicates that almost 39% of LMA is intramuscular fat according to the image analysis by Osawa et al. (2008). De Smet et al. (2004) noted that PUFA/SFA could be a value of 0.05 in breeds that deposit more carcass fat, and increase to 0.5 or greater in very lean (e.g., double-muscled) breeds because PUFA increases at a slower rate than SFA with increasing fatness. The ratio was 0.06 in this study, and hence Japanese Black can be categorized as a fat breed.

Several studies reported heritabilities of carcass traits in Japanese Black cattle. For example, Oyama et al. (2004) estimated heritabilities of the same carcass traits with the present study and showed that the traits had moderate to high heritabilities ranging from 0.38 in RT to 0.56 in BMS. Arakawa et al. (2009) also reported the heritabilities from 0.38 in RT to 0.63 in BMS via both Gibbs sampling and REML. Although we employed a fewer number of carcass records, the heritabilities were similar and estimated between 0.34 in SFT and 0.61 in CW (Table 2).

Heritabilities of specific fatty acids varied largely from 0.00 to 0.78 (Table 2). No genetic variation was observed in C18:3 and C20:0. These 2 traits were minor and comprised only 0.25% of total fatty acids in all. Apart from them, fatty acids were found to be heritable. At present, only a few estimates are available for the heritability of fatty acids. Among them, the estimates by Inoue et al. (2008) are the only ones using Japanese Black. Pitchford et al. (2002) quantified fatty acid composition of 1,215 crossbreds between Hereford cows and 97 sires from 7 breeds and reported relatively low and uniform heritabilities for individual fatty acids ranging from 0.14 to 0.21. Tait et al. (2007) estimated moderate heritabilities (0.108 to 0.455) by the model with lipid percentage as covariate using 916 Angus-sired bulls and steers. Generally, heritabilities estimated herein were greater than those by Pitchford et al. (2002) or Tait et al. (2007) but similar to the estimates from 0.31 to 0.73 using the trapezius muscle of 5,314 Japanese Black cattle from Yamagata prefecture (Inoue et al., 2008). We considered 2 possible reasons for such high heritabilities in Japanese Black. One is that the fatty acids investigated in this study had not been selected at least until the base generation, and thus, substantial genetic variations were left. Another is the existence of some genetic lines (strains), which have been selected for fat quality traits, in the population. We speculate the latter is more probable because no selection necessarily means large genetic variation and quality in many aspects has been emphasized in Japanese Black rather than quantity. Of course, selection in the latter case seems moderate and not strict considering the lack of accurate measurements for such traits. Even so, we cannot deny the possibility that selection for certain strains in the past has inflated the genetic variability of the population. Although heritabilities of fatty acids in these studies were somewhat different in magnitude, it is clear that they are heritable in various breeds and we could observe some consistency in rank orders of heritability: the highest 4 fatty acids in heritabilities were C18:1, C16:1, C14:0, and C16:0 in the present study as they were the same in Tait et al. (2007) and Inoue et al. (2008). The estimates indicated that genetic improvement could be done for most of the fatty acids.

Heritabilities of 0.68, 0.66, and 0.47 were estimated for MUFA, SFA, and PUFA, respectively. These were

Table 2. Estimates of genetic and environmental variances and heritabilities for carcass traits and fatty acid compositions in LM lipid

Trait[1]	Genetic variance	Environmental variance	Heritability ± SE
CW	1,233	775	0.61 ± 0.09
LMA	30.4	31.5	0.49 ± 0.08
RT	0.365	0.386	0.49 ± 0.08
SFT	0.185	0.361	0.34 ± 0.07
YE	1.06	0.87	0.55 ± 0.09
BMS	0.204	0.197	0.51 ± 0.08
C14:0	0.245	0.103	0.70 ± 0.09
C14:1	0.0408	0.0267	0.60 ± 0.09
C16:0	3.12	1.67	0.65 ± 0.09
C16:1	0.483	0.149	0.76 ± 0.09
C17:0	0.00938	0.03494	0.21 ± 0.06
C17:1	0.00929	0.05486	0.14 ± 0.05
C18:0	1.41	1.00	0.59 ± 0.09
C18:1	7.26	2.02	0.78 ± 0.09
C18:2	0.171	0.123	0.58 ± 0.09
C18:3	0.0000	0.0251	0.00 ± 0.01
C20:0	0.0000	0.0203	0.00 ± 0.01
MUFA	6.59	3.16	0.68 ± 0.09
SFA	6.68	3.39	0.66 ± 0.09
PUFA	0.175	0.193	0.47 ± 0.08
MUFA/SFA	0.0225	0.0132	0.63 ± 0.09
PUFA/SFA	0.000132	0.000147	0.47 ± 0.08
DI	6.53	3.28	0.67 ± 0.09
EI	5.53	1.38	0.80 ± 0.09

[1]CW: carcass weight, LMA: LM area, RT: rib thickness, SFT: subcutaneous fat thickness, YE: yield estimate, BMS: beef marbling score, MUFA = C14:1 + C16:1 + C17:1 + C18:1, SFA = C14:0 + C16:0 + C17:0 + C18:0 + C20:0, PUFA = C18:2 + C18:3, DI: desaturation index = 100 [(C16:1 + C18:1)/(C16:0 + C16:1 + C18:0 + C18:1)], EI: elongation index = 100 [(C18:0 + C18:1)/(C16:0 + C16:1 + C18:0 + C18:1)].

