

ORIGINAL ARTICLE

Effects of growth rate during the early fattening period on growth, carcass characteristics and circulating hormones in the different growth hormone genotypes of Japanese black steers

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ABSTRACT

One of the bovine growth hormone (GH) genetic variants is a substitution of leucine (Leu) to valine (Val) at amino acid position 127 of the protein. The GH genotypes of 14 Japanese black steers used in the present study were Leu/Leu (A, $n = 7$) and Val/Val (B, $n = 7$). The steers in each genotype group were divided into two groups based on intended growth rate (high, 1.0 kg/day; low, 0.6 kg/day) during 10–17 months of age. The overall mean concentration of plasma GH was higher ($P < 0.05$) in the A group than in the B group. The serum concentration of insulin-like growth factor-I was higher ($P < 0.05$) in the B group than in the A group. The carcass weight of the A group was greater ($P < 0.01$) than that of the B group. However, there was no significant difference in carcass weights between the 1.0 kg/day and 0.6 kg/day groups ($P > 0.05$). The rib thickness of the 1.0 kg/day group was greater ($P < 0.05$) than that of the 0.6 kg/day group. The crude fat content of longissimus muscle was greater ($P < 0.05$) for the 0.6 kg/day group compared with the 1.0 kg/day group.

Key words: carcass characteristics, circulating hormones, GH genotype, growth rate, Japanese black steer.

INTRODUCTION

Growth hormone (GH) is well known to facilitate growth of animals. GH influences the meat quality of fattening cattle (Dalke *et al.* 1992; Schwarz *et al.* 1993; Preston *et al.* 1995). Chikuni *et al.* (1991, 1994) and Lucy *et al.* (1993) reported polymorphic regions in the fifth exon of the bovine GH gene. Genetic variants of bovine GH include one caused by a substitution of leucine (Leu) to valine (Val) at amino acid position 127 of the protein (Chikuni *et al.* 1991; Lucy *et al.* 1993), and another variant that produces a replacement of threonine (Thr) by methionine (Met) at amino acid position 172 of the protein (Chikuni *et al.* 1994). In Japanese Black cattle, the GH gene genotype consists of gene A (Leu₁₂₇/Thr₁₇₂), gene B (Val₁₂₇/Thr₁₇₂) and gene C (Val₁₂₇/Met₁₇₂) (Chikuni *et al.* 1994). Those polymorphisms were found to be associated with beef production (Schlee *et al.* 1994a; K. Tatsuda *et al.*, unpubl. data, 2004).

Japanese Black cattle have large variations in growth rate and meat quality (Zembayashi 1993; Mitsuhashi *et al.* 1997; Ozawa *et al.* 2000; Oka *et al.* 2002). The cattle of the Tajima strain, which is bred in Hyogo prefecture, is known to be smaller than those bred in Tottori, Okayama and Hiroshima prefecture. The GH genotype might be associated with those variations in Japanese Black cattle. GH (Preston *et al.* 1995; Rausch *et al.* 2002), insulin-like growth factor-I (IGF-I) (Bishop *et al.* 1989; Stick *et al.* 1998), and thyroxin hormone (Hayden *et al.* 1993) affect growth rate of fattening cattle. Exogenous GH decreases the marbling score in fattening cattle (Dalke *et al.* 1992; Schwarz *et al.* 1993; Preston *et al.* 1995), and IGF-I is associated with intramuscular fat content (Gatford *et al.* 1996) or

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beef marbling (Satoh *et al.* 1991). However, there are few studies concerning variation in circulating GH, IGF-I, thyroxin, and triiodothyronine concentrations in different GH genotypes of Japanese Black cattle.

Feed restriction at early fattening period affects growth rate following restriction (Henricks *et al.* 1994; Sainz *et al.* 1995; Yambayamba *et al.* 1996; Loerch & Fluharty 1998) and beef quality (Zembayashi *et al.* 1988; Coleman *et al.* 1993; Wertz *et al.* 2001). The effect of feed restriction on beef quality differed in breeds or biotypes (Zembayashi *et al.* 1988; Coleman *et al.* 1993). It has not been clear how growth restriction at early fattening period affects the following growth rate and beef quality in different GH genotypes of Japanese Black cattle.

In the present study we determined the growth rate, the beef quality and the circulating hormone levels in the GH genotype A and B of Japanese Black steers, and evaluated the effect of high and moderate growth rates during early fattening period on growth and beef quality.

