

Meat produced by Japanese Black cattle and Wagyu



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Implications

- In Japan, Wagyu cattle include four types of Japanese cattle: the Black, Brown, Shorthorn, and Polled breeds. The famous brand name Wagyu includes not only Japanese Black cattle produced in Japan, but also animals or even crossbred Japanese Black cattle produced in foreign countries such as Australia or the USA.
- In recent years, the intramuscular fat percentage of beef from Japanese Black cattle has been greater than 30%. Japanese Black is genetically predisposed to producing carcass lipids containing greater concentrations of monounsaturated fatty acids than other foreign breeds.
- Japanese Black cattle have unique physiological properties and specific dynamics of important intra muscular genes expression. However, there are still unknown reasons for why Japanese Black cattle can produce highly marbled beef.
- The strict management for Japanese Black cattle production has several problems, including its high production costs, circulation of untreated excrement, the requirement for imported feed, and the food security risk resulting from numerous viral diseases introduced by imported feed. The feeding system should shift to be more efficient and provide improved conditions for farmers, food security for consumers, and healthier environments for residents.

Key words: beef, fatty acid composition, Japanese Black, marbling, quality, Wagyu

Japanese Black Cattle and Wagyu

In Japan, Wagyu cattle include four types of Japanese cattle: the Black, Brown, Shorthorn, and Polled breeds. All have played important roles locally and in the history of mixed farming, as well as the synergies that exist between cattle and crops, especially rice. Farmers gradually began replacing the role of cattle as draft animals with farm machinery and industrial fertilizers approximately 50 years ago, and in recent years, Japanese Wagyu cattle have been farmed more specifically for beef production. The famous brand name Wagyu includes not only Japanese Black cattle produced in Japan, but also animals or even crossbred Japanese

Black cattle produced in foreign countries such as Australia or the USA. There are numerous studies investigating the meat quality, quantity, and muscle physiology of crossbreed Wagyu (Japanese Black) in foreign countries (May et al., 1993; Cafe et al., 2006, 2009; Greenwood et al., 2006, 2009). In this review, Wagyu will be referred to as the Japanese Black cattle because of their predominant numbers.

Mishima cattle, which are thought to be a Japanese native, are bred on Mishima Island in the Yamaguchi prefecture. They seem to have maintained the native breed characteristics, and the cattle are expected to improve meat quality when crossed with other breeds. The Mishima steers averaged 517 ± 20 kg ($n = 4$) of body weight at 35.8 ± 0.5 months of age (Morita et al., 2000). Mishima steers generally weigh less compared with fattened Japanese Black steers at 26 months of age (Gotoh et al., 2009; Albrecht et al., 2011). Japanese Black and Japanese Brown breeds were developed by crossing a native similar to Mishima with foreign breeds (e.g., Simmental, Ayrshire, Brown Swiss, Devon, and Hanwoo) approximately 90 years ago to generate draft cattle. However, the crossbreeding of Japanese cattle with foreign breeds caused a decline in meat quality and produced slow-moving draft animals due to an overly large body. Therefore, crossbreeding with foreign breeds was discontinued, and intra-breeding was initiated to improve meat quality. In 1937, the Japanese Black breed was officially established and has been selected for improved meat production for more than 60 years (Morita et al., 2000).

High-performance marbled beef production has caused Japanese Black cattle to comprise the greatest share of the Wagyu cattle population in Japan (Gotoh et al., 2009; Albrecht et al., 2011). Bulls that have been intra-bred to improve the marbling score are an important target because artificial insemination is used in nearly all cattle reproduction in Japan (Figure 1). The intra-beef market for marbling has been markedly enhanced after the decision by the Uruguay Round to allow Japan to import foreign beef beginning in 1991.

Beef greatly contributes to human health as a significant protein source having a high biological value. The intensive concentrate feeding system, necessary to produce marbled beef, results in a more than 30% increase in the fat tissue content of carcasses (Zembayashi and Inayama, 1987). However, it is unclear whether the desirable beef produced by the Japanese Black is based only on the marbling character or also on other factors. Clarification of the skeletal muscle characteristics in Japanese Black cattle using scientific methods has been long awaited.

In 2013, a total 2.64 million head of cattle for beef production were fed in Japan. Approximately 1.77 million head were Japanese Black cattle (MAFF, 2013a), and approximately 870,000 were Holstein cattle for



Figure 1. Japanese Black bull (ItOfuku, Oita prefecture).

production using beef. The number of households raising beef cattle is slowly decreasing in Japan. The number of farmers producing beef was 613,000 in 2013, but 86.5% of these farmers feed less than 50 head. The output of beef cattle was about US\$5 billion in 2012 (MAFF, 2012). In recent times, Japan has exported beef, with an export value in 2013 of US\$51 million (86.3 billion tons; MAFF, 2013b).

The mean body and carcass weights at slaughter were 725 kg and 470 kg for Japanese Black and Holstein cattle, respectively, at 26 to 30 months of age. The carcasses of Japanese Black steers at 26 months of age were 47.7% muscle, 41.7% fat, and 10.6% bone, which is the greatest amount of total fat compared with carcasses of Belgian Blue, German Angus, and Holstein cattle (Gotoh et al., 2009). In conventionally fattened Japanese Black beef ($n = 65$), the mean percentages of moisture, crude fat, and crude protein in the *Longissimus thoracis* muscle at the 12th thoracic vertebra were $47.1 \pm 5.8\%$, $38.4 \pm 7.7\%$, and $13.9 \pm 1.9\%$, respectively (National Livestock Breeding Center, unpublished, 2010). In recent years, the intramuscular fat percentage of beef from Japanese Black cattle averaged greater than 30% (Horie et al., 2009; Albrecht et al., 2011; Figure 2).

Evaluation of Meat Quality Grading in Japanese Black Carcass

Japanese grading system for beef quality and yield

The carcasses of most Japanese breeds, including Japanese Black, are evaluated by accredited graders from the Japan Meat Grading Association (JMGA) in accordance with the beef carcass grading standards. There are nearly 200 accredited graders in Japan. Established in 1988 (JMGA, 1988), the present grading system assigns both a yield grade (A, B, and C) and meat quality grade (1, 2, 3, 4, and 5; Table 1; JMGA, 2014). All beef carcasses in Japan are graded at the sixth to seventh rib section at least 1 hour after ribbing. Four items are independently evaluated: beef marbling; meat color, and brightness; meat firmness and texture; and fat color, luster, and quality. The meat quality grade of the carcass is then assigned according to the lowest grade of these four items.