Table 3. Estimates of genetic correlations[1] between carcass traits and fatty acid compositions in LM lipid[2]

Trait	CW	LMA	RT	SFT	YE	BMS
C14:0	−0.05	−0.01	−0.04	−0.07	0.05	0.00
C14:1	0.00	0.05	0.11	−0.08	0.12	0.09
C16:0	0.00	−0.14	−0.12	−0.21	−0.06	−0.16
C16:1	−0.02	0.08	0.19	0.13	0.11	0.10
C17:0	−0.19	−0.25	−0.13	0.06	−0.17	−0.12
C17:1	−0.20	−0.07	0.12	0.32	0.00	0.18
C18:0	−0.05	−0.21	−0.28	−0.08	−0.22	−0.27
C18:1	−0.01	0.12	0.07	0.17	0.07	0.19
C18:2	0.28	0.36	0.30	0.30	0.11	0.04
MUFA	−0.02	0.14	0.12	0.16	0.11	0.23
SFA	−0.04	−0.21	−0.22	−0.24	−0.15	−0.25
PUFA	0.32	0.37	0.34	0.35	0.09	0.02
MUFA/SFA	0.00	0.17	0.19	0.11	0.13	0.24
PUFA/SFA	0.29	0.39	0.37	0.39	0.12	0.09
DI	0.01	0.19	0.18	0.20	0.14	0.25
EI	0.00	0.10	0.03	0.19	0.02	0.14

[1]SE of genetic correlation ranged from 0.09 to 0.17.

[2]CW: carcass weight, LMA: LM area, RT: rib thickness, SFT: subcutaneous fat thickness, YE: yield estimate, BMS: beef marbling score, MUFA = C14:1 + C16:1 + C17:1 + C18:1, SFA = C14:0 + C16:0 + C17:0 + C18:0 + C20:0, PUFA = C18:2 + C18:3, DI: desaturation index = 100 [(C16:1 + C18:1)/(C16:0 + C16:1 + C18:0 + C18:1)], EI: elongation index = 100 [(C18:0 + C18:1)/(C16:0 + C16:1 + C18:0 + C18:1)].

also greater than 0.17 in MUFA and 0.27 in SFA reported by Pitchford et al. (2002). Inoue et al. (2008) estimated a heritability of 0.44 for the ratio of (C16:1 + C18:1)/(C16:0 + C18:0), which was similar to DI in this study. A few studies suggested the presence of genes with large effect on MUFA in Japanese Black. Genotypes of stearoyl-CoA desaturase (Taniguchi et al., 2004) and sterol regulatory element binding protein-1 (Hoashi et al., 2007) were shown to be responsible for MUFA. These genes indicated the presence of genetic effect in MUFA and may contribute to a high heritability estimate.

Genetic correlations between fatty acid-related traits and carcass traits were generally weak, ranging from −0.28 and 0.39 (Table 3). Both estimated genetic and environmental covariances among traits are listed in Appendix Table A1. Because C18:3 and C20:0 indicated no genetic variation, they were omitted from the estimation of genetic correlations. Among the individual fatty acids, C18:2 showed relatively strong genetic correlations with carcass traits (0.36, 0.30, and 0.30 with LMA, RT, and SFT, respectively). Hence, genetic correlations of C18:2-related traits (PUFA and PUFA/SFA) also indicated similar genetic correlations with the carcass traits. These relationships suggest that selection for larger LMA or RT would lead to greater proportion of C18:2, whereas selection on thinner SFT would lead to less C18:2. Because phenotypic average (Table 1) and genetic variance of C18:2 (Table 2) were small, such genetic correlations would have few practical implications.

Emphasis of selection in Japanese Black has been placed significantly on BMS for 2 decades (Oyama et al., 2002). The average breeding value of BMS increased 0.782 in genetic SD units during the last 20 yr in Tottori. Genetic correlations of BMS with fatty acid-related traits were a matter of interest because genetic improvement in BMS might have changed those traits genetically. The results showed that BMS only weakly correlated with individual fatty acids (−0.27 to 0.19), and it was expected that selection on BMS would not change them significantly. More importantly, it was suggested that these traits could be improved simultaneously. Inoue et al. (2008) also estimated generally weak relationships, ranging from −0.09 to 0.15, of BMS with fatty acids. One exception in their report was BMS with C18:2 (−0.40).