MATERIALS AND METHODS

Animals and dietary treatments

Fourteen 10-month-old Japanese Black steers, which had GH genotype evaluated in advance, were used in the present experiment. The steers were cared for according to the guide for the care and use of experimental animals in Hyogo Prefectural Technology Center of Agriculture, Forestry and Fisheries. GH genotype was determined according to Chikuni *et al.* (1997). The GH genotypes of 14 steers were Leu/Leu (A, $n = 7$) and Val/Val (B, $n = 7$) at amino acid position 127 of the protein and Thr/Thr (all) at amino acid position 172 of the protein. The steers with genotype A were derived from a Hiroshima strain sire (Miyajima, Japan), and the steers with genotype B were derived from a Tajima strain sire (Kikuidoi, Japan). The steers in each genotype group were divided into two groups based on intended growth rate (high, 1.0 kg/day; low, 0.6 kg/day) during 10–17 months of age: A-1.0 ($n = 3$), A-0.6 ($n = 4$), B-1.0 ($n = 3$) and B-0.6 ($n = 4$). The concentrate diets were fed once a day, and were restricted to achieve the intended growth rate during 10–17 months of age (early fattening period) and then were given *ad libitum* during 18–29 months of age (late fattening period). The concentrate diet during early fattening period consisted of 25% rolled barley, 30% flaked corn, 30% wheat bran and 15% soybean meal. That during the late fattening period consisted of

35% rolled barley, 30% flaked corn, 30% wheat bran and 5% soybean meal. The roughages were restricted and fed twice a day. Timothy hay was fed during 10–14 months of age and the amount decreased from 4 to 3 kg/day. Chopped rice straw was fed during 15–29 months of age and the amount decreased from 2.5 to 1.0 kg/day. The animals were housed in pens and individually accessed feed *ad libitum* via electronic gates (American Calan, Northwood, NH, USA). Water and trace-mineralized salt were freely available. Body-weight was measured every 2 weeks at early fattening period and every month at late fattening period. Withers height and heart girth of steers were measured every month. The steers were slaughtered at 29 months of age.

Carcass analysis

The carcasses were chilled for 48 h, and their meat quality was evaluated between the 6th and 7th ribs by official Japanese graders in accordance with the Japan Meat Grading Standards (JMGA 1988). Samples of longissimus muscles were collected at the 7th rib for determination of crude fat content (AOAC 1990) and fatty acid composition in longissimus muscle lipid (Oka *et al.* 2002).

Blood sampling

Blood samples for analyses of IGF-I, urea nitrogen, total cholesterol were collected from the jugular vein 2–3 h after concentrate feeding at the ages of 10, 16, 22 and 28 months. The serum was obtained by centrifugation and frozen at -40°C until assayed. Series of blood samples for analyses of GH were taken from each animal at 10 and 17 months of age. Blood samples were collected via indwelling jugular catheters at 15 min intervals for 6 h beginning at 10.00 hours. Jugular catheters were inserted on the afternoon of the day before sampling. The animals were given *ad libitum* access to water during the sampling period. Blood samples were drawn into heparinized tubes and centrifuged at 4°C . Plasma samples were stored at -40°C until assayed for GH.

Blood constituents

Serum levels of total cholesterol and urea nitrogen were measured on an autoanalyzer (Model Dri-Chem 5500; Fuji Photo Film, Tokyo, Japan). Serum levels of free fatty acid were determined with a commercial test kit (NEFA-C-test; Wako Pure Chemical, Osaka, Japan). The radioimmunoassays for the serum IGF-I, thyroxin and triiodothyronine were performed using

Table 1 Effects of GH genotype and growth rate during early fattening period on feed intake

Item	GH genotype		Intended growth rate (kg/day)		Significance	
	A	B	1.0	0.6	Genotype	Growth rate
Dry matter intakes (kg)						
Concentrate (kg)						
10–17 months of age	935	836	1029	743	**	**
17–29 months of age	2589	1839	2206	2222	**	
Total	3524	2675	3235	2966	**	
Roughage (kg)						
10–17 months of age	627	589	598	619	**	**
17–29 months of age	383	365	369	379	*	
Total	1010	954	967	998	**	**
TDN intake (kg)						
10–17 months of age	1119	1017	1183	953	**	**
17–29 months of age	2333	1696	2005	2023	**	
Total	3453	2713	3189	2977	**	

* $P < 0.05$, ** $P < 0.01$.