Beef marbling

In 1988, the marbling levels were assigned by the Beef Marbling Standard (BMS) using a plastic model made from silicone resin. This standard was calculated based on the circumference and area percentage of marbling

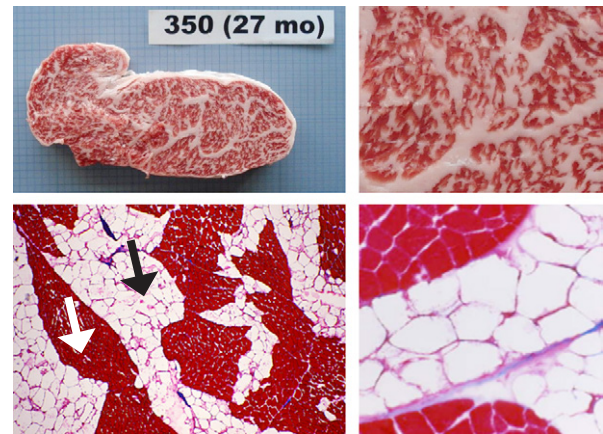


Figure 2. Meat produced by Japanese Black steers. **Left top:** marbled beef at 12 thoracic vertebrae level of *Longissimus thoracis* muscle (BMS No. 7). **Right top:** Macro appearance of marbled fat depots. **Left bottom:** Azan staining of transverse section (thickness: 10 mm) in the *Longissimus thoracis* muscle of the best grade Japanese Black marbled beef. Myofiber bundles (white arrow) look like islands in a sea of adipose tissue (black arrow; Gotoh et al., 2003). **Right bottom:** Azan staining of adipocytes.

particles in the rib eye section (*Longissimus dorsi*). In October of 2008, a new marbling standard utilizing carcass photographs replaced the 1988 standard, and in March 2014, an even newer marbling standard was implemented (Figure 3). Graders determine the BMS number (1 to 12) by comparing the actual carcass marbling and the marbling standard photograph. During this process, any large inclusions of fat at the periphery of the rib eye are not considered marbling according to the Japanese grading system (Figure 4).

The photographs were selected using a combination of marbling percentage (fat to muscle ratio) and fineness index developed by the authors (Kato et al., 2014). This combination theory has a patent pending in several countries, including Japan, and may become a global standard for beef marbling evaluation worldwide. Digital imaging to objectively assess beef marbling is becoming popular to genetically improve the Australian Wagyu (Maeda et al., 2013).

The mean BMS varies greatly according to the breed and geographical origin of animals. In Japan, most Shorthorn and Holstein steers fattened for meat have carcasses designated a BMS of 2, but the mean BMS of Japanese Black steers in 2011 was 5.8. The Japanese government has recently changed the focus of numerical targets of marbling (BMS value) for genetic improvement of Japanese Black to focus on other traits of economic importance.

Meat color and brightness

Color and brightness is a grade determined by the complex decision of color and brightness. The meat color is determined using the Beef Color Standard (BCS), which is made of silicone. The BCS is scored in seven steps from 1 to 7; number 1 is pale red, and the scores become progressively darkened until reaching dark red at number 7. During meat color assessment of refrigerated carcasses, a specialized flashlight is used. A BCS number of 3 or 4 corresponds to the preferred meat color.

Table 1. Relationship between Beef Marbling Standard (BMS) number and classification of BMS grade.

BMS No.	1	2	3	4	5	6	7	8	9	10	11	12
Grade	1	2	3		4					5		

Source: JMGA, 1988.

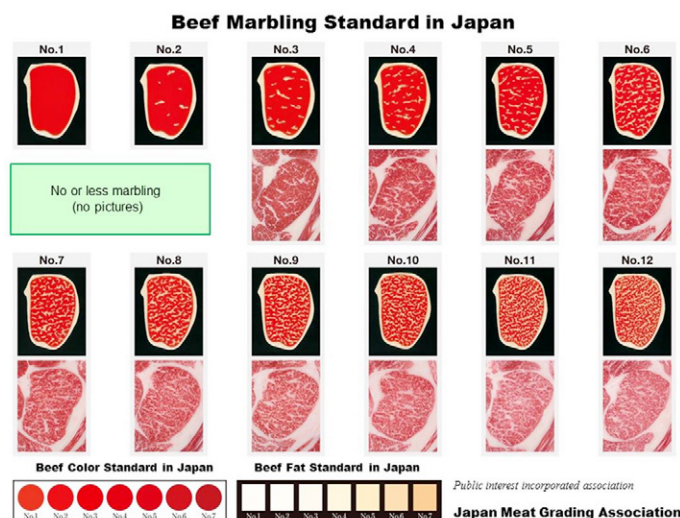


Figure 3. Official picture standard of BMS (Beef Marbling Standard), BCS (Beef Color Standard), and BFS (Beef Fat Standard) by the Japan Meat Grading Association.

In general, a carcass with superior marbling has good color (Figure 3), and the correlation coefficient between the color and brightness grade and the BMS number is extremely high ($r = 0.89$). The color and brightness grade is determined as shown in Table 2.

Meat firmness and texture

The firmness of meat is determined by visual assessment of the amount of exudate on the cut muscle surface as bound water containing protein released from the muscle and the degree of depression in the incision surface. Highly marbled meat has a high water-holding capacity and good firmness. In general, young aged muscle, which has a greater moisture level, has poor firmness.

The meat texture is highly correlated with the diameter of the primary muscle bundles forming the muscle. This diameter is the primary determinant of fine or coarse texture. However, the cut surface of muscle which has fine muscle bundles bound by dense connective tissue is also smooth.

Fat color, luster, and quality

The color, luster, and quality for fat grade is determined using the Beef Fat Standard (BFS) made of silicone resin (Figure 3). In BFS, white color is number 1, and the colors transition to pale cream, cream, and yellow up to number 7. The color, luster, and quality of fat grade is determined as shown in Table 3. This BFS grade, which is evaluated by the trained referees belonging to JMGA, is moderately correlated with the BMS ($r = 0.47$).

Table 2. Classification of color and brightness grade.

Grade		BCS No.	Brightness
5	very good	3~5	very good
4	good	2~6	good
3	average	1~6	average
2	below average	1~7	below average
1	inferior	except Grade 5~2	

Source: JMGA, 1988.

Thickness of ribs part including meat (cm)

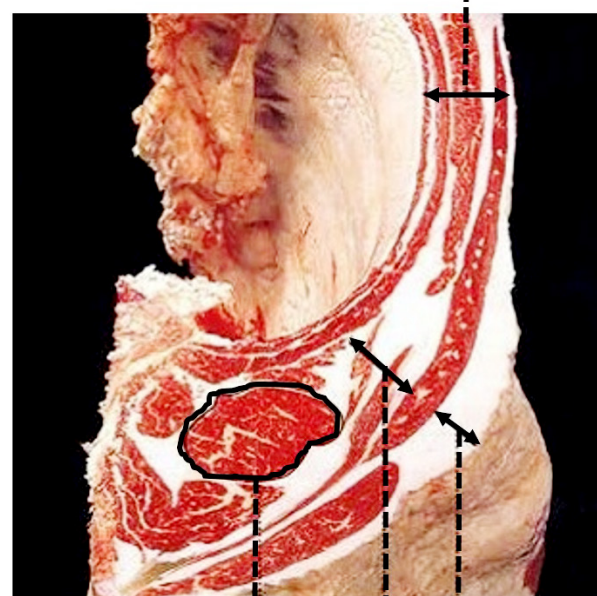


Figure 4. The location of carcass grading in Japan.

Meat yield percentage

Meat yield percentage is calculated by using the following equation: Dressing percentage value = $67.37 + [0.130 \times \text{cross-sectional area of } \textit{Longissimus thoracis} \text{ muscle at 6-7 thoracic vertebrae (cm}^2\text{)}] + [0.667 \times \text{thickness of ribs part including meat (cm)}] - [0.025 \times \text{half carcass weight (kg)}] - [0.896 \times \text{subcutaneous fat thickness (cm)}]$ (Figure 4). We grade A as more than 72, B as 69 to 72, and C as less than 69; (Figure 4; JMGA, 1988).