Genetic correlations of BMS with C18:1 and MUFA were small but positive (0.19 and 0.23, respectively). Positive correlations were also estimated between MUFA and LMA, RT, or SFT. These relationships indicate that selection on MUFA in Japanese Black cattle may not disturb the genetic improvement of carcass traits except for SFT. However, the estimates between intramuscular fat content and C18:1 by Pitchford et al. (2002) and Inoue et al. (2008) were both negative and were not consistent with this study. Further research seems to be required to investigate this discrepancy.

Principal components analysis was performed on the genetic correlation matrix among individual fatty acids. Two fatty acids without genetic variation (C18:3 and C20:0) were excluded. Factor loadings of the first and second principal components obtained from the analysis are shown in Figure 1. Four major fatty acids in phenotype (C18:1, C16:0, C18:0, and C16:1) are located in each quadrant indicating their genetic independence. All the SFA were placed on the upper half of the diagram, whereas unsaturated fatty acids were on the bottom. Moreover, the fatty acids with longer chains were found in the left. The figure clearly shows that the first

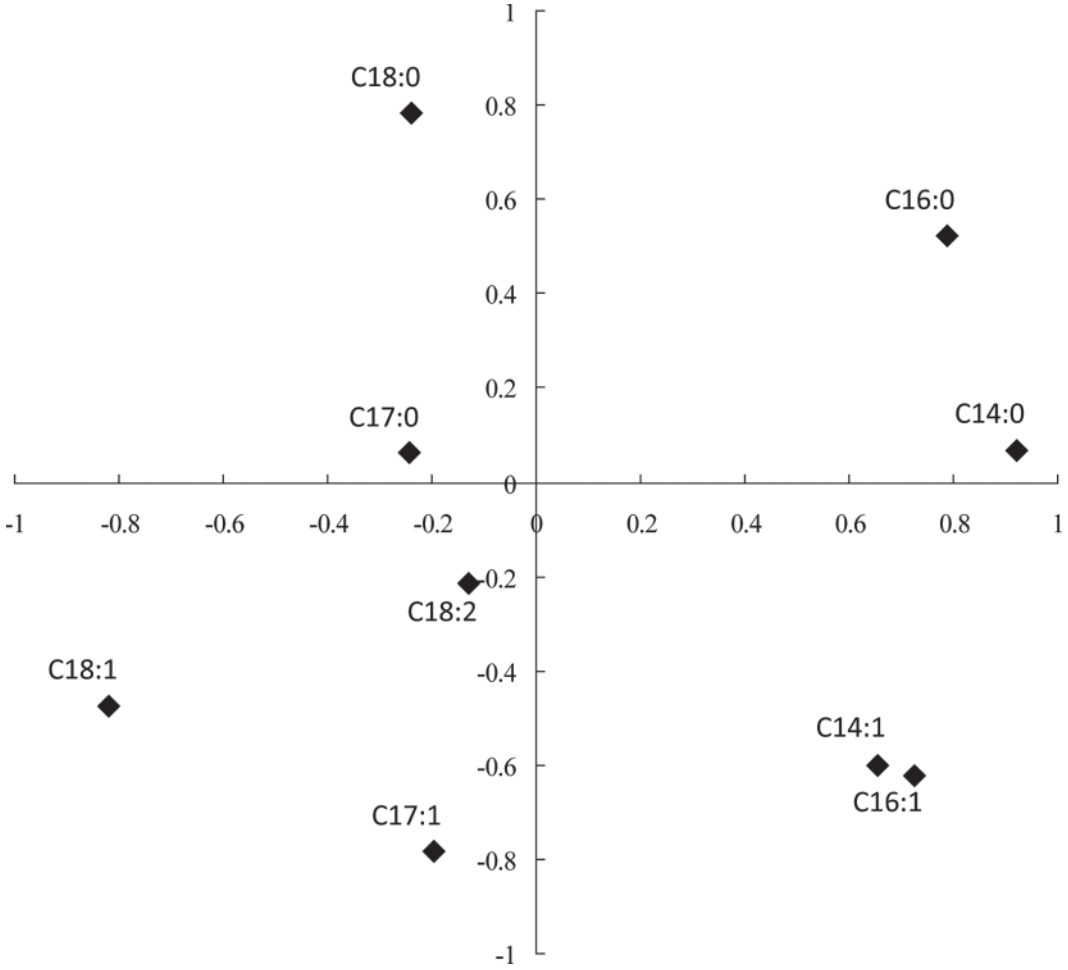

Figure 1. Factor loadings of principal components analysis on the genetic correlation matrix among fatty acids. Horizontal and vertical axes denote the first and second principal components, respectively. The first 2 principal components accounted for 64% of the total variation.

and second principal components represented the elongation and desaturation factors, respectively. The only PUFA, C18:2, was in the third quadrant but close to the origin. It seems C18:2 is genetically independent of other fatty acids, reflecting the fact that it is the fatty acid of dietary origin.