GH, growth hormone; TDN, total digestible nutrients.

commercial test kits (Somatomedin C-II; Bayer Medical, Tokyo, Japan; Amerlex-M T4, Amerlex-M T3; Ortho-Clinical Diagnostics, Tokyo, Japan). Plasma concentrations of GH were determined with a double-antibody radioimmunoassay using bovine GH (Biogenesis, Poole, UK) as standard, bovine GH antiserum (rabbit anti-bovine GH; Biogenesis) as a first antibody, and antirabbit serum (sheep antirabbit IgG; Biogenesis) as a second antibody. Bovine GH was radiolabeled with ^{125}I (Fraker & Speck 1978). The intra-assay CV was $<10\%$, and the inter-assay CV was $<15\%$.

Statistical analysis

Plasma GH values were subjected to CLUSTER pulse analysis procedures (Veldhuis & Johnson 1986) to determine the mean concentrations, area under the curve, peak number, and peak height estimates. Data were analyzed using the general liner model (GLM) procedures of the statistical analysis system (SAS Institute, Cary, NC, USA). The model included GH genotype, growth rate during the early fattening period, and genotype \times growth rate interaction as main effects. Differences were considered significant at $P < 0.05$. There was no significant interaction of genotype \times growth rate in any item ($P > 0.05$).

RESULTS

Feed intake, bodyweight, withers height and heart girth

The A group had greater ($P < 0.01$) dry matter intake (DMI) and total digestible nutrients (TDN) intake than

the B group (Table 1). The high growth rate group (1.0 kg/day) had greater ($P < 0.01$) DMI of concentrate and TDN intake than the low growth rate group (0.6 kg/day) during the early fattening period. However, there was no significant difference in the total DMI of concentrates and the total TDN intake between the 1.0 and 0.6 kg/day groups ($P > 0.05$). The DMI of roughage at the early fattening period was lower ($P < 0.01$) for the 1.0 kg/day group compared with the 0.6 kg/day group. Although the steers were fed the same amount of roughage, the steers in the 1.0 kg/day group did not finish their feed.

The bodyweights at the ages of 10, 17 and 29 months were greater ($P < 0.05$) for the A group compared with the B group (Table 2). The bodyweight at the age of 17 months and the average daily gain (ADG) during the early fattening period were greater ($P < 0.05$) for the 1.0 kg/day group compared with the 0.6 kg/day group. However, there was no significant difference in the bodyweight at the age of 29 months or ADG during the experimental period between the 1.0 and 0.6 kg/day groups ($P > 0.05$). The ADG of the 0.6 kg/day group during the early fattening period were approximately established values. However, that of the 1.0 kg/day group was lower than the established value because the steers in the B-1.0 group could not finish the feed. There was no significant difference in the withers height between the A and B groups, or between the 1.0 and 0.6 kg/day groups ($P > 0.05$). The final heart girth was greater ($P < 0.01$) for the A group compared with the B group. The heart girths at the ages of 17 and 29 months were greater ($P < 0.05$) for

Table 2 Effects of GH genotype and growth rate during early fattening period on bodyweight, withers height, heart girth and ADG

Item	GH genotype		Intended growth rate (kg/day)		Significance	
	A	B	1.0	0.6	Genotype	Growth rate
Bodyweight (kg)						
10 months of age	317.0	287.0	303.3	300.6	*	
17 months of age	486.9	422.1	489.7	439.4	*	*
29 months of age	736.6	597.9	677.5	657.0	**	
ADG (kg/day)						
10–17 months of age	0.81	0.73	0.88	0.66		**
17–29 months of age	0.70	0.44	0.53	0.61	**	
total	0.74	0.54	0.65	0.63	**	
Withers height (cm)						
10 months of age	119.7	118.3	119.2	118.8		
17 months of age	131.7	130.1	132.0	129.8		
29 months of age	143.0	141.9	142.7	142.2		
Heart girth (cm)						
10 months of age	157.2	157.8	158.3	156.6		
17 months of age	187.0	185.1	190.0	182.1		*
29 months of age	222.0	209.8	218.7	213.1	**	*

* $P < 0.05$, ** $P < 0.01$.

ADG, average daily gain; GH, growth hormone.

the 1.0 kg/day group compared with the 0.6 kg/day group.