Cattle slaughter

Japan upholds the best practice in the world for animal welfare during the slaughtering process of cattle (Ministry of the Environment, 1995). The slaughtering process is undertaken in two steps: 1) Stunning: The majority of cattle slaughtered in Japan undergo percussion stunning, which produces a physical shock to the brain to render an animal unconscious and eliminate all stress, pain, and discomfort (Ministry of the Environment, 1995). A smaller proportion of cattle undergo electrical stunning or carbon dioxide gas stunning. 2) Bleeding: This process involves severing

Table 3. Classification of fat, color, luster, and quality grade.

Grade		BFS No.	Luster and quality
5	excellent	1~4	excellent
4	good	1~5	good
3	average	1~6	average
2	below average	1~7	below average
1	inferior	except Grade 5~2	

Source: JMGA, 1988.

the aorta and other major blood vessels of the neck of the animal after the animal is unconscious from the stunning process. The animal dies from cerebral anoxia as a result of exsanguination. Upon commencement of testing for bovine spongiform encephalopathy (BSE), the process of pithing of the brainstem after stunning was abolished in Japan. This ensures sampling for pathology testing is not adversely impacted. There are approximately 90 registered slaughter houses for cattle in Japan. Processing capacity of the largest slaughter house in Japan is 350 animals per day.

Histochemical Properties of Muscle in Japanese Black Cattle

Meat is mainly skeletal muscle, which is predominated by three myofiber types: type I myofiber (slow-twitch oxidative); type IIA myofiber (fast-twitch oxidative glycolytic); and type IIB myofiber (fast-twitch glycolytic). The myofiber type and size within specific muscles are important factors affecting meat quality because they influence many of the peri- and post-mortem biochemical processes in muscles (Klont et al., 1998). Iwamoto et al. (1991) compared the histochemical fiber composition between Japanese Black, Japanese Brown, and Holstein cattle. A larger percentage of type IIB muscle fibers were observed in the Japanese Brown and Holstein, and a larger percentage of type I or type IIA muscle fibers was observed in the Japanese Black. Moreover, the Japanese Black had larger type I fibers at a higher frequency than the two other breeds in the *Longissimus thoracis*, *Semimembranosus*, *Triceps brachii*/caput longum, *Gluteus medialis*, and *Vastus medialis* muscles. Morita et al. (2000) compared the muscle fiber types composing the *Longissimus* muscle between Mishima and the Japanese Black cattle, including regional variations. The size of type I myofibers in the *Longissimus* muscle was larger in the Mishima cattle than in Japanese Black, but the percentage of type I fibers was greater in Japanese Black cattle than in Mishima cattle (Gotoh, 2003; Morita et al., 1999, 2000). However, the percentage area of type I myofibers to total area was nearly identical between the breeds. Similar results were obtained in other muscles. Solomon (1985) and Rahelic and Puac (1981) suggested that type I myofibers are larger in wild pigs than in domestic ones. They concluded that these results indicate that Mishima cattle have maintained certain histochemical myofiber properties characteristic of the native breed (Gotoh, 2003).

Fatty Acid Composition of Current Japanese Black Beef

Current meat quality of Japanese Black cattle

As described previously, current beef produced by Japanese Black cattle contains greater than 30% intramuscular fat. The physiochemical properties and fatty acid composition of *Longissimus* muscle is shown in Table 4 (Gotoh et al., 2011).

Zembayashi et al. (1995) investigated the effect of breed type, including Japanese Black, and sex on the fatty acid composition of subcutaneous and intramuscular lipids in finishing steers and heifers of pure Japanese Black and Holstein, as well as crossbred Japanese Black, Holstein, Japanese Brown, and Charolais. They reported that the Japanese Black is genetically predisposed to producing carcass lipids containing greater concentrations of monounsaturated fatty acids than Holstein, Japanese Brown, or Charolais steers. Sturdivant et al. (1992) also concluded that beef from purebred Wagyu cattle raised in Japan is rich in monounsaturated fatty acids (MUFA).

Table 4. Comparison of intramuscular fatty acid compositions in longissimus muscle between Wagyu and Holstein steers fattened by an identical conventional fattening system.

Fatty acid	Wagyu (n = 6)	Holstein (n = 5)	P-value
IMF (%)*	32.066 ± 2.805	17.34 ± 2.864	<0.01
12:0	0.052 ± 0.004	0.037 ± 0.004	<0.05
14:0	2.840 ± 0.172	2.726 ± 0.282	n.s.
14:1	0.848 ± 0.103	0.798 ± 0.121	n.s.
15:0	0.402 ± 0.037	0.351 ± 0.039	n.s.
15:1	0.025 ± 0.002	0.024 ± 0.002	n.s.
16:0	26.144 ± 0.546	28.009 ± 0.661	0.055
16:1	4.069 ± 0.225	3.833 ± 0.162	n.s.
17:0	1.037 ± 0.087	1.004 ± 0.117	n.s.
17:1	0.986 ± 0.082	0.825 ± 0.114	n.s.
18:0	10.484 ± 0.266	12.267 ± 0.516	<0.05
18:1	50.040 ± 0.911	47.465 ± 0.98	n.s.
18:2 n-6	2.116 ± 0.911	1.926 ± 0.129	n.s.
18:3 0-3	0.121 ± 0.036	0.175 ± 0.062	n.s.
CLA9c,11t	0.302 ± 0.031	0.260 ± 0.015	n.s.
20:0	0.071 ± 0.003	0.128 ± 0.027	0.051
20:1	0.457 ± 0.046	0.164 ± 0.028	<0.001
ΣSFA†	41.033 ± 0.562	44.524 ± 0.842	<0.01
ΣMUFA††	56.427 ± 0.704	53.112 ± 0.853	<0.05
ΣPUFA†††	2.539 ± 0.225	2.363 ± 0.094	n.s.

Values are expressed as mean (%) ± S.E. *IMF: intramuscular fat. †SFA: saturated fatty acid. ††MUFA: monounsaturated fatty acid. †††PUFA: polyunsaturated fatty acid. Student's t-test. (Data from Gotoh et al., 2011.) n.s. = not significant.

Gotoh et al. (2011) compared intramuscular fatty acid composition of *Longissimus* muscle in 26-month-old Japanese Black steers and Holstein steers reared and fattened using a standard fattening system with concentrate feed bases in a conventional Japanese fattening system though normally a fattening period of Holstein cattle is shorter (20 to 22 months). In *Longissimus* muscle, there was a greater percentage of unsaturated fatty acid in Japanese Black steers than in Holstein steers (Table 4). The intramuscular fat content and intramuscular fatty acid composition of 21 major skeletal muscles using the same animals revealed that muscles from the Japanese Black cattle contained a greater proportion of numerous fatty acids, particularly C16:1, C18:1, C20:1, and monounsaturated fatty acids, compared with fatty acids in the Holstein cattle. In Japanese Black cattle, the proportion of C18:0 and saturated fatty acids was much less (Gotoh et al., 2011).

Sasaki et al. (2001) reported the relationship of crude fat content to lipid peroxidation during storage of beef *Longissimus* muscle samples (fat content: 6.5 to 39.4%) from 27 Japanese Black steers. They concluded that 1) high-fat beef had high-preservative properties and 2) thiobarbituric acid reactive substances (TBARS) formation was correlated with lipid hydroperoxides (LOOH) derived from phospholipid oxidation in the initial period of storage, and the relationship was correlated directly with fat content in a later period.