Oka et al. (2002) identified fatty acid compositions of 293 Japanese Black steers derived from 34 sires (6 to 10 progeny per sire). Oka et al. (2002) compared least squares means of MUFA for the sires and found approximately 7% of difference in MUFA. In our data, there were 99 sires, which produced 5 or more progeny with observations. Predicted breeding values of those sires ranged from −3.0 to 5.4% in MUFA. The variation is not negligible and should be used for genetic improvement.

De Smet et al. (2004) questioned the inclusion of fatty acids in the breeding program because which and how many acids should be included are not clear and measuring the acids on a large scale is not feasible at present. Their indications are partly correct, and more research should be conducted on the effect of fatty acids on palatability through sensory testing. On the other hand, a convenient means of estimating porcine and bovine fat quality using fiber-optic technology has been developed (Irie, 1999; Irie et al., 2003). It is anticipated that such a method can be an additional tool in accurately predicting fatty acids of large numbers of cattle soon.

In conclusion, it seems that the genetic improvement of beef cattle should be directed to fat quality traits such as fatty acid composition because it is known that they affect not only palatability of beef but also human health. The present study revealed the existence of genetic variability and hence possibility of genetic improvement in fatty acid composition in beef cattle. It seems very important to carefully find out what consumers really demand because this can change the carcass evaluation system and the profits of the producer. Such changes will make the improvement more efficient and fruitful. The genetic relationship between carcass and fatty acid composition traits were low and severe genetic antagonism was not observed, indicating that these traits could be improved simultaneously, if desired.

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APPENDIX

Table A1. Estimates of genetic (above diagonal) and environmental (below diagonal) covariances among carcass traits and fatty acid compositions in LM lipid[1]

Trait	CW	LMA	RT	SFT	YE	BMS	C14:0	C14:1	C16:0	C16:1	C17:0	C17:1	C18:0	C18:1	C18:2
CW		47.941	14.578	2.854	−1.714	0.649	−0.914	0.029	−0.102	−0.480	−0.645	−0.690	−1.972	−0.816	4.005
LMA	89.564		0.895	−0.899	4.942	1.517	−0.020	0.051	−1.357	0.291	−0.136	−0.039	−1.399	1.752	0.821
RT	10.236	1.589		0.015	0.164	0.050	−0.012	0.014	−0.129	0.080	−0.008	0.007	−0.203	0.121	0.075
SFT	6.583	0.176	0.118		−0.302	−0.034	−0.014	−0.007	−0.160	0.038	0.003	0.013	−0.039	0.196	0.053
YE	2.781	3.690	0.229	−0.307		0.271	0.024	0.026	−0.102	0.078	−0.017	0.000	−0.268	0.181	0.046
BMS	5.167	1.048	0.124	0.015	0.127		−0.001	0.008	−0.129	0.030	−0.005	0.008	−0.146	0.235	0.007
C14:0	0.899	−0.097	0.020	0.013	−0.031	0.006		0.051	0.576	0.222	−0.006	−0.009	−0.056	−1.079	−0.023
C14:1	0.830	0.087	0.014	0.019	−0.009	0.003	0.036		0.084	0.099	−0.003	0.007	−0.146	−0.134	−0.003
C16:0	−7.538	−0.595	−0.144	−0.026	−0.061	−0.009	0.094	−0.020		0.266	−0.018	−0.099	0.355	−4.401	−0.060
C16:1	3.002	0.238	0.053	0.039	−0.020	0.009	−0.018	0.035	−0.317		−0.014	0.034	−0.506	−0.677	−0.029
C17:0	−0.138	−0.062	−0.006	−0.004	−0.007	−0.003	0.029	0.007	−0.008	0.003		0.004	0.042	−0.018	0.002
C17:1	0.575	0.033	0.006	−0.004	0.001	−0.004	0.010	0.006	−0.075	0.009	0.032		−0.021	0.094	0.013
C18:0	−8.694	−0.680	−0.172	−0.105	0.009	0.021	0.047	−0.042	0.122	−0.236	0.040	−0.034		−1.154	−0.071
C18:1	14.040	1.766	0.302	0.042	0.184	0.012	−0.207	−0.034	−1.174	0.469	−0.149	−0.052	−0.735		−0.012
C18:2	−1.946	−0.608	−0.031	−0.038	−0.033	−0.035	−0.041	−0.013	−0.117	−0.002	0.001	0.007	−0.073	0.079	

[1]CW: carcass weight, LMA: LM area, RT: rib thickness, SFT: subcutaneous fat thickness, YE: yield estimate, BMS: beef marbling score.