Blood constituents

The serum concentration of urea nitrogen was higher ($P < 0.05$) in the B group than in the A group at the ages of 10, 16 and 22 months and greater ($P < 0.01$) in the 1.0 kg/day group than in the 0.6 kg/day group at the age of 16 months (Table 3). There was no significant difference in the serum concentrations of total cholesterol or free fatty acid between the A and B groups, or between the 1.0 and 0.6 kg/day groups. The serum concentration of thyroxin at the age of 28 months was higher ($P < 0.01$) in the A group than in the B group. The serum concentrations of thyroxin and triiodothyronine at the age of 16 months were higher ($P < 0.05$) in the 1.0 kg/day group than in the 0.6 kg/day group. The serum concentration of IGF-I was higher ($P < 0.05$) in the B group than in the A group at the ages of 10, 22 and 28 months, but there was no significant difference between the 1.0 and 0.6 kg/day groups ($P > 0.05$).

Growth hormone secretion

The overall mean concentrations of plasma GH at the ages of 10 and 17 months was higher ($P < 0.05$) in the A group than in the B group (Table 4). The peak height and area under the curve of plasma GH at the age of 17 months were also greater ($P < 0.05$) in the A group

than in the B group. The overall mean concentration and peak height of plasma GH at the age of 17 months were greater ($P < 0.01$) in the 1.0 kg/day group than in the 0.6 kg/day group.

Carcass characteristics

The carcass weight of the A group was greater ($P < 0.01$) than that of the B group. However, there was no significant difference in carcass weights between the 1.0 and 0.6 kg/day groups ($P > 0.05$; Table 5). The rib thickness of the 1.0 kg/day group was greater ($P < 0.05$) than that of the 0.6 kg/day group. The crude fat content of the longissimus muscle was greater ($P < 0.05$) for the 0.6 kg/day group compared with the 1.0 kg/day group. There was no significant difference in the marbling score, beef color, longissimus muscle area, intermuscular fat thickness or subcutaneous fat thickness between the A and B groups, or between the 1.0 and 0.6 kg/day groups.

The steers in the A group had higher ($P < 0.01$) percentages of myristoleic (14:1) and palmitoleic (16:1) acids, and lower ($P < 0.01$) percentage of stearic acid (18:0) in intramuscular lipid than those in the B group (Table 6).

DISCUSSION

The carcass weight breeding value was significantly higher in Simmental bull with the Leu/Leu genotype

Table 3 Effects of GH genotype and growth rate during early fattening period on blood constituents

Item	GH genotype		Intended growth rate (kg/day)		Significance	
	A	B	1.0	0.6	Genotype	Growth rate
Urea nitrogen (mg/dL)						
10 months of age	5.5	7.9	6.2	7.2	**	
16 months of age	17.3	22.1	22.3	17.2	**	**
22 months of age	15.3	18.0	15.8	17.5	*	
28 months of age	17.7	19.2	19.2	17.7		
Total cholesterol (mg/dL)						
10 months of age	90.8	87.5	85.8	92.4		
16 months of age	149.4	132.6	144.5	137.5		
22 months of age	164.1	151.1	148.5	166.8		
28 months of age	146.1	142.2	146.2	142.1		
Free fatty acid (μ Eq/L)						
10 months of age	131.9	125.2	119.3	137.8		
16 months of age	78.8	93.0	91.3	80.5		
22 months of age	286.0	245.4	274.8	256.5		
28 months of age	115.7	114.4	119.2	110.9		
Thyroxin (ng/mL)						
10 months of age	72.0	77.0	73.7	75.4		
16 months of age	77.2	82.3	83.0	76.4		*
22 months of age	83.8	87.4	84.7	86.5		
28 months of age	88.0	79.3	83.4	84.0	**	
Triiodothyronine (ng/mL)						
10 months of age	1.3	1.3	1.3	1.2		
16 months of age	1.2	1.2	1.3	1.1		*
22 months of age	1.1	1.0	1.1	1.0		
28 months of age	1.1	0.9	1.0	1.0		
Insulin-like growth factor-I (ng/mL)						
10 months of age	235.4	295.6	279.6	251.4	*	
16 months of age	233.8	253.5	215.1	272.2		
22 months of age	170.9	231.6	203.4	199.1	*	
28 months of age	134.3	190.2	147.6	176.9	*	

* $P < 0.05$, ** $P < 0.01$.
GH, growth hormone.