Genes Associated with Beef Quality in Japanese Black Cattle

In addition to its valuable, highly marbled meat, Japanese Black beef has a greater percentage of MUFA within the fat than do other breeds (Yang et al., 1999a). A greater percentage of MUFA leads to a reduced fat-

melting point, which contributes to the softness of bovine fat and favorable beef flavor, and may decrease the circulating concentration of LDL (low density lipid) cholesterol in consumers (Melton et al., 1982; Rudel et al., 1995; Smith, 1994). Therefore, the fatty acid composition of beef has recently become an important trait in the beef industry, especially in Japanese Black cattle.

The fatty acid composition in cattle is much less dependent on diet because microorganisms within the rumen hydrogenate the majority of dietary unsaturated fatty acids, which are mostly absorbed as saturated fatty acids (Jenkins, 1993). However, diet does influence the bovine fatty acid composition (Edwards et al., 1961; Cabezas et al., 1965). Oka et al. (2002) demonstrated that sires significantly affected the fatty acid composition in Japanese Black cattle, suggesting that fatty acid composition may be controlled by genetic factors such as lipid synthesis and fatty acid metabolism genes. Recently, the genes responsible for fatty acid composition have been identified in Japanese Black cattle as described below.

Stearoyl-CoA desaturase (SCD) was first identified and reported as one of the genes associated with beef fatty acid composition (Taniguchi et al., 2004). This enzyme converts saturated fatty acids into MUFA in mammalian adipocytes. The composition of fatty acids stored in fat depots reflects the earlier action of SCD on substrates such as stearic acid or palmitic acid (Kim and Ntambi, 1999). Yang et al. (1999b) reported interesting correlations between the SCD enzyme activity and fatty acid composition in bovine adipose tissue.

The bovine SCD gene has 1080 nucleotides, coding 359 amino acids. The nucleotide substitutions at base pair (bp) 878 in the protein coding region cause replacement of the amino acid valine (V type) to alanine (A type) in the SCD peptide. A study on the association between the SCD genotypes and fatty acid composition showed the MUFA percentage differed significantly among the genotypes (high in type AA, medium in type AV, and low in type VV; Taniguchi et al., 2004). The melting point was also significantly different between the genotypes (high in type VV, medium in type AV, and low in type AA). The mean effects of gene substitution of the A allele on the MUFA percentage and melting point of intramuscular fat were +0.805 and -1.03, respectively. The genotypes explained 4% of the total variation in MUFA and 3% of the melting point of intramuscular fat. The genetic effects on fatty acid composition have been confirmed by subsequent studies (Ohsaki et al., 2009; Ishii et al., 2013; Kelly et al., 2014).

Since the report describing SCD, several candidate genes affecting fatty acid composition have been identified. Sterol regulatory element binding protein-1 (SREBP-1) regulates gene transcription activation by binding to the sterol regulatory element sequences contained in the promoters of downstream genes, including the SCD gene (Shimano, 2001). The intron polymorphism of SREBP-1 also effects the fatty acid composition in bovine adipose tissue (Hoashi et al., 2007). Bovine fatty acid synthase (FASN) generates a multifunctional enzyme that regulates de novo biosynthesis of long-chain fatty acids in mammals (Smith, 1994). Abe et al. (2009) revealed that the FASN genotypes significantly affected the fatty acid composition of dorsal, intramuscular, and intermuscular fat in an F₂ population generated from Japanese Black and Limousin cattle.

Additional genetic markers associated with fatty acid composition have been surveyed primarily by Japanese scientists. The following genes were reported as responsible or candidate genes affecting fatty acid composition: FABP4, LXR α , ELOVL5, FADS2, ACACA, and UTS2R (Hoashi et al., 2008; Matsumoto et al., 2012, 2013, 2014; Sasazaki et al., 2014).

In general, economic traits in cattle such as the fatty acid composition have been considered polygenic. Although the adipogenic mechanism is

extremely complicated, several genes have been identified and confirmed as either associated with or responsible for fatty acid composition in Japanese Black cattle. Representative genes such as SCD and FASN have already been used as DNA markers to select elite sires in Japanese breeding programs. These genetic markers may also contribute to the beef industry and human nutrition worldwide.

Why is Highly Marbled Beef Extremely Tender?

Marbling (intramuscular fat) is one of the most important factors in determining meat quality, especially with reference to texture and flavor. Japanese Black cattle are characterized by the ability to deposit very large amounts of intramuscular fat (Zembayashi, 1994; Gotoh et al., 2009; Albrecht et al., 2011). We have shown that the shear force value of the *Longissimus* muscle in Japanese Black steers decreases after 20 months of age, concomitant with the rapid increase in the fat content (Nishimura et al., 1999). There was a high and inverse correlation coefficient between the crude fat content and shear force value of raw *Longissimus* muscle in Japanese Black cattle after 20 months of age. A greater level of marbling is most likely closely related to meat tenderness.

Nishimura et al. (1999) have shown structural changes in the intramuscular connective tissues during fattening of Japanese Black steers using the cell maceration method for scanning electron microscopy. During the early fattening period from 9 to 20 months of age, collagen fibrils within the endomysium in the *Longissimus* muscle associate more closely with each other, the collagen fibers in the perimysium become increasingly thick, and their wavy pattern grows more regular (Figure 5). These changes are closely related to the increased mechanical strength of the intramuscular connective tissue, resulting in toughening of the beef during this period. The shear force value of the *Longissimus* muscle decreases after 20 months of age, concomitant with the rapid increase in the fat content. Scanning electron micrographs of the *Longissimus* muscle dissected from 32-month-old steers clearly showed that the adipose tissues formed between the muscle fiber bundles, that the honeycomb structure of the endomysium was partially broken, and that the perimysium separated into thinner collagen fibers. By contrast, in the semitendinosus muscle, which has a comparatively lesser crude fat content, the structure within the intramuscular connective tissue remained rigid at 32 months of age, and the shear force value of the muscle increased even during the late fattening period from 20 to 32 months of age. Thus, the development of adipose tissues in the *Longissimus* muscle appears to disrupt the structure of intramuscular connective tissues and contributes to the tenderness of highly marbled beef from Japanese Black cattle (Nishimura, 2010; Figure 5).

Physiological Aspects Related to Meat Quality in Japanese Black Cattle

Japanese Black cattle produce high quality meat with more marbling compared with purebred Holstein cattle (Lunt et al., 1993; Gotoh et al., 2009; Albrecht et al., 2011). The formation of marbling in Japanese Black cattle is closely related to the endocrine system. Many reports suggest that there are differences in plasma hormone concentrations between Japanese Black cattle and other breeds.

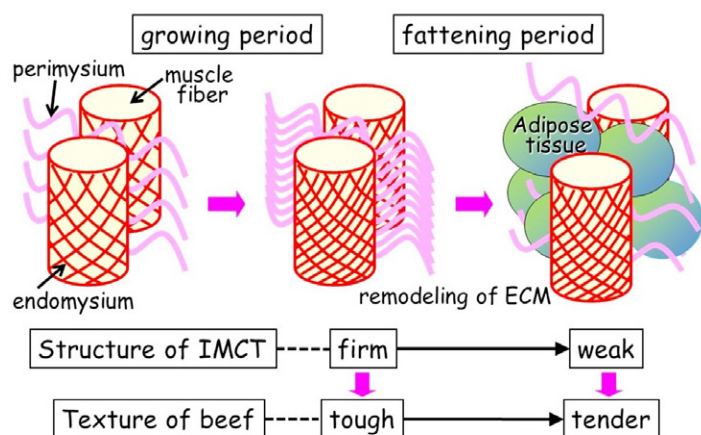


Figure 5. Effect of intramuscular fat deposition on the structure of intramuscular connective tissue (IMCT). With animal growth, collagen crosslinks become more stable, and the structural integrity of IMCT increases. These changes increase the mechanical properties of IMCT, contributing to the toughening of meat. The intramuscular fat deposits mainly in the perimysium (between muscle fiber bundles), resulting in marbling. This causes the remodeling of extracellular matrix (ECM) and reduces the mechanical strength of IMCT, contributing to the tenderization of beef (Nishimura, 2010).