Table 4 Effects of GH genotype and growth rate during early fattening period on plasma GH concentrations

Item	GH genotype		Intended growth rate (kg/day)		Significance	
	A	B	1.0	0.6	Genotype	Growth rate
10 months of age						
Overall mean (ng/mL)	17.8	12.5	17.2	13.2	*	
Peak number (no.per 6 h)	3.0	2.7	2.7	3.0		
Peak height (ng/mL)	24.4	18.2	23.8	18.8		
Area under the curve (ng/mL)	501.8	265.2	471.1	295.8		
17 months of age						
Overall mean (ng/mL)	11.7	6.7	12.1	6.3	**	**
Peak number (no.per 6 h)	2.5	2.7	2.7	2.5		
Peak height (ng/mL)	16.3	10.2	16.7	9.9	**	**
Area under the curve (ng/mL)	301.1	162.5	269.0	194.7	*	

* $P < 0.05$, ** $P < 0.01$.
GH, growth hormone.

Table 5 Effects of GH genotype and growth rate during early fattening period on carcass characteristics

Item	GH genotype		Intended growth rate (kg/day)		Significance	
	A	B	1.0	0.6	Genotype	Growth rate
Carcass weight (kg)	455.7	369.0	420.7	404.0	**	
Marbling score (BMS No.)†	3.6	4.0	3.5	4.1		
Beef color (BCS No.)‡	3.9	4.6	4.3	4.1		
Longissimus muscle area (cm ²)	52.3	44.8	50.5	46.6		
Rib thickness (cm)	6.9	6.9	7.2	6.6		*
Intermuscular fat thickness (cm)	6.6	6.6	7.0	6.2		
Subcutaneous fat thickness (cm)	2.7	2.2	2.6	2.2		
Intramuscular fat (%)§	27.4	29.6	25.0	31.9		**

* $P < 0.05$, ** $P < 0.01$. †Beef marbling standard numbers (JMGA 1988). ‡Beef color standard numbers (JMGA 1988). §Determined in longissimus muscle obtained the 7th ribs.

GH, growth hormone.

Table 6 Effects of GH genotype and growth rate during early fattening period on fatty acid composition of longissimus muscle

Item	GH genotype		Intended growth rate (kg/day)		Significance	
	A	B	1.0	0.6	Genotype	Growth rate
Myristic acid (14:0)	3.6	3.2	3.5	3.3		
Myristoleic acid (14:1)	1.4	1.0	1.2	1.2	**	
Palmitic acid (16:0)	29.7	28.6	29.5	28.8		
Palmitoleic acid (16:1)	4.4	3.5	4.1	3.8	**	
Stearic acid (18:0)	10.5	12.2	11.3	11.4	**	
Oleic acid (18:1)	45.9	47.3	46.1	47.1		
Linoleic acid (18:2)	1.9	1.7	1.9	1.7		
SFA	45.1	45.3	45.6	44.8		
MUFA	52.9	52.9	52.5	53.4		
PUFA	2.0	1.8	2.0	1.8		

** $P < 0.01$.

SFA, saturated fatty acids (sum of 14:0, 16:0, and 18:0); MUFA, mono-unsaturated fatty acids (sum of 14:1, 16:1, and 18:1); PUFA, polyunsaturated fatty acids (sum of 18:2 and 18:3).

than in that with the Val/Val genotype at amino acid residue 127 in the GH gene (Schlee *et al.* 1994a). Japanese Black cattle with genotype A (Leu/Leu) had greater carcass weight than those with genotype B (Val/Val) (K. Tatsuda *et al.*, unpubl. data, 2004). In the present study, the feed intake, bodyweight and carcass weight of genotype A were greater than those of genotype B. These findings suggest that cattle with genotype A are heavier than those with genotype B, and that the difference of bodyweight between the two genotypes is probably due to difference of feed intake.

Schlee *et al.* (1994a) also indicated that meat classification score breeding value was significantly higher in Simmental bull with the Val/Val genotype than that with the Leu/Leu genotype. The beef marbling score of Japanese Black cattle with genotype B tended to be higher than that of genotype A but the difference was

not significant (K. Tatsuda *et al.*, unpubl. data, 2004). In the present study there was no significant difference in marbling score or intramuscular fat content between genotypes A and B. The beef marbling score of Japanese Black cattle may not be different between genotype A and B.

In general, cattle recovering from feed or growth restriction exhibited more rapid compensatory growth upon refeeding (Henricks *et al.* 1994; Sainz *et al.* 1995; Yambayamba *et al.* 1996). Feeding at a restricted intake early in the feeding period does not reduce steer performance if followed by approximately 100 days of ad libitum feeding (Loerch & Fluharty 1998). Matsuzaki *et al.* (2001) also reported that restricted concentrate intake during rearing period (5–8 months old) did not affect the finishing weight of Holstein steers. In agreement with these reports, in the present

study there was no significant difference in the bodyweight at the end of the experiment or ADG during the experimental period between the 1.0 and 0.6 kg/day groups, although ADG during the early fattening period was greater for the 1.0 kg/day group compared with the 0.6 kg/day group. This result suggests that moderate growth restriction (0.6 kg/day) during the early fattening period does not affect the bodyweight at the end of the fattening period.