Growth hormone

Growth hormone (GH) is a 191-amino-acid peptide secreted by the anterior pituitary gland (Muller et al., 1987) that may influence the meat quality during fattening (Preston et al., 1995). Japanese Black heifers have a lesser basal plasma GH concentration than do Holstein heifers at 22 months of age (Satoh et al., 1998). Exogenous GH decreases the marbling score during fattening (Dalke et al., 1992). Additionally, the GH gene occurs as three genotypes (haplotype A, B, and C) in Japanese Black cattle, and haplotype C may play a key role in marbling. The haplotypes differ by amino acid mutations at positions 127 and 172 in the fifth exon, a difference that influences the meat quality (Tatsuda et al., 2008). In particular, haplotype C was found in Japanese Black cattle and Japanese Brown cattle and was not observed in other breeds (Chikuni et al., 1994). Tatsuda et al. (2008) reported that beef marbling was highest in haplotype C than in another haplotype. Ardiyanti et al. (2009) reported the GH haplotype C influences fat deposition and is related to increases in MUFA and unsaturated fatty acids, including that synthase activity. However, the mechanism is still unclear, however. Thus, the greater rate of intramuscular fat deposition and marbling in Japanese Black cattle compared with other cattle may be due to the effect of GH secretion and the presence of the GH gene haplotype C.

Insulin like growth factor-1

Insulin like growth factor-1 (IGF-1) is associated with muscle growth and, along with GH, helps determine the number of pre-adipocytes (Harper and Pethick, 2004) or beef marbling (Satoh et al., 1991). Plasma IGF-1 increases as crude protein intake increases. Additionally, some reports suggest that the plasma IGF-1 concentration is related to increased weight and daily gain.

A previous study reported that steers had greater circulating IGF-1 concentrations than heifers (Brandt et al., 2007). The steers also had a greater carcass weight, daily gain of carcass weight, and rib eye area than did heifers (Tanner et al., 1970; Brandt et al., 2007). These reports indicate that the high IGF-1 concentration may promote lean meat growth

during the fattening phase. In contrast, Japanese Black steers have lesser plasma IGF-1 concentrations compared with Holstein steers (Matsuzaki et al., 2001). The marbling score of Japanese Black steers was greater than that of Holsteins at the same carcass weight (Matsuzaki et al., 2001). The differences in the muscle quality between Japanese Black cattle and Holsteins may be influenced by the difference in IGF-1 concentration.

The production system of Japanese Black cattle in Japan suppresses vitamin A intake during the fattening phases to encourage marbling. Beef marbling in cattle fed a low vitamin A feed was superior to marbling in cattle consuming a high vitamin A feed (Oka et al., 1998a). Additionally, IGF-1 secretion has been linked to dietary vitamin A. In Japanese Black cattle, the serum IGF-1 concentrations in cattle consuming an experimental low vitamin A feed from 14 months of age gradually decreased, and after 18 months of age were less than the baseline IGF-1 concentrations before intervention (Oka et al., 1998a). These findings suggest that control of IGF-1 through vitamin A supplementation may be a method to increase the marbling in other cattle as well as Japanese Black cattle.

Insulin

Insulin increases lipogenesis and decreases lipolysis (Rhoades et al., 2007). However, there is little information detailing the relationship between insulin secretion and marbling in Japanese Black cattle. Insulin secretion is increased by plasma propionate, butyrate, or glucose in steers. McAtee and Trenkle (1971) reported that plasma insulin concentration increased following intravenous infusion of propionate or butyrate in steers. Additionally, the two short-chain fatty acids produced a greater response in insulin secretion compared with that of glucose. High grain diets also stimulate insulin secretion in cattle (Trenkle, 1970). Plasma insulin concentration is positively correlated with carcass adiposity (Trenkle and Topel, 1978). Matsuzaki et al. (1997) reported that the plasma insulin concentration and carcass fat proportion were greater in Wagyu (600 kg slaughter weight) than in Holstein cattle (700 kg slaughter weight). Japanese Black heifers also have greater insulin concentrations than do Holstein heifers at 18 and 22 months of age, and glucose-induced insulin secretion was greater in Japanese Black heifers than in Holstein heifers at 18 months of age (Shingu et al., 2001). These reports indicate that the production of intramuscular fat in Japanese Black cattle may possibly be associated with insulin secretion.

Hormones are an important factor for improving growth and meat quality in livestock. Differences in hormone secretion between Japanese Black cattle and Holstein reflect genetic differences. Japanese Black cattle have been selected for an increased meat quantity and quality (intramuscular fat content). Therefore, anabolic function in Japanese Black cattle is important for nutrient utilization. In contrast, Holstein cattle have been selected for increased milk production. Accordingly, catabolic function is important in Holsteins to increase milk yield. Japanese Black cattle may differ in their nutritional metabolism of fat and muscle compared with other breeds, and as a result, they may possess endocrine properties favoring marbling.

Feeding Japanese Black Cattle

To produce beef satisfying the Japanese beef market, appropriate nutritional management is imperative for high quality Japanese Black beef. Nutritional management programs must consider many factors including the growth rate, feed efficiency, health, animal welfare, disease intolerance, and the intramuscular fat accumulation. In Japan, animals are raised in a pen with group feeding using the standard system for marbled beef



Figure 6. Japanese Black cattle fattened in the pen.

production (Gotoh et al., 2009; Figure 6). Each prefecture in Japan has a recommended fattening system. Japanese Black cattle are usually fed a high concentrate diet from 11 to 30 months of age to induce greater accumulation of intramuscular fat, which is the most critical goal of Japanese Black cattle farmers. In particular, during the finishing period of fattening, the most common fattening program is to provide as much concentrate as possible and rice ad libitum. For example, cattle are fed a high-energy diet twice daily starting at 11 months of age until slaughter (28 to 30 months of age). From 11 to 18 months of age, the diet comprises increasing amounts of concentrate (36.8 to 86.4%, formula feed) and decreasing amounts of roughage [Jamboree (beer bran), hay, and rice straw]. During the final stage from 18 months to slaughter, the diet comprises 86.4 to 84.2% concentrate and 13.6 to 15.8% roughage. All cattle have constant access to water and mineral salt blocks containing minerals, salt, and a diuretic. The total feed consumption during fattening is normally 4,000 to 5,000 kg/animal. For fattening until 26 and 30 months of age, 4,344 kg and 5,167 kg of concentrate was needed (Gotoh, unpublished data, 1997). More than 90% of the concentrates for fattening Japanese Black cattle are imported.

In Japan in recent years, farmers have considered manipulating vitamin A level to improve marbling during fattening of Japanese Black cattle. Vitamin A derivatives (retinoids) play a key role in mammalian development and cell differentiation (Villarroya et al., 1999). In most cases, retinoic acid impairs adipocyte differentiation. Oka et al. (1998b) and Nade et al. (2007) demonstrated the influence of vitamin A on beef quality in Japanese Black cattle. They suggested that regulating the serum vitamin A concentration could produce a higher marbling score without increasing subcutaneous fat in animals genetically predisposed to marbling. Currently, farmers keep the vitamin A concentration low only during the middle fattening period; during the finishing period, low vitamin A concentration often induces severe hepatic disease and swelling.

Originally cattle should eat grass. But to produce marbled beef in Japanese Black cattle, much grain feed needs to be imported. Although Japanese Black cattle can produce excellent marbled beef, they also discharge a large amount of excrement derived from imported grain feed. Totally, about 23.7 million tons excrement (feces and urine) per year were discharged in beef cattle production in 1996 (Haga, 1992). This is a cause of soil pollution because of increased nitrogen concentrations. The outbreak of BSE in September 2001 and foot-and-mouth disease in 2000 and 2010 are thought to be related to imported feed. Heavy dependence on imported feed might be dangerous in food security in Japan. Moreover, Japanese Black cattle carcasses produce a large amount of wasted fat like subcu-

taneous fat and abdominal fat of more than 200 kg per carcass (Gotoh et al., 2009). Lately, Japanese beef production has many problems such as food safety, excreta from livestock, and the sudden price increase of grain. Accordingly, we might have to shift the system to produce beef while maximizing the use of domestic grass resources.

Conclusion

The quality of beef produced by Japanese Black cattle is excellent and contains greater than 30% intramuscular fat and a significant concentration of monounsaturated fatty acids. Japanese Black cattle have unique physiological properties and specific dynamics of important intra muscular gene expression like SCD and FASN. However, it is still unknown why Japanese Black can produce excellent marbled beef. In the production system, there are numerous problems concerning the strict management, including high production costs, circulation of untreated excrement, the requirement for imported feed, and the food security risk resulting from numerous viral diseases introduced by imported feed. Livestock epidemics, such as BSE and foot-and-mouth disease, have caused significant damage to the beef industry in Japan. Among the worldwide Japanese beef market, 248 head and more than 5,000 straws of frozen semen of Japanese Black cattle have been exported at present, and Japanese Black cattle are fed in 18 foreign countries (NHK, 2013). Japanese Black cattle, known as Wagyu outside Japan, are specially regarded by cattle breeders in the USA, Canada, Germany, Austria, France, Thailand, China, Mexico, Australia, and other countries who aim to improve beef quality, especially by improving marbling and tenderness. The beef of crossbred Wagyu cattle is also sold as Wagyu beef worldwide (NHK, 2013) and is relatively inexpensive compared with the original Japanese Black beef. Considering the global distribution of Japanese Black and Wagyu beef, new strategies are needed for Japanese farmers to produce and sell Japanese Black beef in the global market.

Literature Cited

- Abe, T., J. Saburi, H. Hasebe, T. Nakagawa, S. Misumi, T. Nade, H. Nakajima, N. Shoji, M. Kobayashi, and E. Kobayashi. 2009. Novel mutations of the FASN gene and their effect on fatty acid composition in Japanese Black beef. *Biochem. Genet.* 47:397–411.
- Albrecht, E., T. Gotoh, F. Ebara, J.X. Xu, T. Viergutz, G. Nuernberg, S. Maak, and J. Wegner. 2011. Cellular conditions for intramuscular fat deposition in Japanese Black and Holstein steers. *Meat Sci.* 89:13–20.
- Ardiyanti, A., Y. Oki, Y. Suda, K. Suzuki, K. Chikuni, Y. Obara, and K. Katoh. 2009. Effects of GH gene polymorphism and sex on carcass traits and fatty acid compositions in Japanese Black cattle. *Anim. Sci. J.* 80:62–69.
- Brandt, M.M., D.H. Keisler, D.L. Meyer, T.B. Schmidt, and E.P. Berg. 2007. Serum hormone concentrations relative to carcass composition of a random allotment of commercial-fed beef cattle. *J. Anim. Sci.* 85:267–275.
- Cabezas, M., J. Hentges, J. Moore, and J. Olson. 1965. Effect of diet on fatty acid composition of body fat in steers. *J. Anim. Sci.* 24:57–61.
- Cafe, L.M., D.W. Hennessy, H. Hearnshaw, S.G. Morris, and P.L. Greenwood. 2006. Influences of nutrition during pregnancy and lactation on birthweights and growth to weaning of calves sired by Piedmontese or Wagyu bulls. *Aust. J. Exp. Agric.* 46:245–255.
- Cafe, L.M., D.W. Hennessy, H. Hearnshaw, S.G. Morris, and P.L. Greenwood. 2009. Consequence of prenatal and preweaning growth for feedlot growth, intake and efficiency of Piedmontese and Wagyu-sired cattle. *Anim. Prod. Sci.* 49:461–467.
- Chikuni, K., T. Nagatsuma, T. Tabata, M. Monma, M. Saito, S. Ozawa, and K. Ozutsumi. 1994. Genetic variants of the growth hormone gene in Japanese cattle. *Anim. Sci. Technol.* 65:340–346.

- Dalke, B.S., R.A. Roeder, T.R. Kasser, J.J. Veenhuizen, C.W. Hunt, D.D. Hinman, and G.T. Schelling. 1992. Dose-response effects of recombinant bovine somatotropin implants on feedlot performance in steers. *J. Anim. Sci.* 70:2130–2137.
- Edwards, R., S. Tove, T. Blumer, and E. Barrick. 1961. Effects of added dietary fat on fatty acid composition and carcass characteristics of fattening steers. *J. Anim. Sci.* 20:712–717.
- Gotoh, T. 2003. Histochemical properties of skeletal muscles in Japanese cattle and their meat production ability. *Anim. Sci. J.* 74:339–354.
- Gotoh, T., E. Albrecht, F. Teuscher, K. Kawabata, K. Sakashita, H. Iwamoto, and J. Wegner. 2009. Differences in muscle and fat accretion in Japanese Black and European cattle. *Meat Sci.* 82:300–308.
- Gotoh, T., S. Olavanh, M. Shiota, B. Shirouchi, M. Satoh, E. Albrecht, S. Maak, J. Wegner, Y. Nakamura, K. Etoh, Y. Shiotsuka, K. Hayashi, F. Ebara, T. Etoh, and H. Ida. 2011. Relationship between myofiber type and fatty acid composition in skeletal muscles of Wagyu (Japanese Black) and Holstein cattle. *Proceedings of 57th International Congress of Meat Science and Technology (57th ICoMST)*, 7–12 Aug. 2011, Ghent, Belgium. (Abstr.)
- Greenwood, P.L., L.M. Cafe, H. Hearnshaw, D.W. Hennessy, and S.G. Morris. 2009. Consequence of prenatal and preweaning growth for yield of primal cuts from 30 months-of-old Piedmontese- and Wagyu-sired cattle. *Anim. Prod. Sci.* 49:468–478.
- Greenwood, P.L., L.M. Cafe, H. Hearnshaw, D.W. Hennessy, J.M. Thopson, and S.G. Morris. 2006. Long-term consequences of birth weight and growth to weaning for carcasses, yield and beef quality characteristics of Piedmontese- and Wagyu-sired cattle. *Aust. J. Exp. Agric.* 46:257–269.
- Haga, K. 1992. Clean energy and agriculture. Utilization of biomass for energy. *J. Agric. Eng. Soc.* 60:945–950.
- Harper, G.S., and D.W. Pethick. 2004. How might marbling begin? *Aust. J. Exp. Agric.* 44: 653–662.
- Hoashi S, N. Ashida, H. Ohsaki, T. Utsugi, S. Sasazaki, T. Taniguchi, K. Oyama, F. Mukai, H. Mannen. 2007. Genotype of bovine sterol regulatory element binding protein-1 (SREBP-1) is associated with fatty acid composition in Japanese Black cattle. *Mamm. Genome* 18:880–886.
- Hoashi, S., T. Hinenoya, A. Tanaka, H. Ohsaki, S. Sasazaki, M. Taniguchi, K. Oyama, F. Mukai, and H. Mannen. 2008. Association between fatty acid compositions and genotypes of FABP4 and LXR α in Japanese Black cattle. *BMC Genet.* 9:84.
- Horii, H., Y. Sakurai, Y. Kanbe, K. Kasai, K. Ono, T. Asada, T. Mori, M. Kobayashi, A. Iguchi, M. Yamada, M. Hayashi, and K. Hodate. 2009. Relationship between Japanese Beef Marbling Standard numbers and intramuscular lipid in *M. longissimus thoracis* of Japanese Black steers from 1996 to 2004. *Nihon Chikusan Gakkaiho* 80(1):55–61.
- Ishii, A., K. Yamaji, Y. Uemoto, N. Sasago, E. Kobayashi, N. Kobayashi, T. Matsuhashi, S. Maruyama, H. Matsumoto, S. Sasazaki, and H. Mannen. 2013. Genome wide association study for fatty acid composition in Japanese Black cattle. *Anim. Sci. J.* 84(10):675–682.
- Iwamoto, H., Y. Ono, T. Goto, S. Nishimura, Y. Nakanishi, R. Umezu, and H. Takahara. 1991. Comparative studies on the composition of muscle fiber types in Japanese Black, Japanese Brown and Holstein steers. *Anim. Sci. Technol.* 62(7):674–682 (in Japanese).
- Jenkins, C. 1993. Lipid metabolism in the rumen. *J. Dairy Sci.* 76:3851–3863.
- JMGA. 1988. Meat grading standard. Japan Meat Grading Association.
- JMGA. 2014. Beef carcass trading standards. Japan Meat Grading Association.
- Kato, K., S. Maeda, and K. Kuchida. 2014. Genetic parameters for fineness of marbling in *M. longissimus thoracis* of Japanese Black cattle. *Nihon Chikusan Gakkaiho* 85:21–26.
- Kelly, M.J., R.K. Tume, M. Fortes, J.M. Thompson. 2014. Whole-genome association study of fatty acid composition in a diverse range of beef cattle breeds. *J. Anim. Sci.* 92(5):1895–1901.
- Kim, Y.C., and J.M. Ntambi. 1999. Regulation of stearoyl-CoA desaturase genes: Role in cellular metabolism and preadipocyte differentiation. *Biochem. Biophys. Res. Commun.* 266:1–4.
- Klont, R.E., L. Brocks, and G. Eikelenboom. 1998. Muscle fiber type and meat quality. *Meat Sci.* 49:S219–S229.
- Lunt, D.K., R.R. Riley, and S.B. Smith. 1993. Growth and carcass characteristics of Angus and American Wagyu steers. *Meat Sci.* 34:327–334.
- Maeda, S., J. Grose, K. Kato, and K. Kuchida. 2013. Comparing AUS-MEAT marbling scores using image analysis traits to estimate genetic parameters for marbling of Japanese Black cattle in Australia. *Anim. Prod. Sci.* 54:557–563.
- MAFF. 2012. Statistics of agriculture, forestry and fisheries. Ministry of Agriculture, Forestry, and Fisheries (in Japanese).
- MAFF. 2013a. Statistics. V. Livestock and poultry, number of farm households feeding livestock, and number of livestock fed. Ministry of Agriculture, Forestry, and Fisheries.
- MAFF. 2013b. Strategy of export for Beef. Ministry of Agriculture, Forestry, and Fisheries (in Japanese).
- Matsumoto, H., T. Nogi, I. Tabuchi, K. Oyama, H. Mannen, and S. Sasazaki. 2014. The SNPs in the promoter regions of the bovine FADS2 and FABP4 genes are associated with beef quality traits. *Livest. Sci.* 163:34–40.
- Matsumoto, H., K. Sasaki, T. Bessho, E. Kobayashi, T. Abe, S. Sasazaki, K. Oyama, and H. Mannen. 2012. The SNPs in the ACACA gene are effective on fatty acid composition in cattle. *Mol. Biol. Rep.* 39(9):8637–8644.
- Matsumoto, H., Y. Shimizu, A. Tanaka, T. Nogi, I. Tabuchi, K. Oyama, M. Taniguchi, H. Mannen, and S. Sasazaki. 2013. The SNP in the promoter region of the bovine ELOVL5 gene influences economic traits including subcutaneous fat thickness. *Mol. Biol. Rep.* 40(4):3231–3237.
- Matsuzaki, M., T. Sato, S. Morita, N. Shiba, E. Tsuneishi, S. Hara, K. Ozutsumi, and T. Yamaguchi. 2001. Pulsatile growth hormone secretion, circulating insulin-like growth factor-1 concentration and cellular density of somatotrophs differ between Wagyu and Holstein steers. *Tohoku J. Anim. Sci. Technol.* 48:7–13.
- Matsuzaki, M., S. Takizawa, and M. Ogawa. 1997. Plasma insulin, metabolite concentrations, and carcass characteristics of Japanese Black, Japanese Brown, and Holstein steers. *J. Anim. Sci.* 75:3287–3293.
- May, S.G., C.A. Sturdivant, S.K. Lunt, R.K. Miller, and S.B. Smith. 1993. Comparison of sensory characteristics and fatty acid composition between Wagyu and crossbred and Angus steers. *Meat Sci.* 35:289–298.
- McAtee, J.W., and A. Trenkle. 1971. Metabolic regulation of plasma insulin levels in cattle. *J. Anim. Sci.* 33:438–442.
- Melton, L., M. Amiri, W. Davis, and R. Backus. 1982. Flavor and chemical characteristics of ground beef from grass-, forage-grain- and grain-finished steers. *J. Anim. Sci.* 55:77–87.
- Ministry of the Environment. 1995. *Doubutsu no satsushobun houhou ni kansuru shishin* (in Japanese).
- Morita, S., H. Iwamoto, Y. Fukumitsu, T. Gotoh, S. Nishimura, and Y. Ono. 1999. Heterogeneous composition of histochemical fibre types in the different parts of *M. longissimus thoracis* from Mishima (Japanese native) steers. *Meat Sci.* 54:59–63.
- Morita, S., H. Iwamoto, Y. Fukumitsu, T. Gotoh, S. Nishimura, and Y. Ono. 2000. Histochemical studies on the skeletal muscles in fattened Mishima steers. *Anim. Sci. J.* 71:J51–J59.
- Muller, E.E. 1987. Neural control of somatotrophic function. *Physiol. Rev.* 67:962–1053.
- Nade, T., Y. Masuda, S. Misumi, and K. Fujita. 2007. Effects of vitamin A restriction on growth and carcass characteristics of Japanese Black steers measured by ultrasonic equipment. *Nihon Chikusan Gakkaiho* 78:161–166.
- NHK (Japan Broadcasting Cooperation). 2013. Gachi Asia. <http://www.nhk.or.jp/fukuoka/gachiasia/back/bk131220.html> (in Japanese)
- Nishimura, T. 2010. The role of intramuscular connective tissue in meat texture. *Anim. Sci. J.* 81:21–27.
- Nishimura, T., A. Hattori, and K. Takahashi. 1999. Structural changes in intramuscular connective tissue during the fattening of Japanese Black cattle: Effect of marbling on beef tenderization. *J. Anim. Sci.* 77:93–104.
- Ohsaki, H., A. Tanaka, S. Hoashi, S. Sasazaki, K. Oyama, M. Taniguchi, F. Mukai, and H. Mannen. 2009. Effect of SCD and SREBP genotypes on fatty acid composition in adipose tissue of Japanese Black cattle herds. *Anim. Sci. J.* 80:225–232.
- Oka, A., T. Dohgo, M. Juen, and T. Saito. 1998a. Effects of vitamin A on beef quality, weight gain, and serum concentration of thyroid hormones, insulin-like growth factor-I, and insulin in Japanese black steers. *Meat Sci.* 48:159–167.
- Oka, A., F. Iwaki, T. Dohgo, S. Ohtagaki, M. Noda, T. Shiozaki, O. Endoh, and M. Ozaki. 2002. Genetic effects on fatty acid composition of carcass fat of Japanese Black Wagyu steers. *J. Anim. Sci.* 80:1005–1011.
- Oka, A., Y. Maruo, T. Miki, T. Yamasaki, and T. Saito. 1998b. Influence of vitamin A on the quality of beef from the Tajima strain of Japanese Black cattle. *Meat Sci.* 48:159–167.
- Preston, R.L., S.J. Bartle, T.R. Kasser, J.W. Day, J.J. Veenhuizen, and C.A. Baile. 1995. Comparative effectiveness of somatotropin and anabolic steroids in feedlot steers. *J. Anim. Sci.* 73:1038–1047.

- Rahelic, S., and S. Puac. 1981. Fibre types in *longissimus dorsi* from wild and highly selected pig breeds. *Meat Sci.* 5:439–450.
- Rhoades, R.D., J.E. Sawyer, K.Y. Chung, M.L. Schell, D.K. Lunt and S.B. Smith. 2007. Effect of dietary energy source on in vitro substrate utilization and insulin sensitivity of muscle and adipose tissues of Angus and Wagyu steers. *J. Anim. Sci.* 85:1719–1726.
- Rudel, L., S. Park, and K. Sawyer. 1995. Compared with dietary monounsaturated and saturated fat, polyunsaturated fat protects African green monkeys from coronary artery atherosclerosis. *Arterioscler. Thromb. Vasc. Biol.* 15:2101–2110.
- Sasaki, K., M. Mitsumoto, and K. Kawabata. 2001. Relationship between lipid peroxidation and fat content in Japanese Black beef *Longissimus* muscle during storage. *Meat Sci.* 59:407–410.
- Sasazaki, S., K. Akiyama, T. Narukami, H. Matsumoto, K. Oyama, and H. Mannen. 2014. UTS2R gene polymorphisms are associated with fatty acid composition in Japanese beef cattle. *Anim. Sci. J.* 85(5):499–505.
- Satoh, H., K. Chiba, M. Takeda, and A. Hagino. 1998. Comparison of plasma metabolic hormones concentrations in Japanese Black and Holstein cattle. *Anim. Sci. Technol.* 69:483–488.
- Satoh, H., S. Ujiie, S. Onodera, and S. Oda. 1991. Correlation between carcass characteristics and plasma insulin-like growth factor-I level in Japanese Black beef cattle. *Anim. Sci. Technol.* 62:774–776.
- Shimano, H. 2001. Sterol regulatory element-binding proteins (SREBPs), transcriptional regulators of lipid synthetic genes. *Prog. Lipid Res.* 40:439–452.
- Shingu, H., K. Hodate, S. Kushibiki, Y. Ueda, A. Watanabe, M. Shinoda, and M. Matsumoto. 2001. Profiles of growth hormone and insulin secretion, and glucose response to insulin in growing Japanese Black heifers (beef type): Comparison with Holstein heifers (dairy type). *Comp. Biochem. Physiol. Part Toxicol. Pharmacol.* 130:259–270.
- Smith, S. 1994. The animal fatty acid synthase: One gene, one polypeptide, seven enzymes. *FASEB J.* 8:1248–1259.
- Solomon, M.B. 1985. Profile of fiber types in muscles from wild pigs native to the United States. *Meat Sci.* 13:247–254.
- Sturdivant, C.A., D.K. Lunt, G.C. Smith, and S.B. Smith. 1992. Fatty acid composition of subcutaneous and intramuscular adipose tissues and *M. longissimus dorsi* of Wagyu cattle. *Meat Sci.* 32:449–458.
- Taniguchi, M., T. Utsugi, K. Oyama, H. Mannen, M. Kobayashi, Y. Tanabe, A. Ogino, and S. Tsuji. 2004. Genotype of stearoyl-CoA desaturase is associated with fatty acid composition in Japanese Black cattle. *Mamm. Genome* 15:142–148.
- Tanner, J.E., R.R. Frahm, R.L. Willham, and J.V. Whiteman. 1970. Sire \times sex interactions and sex differences in growth and carcass traits of Angus bulls, steers, and heifers. *J. Anim. Sci.* 31:1058–1064.
- Tatsuda, K., A. Oka, E. Iwamoto, Y. Kuroda, H. Takeshita, H. Kataoka, and S. Kouno. 2008. Relationship of the bovine growth hormone gene to carcass traits in Japanese Black cattle. *J. Anim. Breed. Genet.* 125:45–49.
- Trenkle, A. 1970. Plasma levels of growth hormone, insulin and plasma protein-bound iodine in finishing cattle. *J. Anim. Sci.* 31:389.
- Trenkle, A., and D.G. Topel. 1978. Relationship of some endocrine measurements to growth and carcass composition of cattle. *J. Anim. Sci.* 46:1604–1609.
- Villarroya, F., M. Giral, and R. Iglesias. 1999. Retinoids and adipose tissues: Metabolism, cell differentiation and gene expression. *Int. J. Obes.* 23:1–6.
- Yang, A., T.W. Larsen, H. Powell, and K. Tume. 1999a. A comparison of fat composition of Japanese and long-term grain-fed Australian steers. *Meat Sci.* 51:1–9.
- Yang, A., T.W. Larsen, S.B. Smith, and R.K. Tume. 1999b. $\Delta 9$ desaturase activity in bovine subcutaneous fatty acid composition. *Lipids* 34:971–978.
- Zembayashi, M. 1994. Effects of nutritional planes and breeds on intramuscular-lipid deposition in *M. longissimus dorsi* of steers. *Meat Sci.* 38:367–374.
- Zembayashi, M., and M. Inayama. 1987. Fat partition and its distribution in Japanese Black, Japanese Shorthorn and Holstein steer carcass. *Jpn. J. Zootech. Sci.* 58:381–387.
- Zembayashi, M., K. Nishimura, D.K. Lunt, and S.B. Smith. 1995. Effect of breed type and sex on the fatty acid composition of subcutaneous and intramuscular lipids of finishing steers and heifers. *J. Anim. Sci.* 73:3325–3332.

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