Several studies have indicated that cattle with feed restriction and re-alimentation accumulated more fat and had higher marbling scores than cattle fed *ad libitum* (Coleman *et al.* 1993; Wertz *et al.* 2001). Zembayashi *et al.* (1988) reported that steers on a medium-high nutritional level had greater intramuscular fat contents than steers on a high nutritional level in Japanese Black breed. In the present study, the growth restriction during the early fattening period increased fat content of the longissimus muscle. These findings suggest that Japanese Black steers have higher intramuscular fat content on growth restriction during the early fattening period and subsequent re-alimentation.

In the present study, the heart girths and the rib thickness were increased at a high growth rate. The rib thickness of the 1.0 kg/day group was significantly greater than that of the 0.6 kg/day group. However, the difference in the longissimus muscle area was not significant between the two groups. Therkildsen *et al.* (2002) and Vestergaard *et al.* (2003) reported that high growth rate increased skeletal muscle weight, although different types of muscles reacted differently to high growth rate. High growth rate at early fattening period might stimulate growth of muscles associated with rib thickness.

We previously reported that fatty acid composition of carcass fat was affected by genetic factors in Japanese Black cattle (Oka *et al.* 2002). In the present study, the steer with genotype A had higher percentages of 14:1 and 16:1 acids, and lower percentage of 18:0 in intramuscular lipid than the steers with genotype B. Fatty acid composition of carcass fat might be affected by GH genotype.

The overall mean concentration of plasma GH was higher in genotype A than in genotype B, and the peak height and area under the curve of plasma GH at the age of 17 months were greater in genotype A than in genotype B. Similar to the present study, Danish Jersey calves with Leu/Leu genotype had a higher peak and rate of GH release after inducement with GH-releasing hormone than those with the Val/Val

genotype (Sørensen *et al.* 2002). Schlee *et al.* (1994b) reported that the Leu/Leu genotype was associated with higher plasma concentration of GH than Leu/Val genotype in German Black and White bulls. The serum concentration of IGF-I was higher in genotype B than in genotype A. The plasma concentration of IGF-I was higher in the Leu/Val genotype than in the Leu/Leu genotype in Simmental bulls (Schlee *et al.* 1994b). These findings suggest that the Val allele is associated with lower plasma GH level and higher circulating IGF-I level.

Feed restriction was associated with higher plasma concentrations of free fatty acid and lower concentrations of IGF-I, thyroxin, triiodothyronine and urea nitrogen (Blum *et al.* 1985; Ellenberger *et al.* 1989; Yambayamba *et al.* 1996). In the present experiment, serum concentrations of urea nitrogen, thyroxin and triiodothyronine decreased during restricted growth, but serum concentrations of free fatty acid and IGF-I were not affected by restricted growth. Hall *et al.* (1995) reported that heifers fed to achieve moderate growth rate (0.6 kg/day) had lower concentration of blood urea nitrogen than those fed to achieve high growth rate (1.0 kg/day), but serum concentrations of IGF-I were not different between the two groups. The growth rates during restricted growth in the studies by Blum *et al.* (1985), Ellenberger *et al.* (1989) and Yambayamba *et al.* (1996) were very low (0.128, 0.37 and 0.07 kg/day, respectively), but those in the Hall *et al.* (1995) and present studies were not extremely low (0.6 kg/day). These findings suggest that moderate growth restriction (0.6 kg/day) does not influence serum concentrations of free fatty acid and IGF-I during the early fattening period.

In the present study, the plasma overall mean concentration and the peak height of GH in the 0.6 kg/day group in which feed was restricted for 7 months were lower than those in the 1.0 kg/day group. Several studies reported a higher plasma mean concentration of GH in cattle on feeding restrictions (Blum *et al.* 1985; Ellenberger *et al.* 1989; Henricks *et al.* 1994; Yambayamba *et al.* 1996). The durations of feed restriction in these studies were shorter than 200 days. Hornick *et al.* (1998) reported that the longer that feed was restricted, the less effect was observed on GH levels in bulls. Radcliff *et al.* (2004) indicated that feed restriction for more than 200 days no longer affected the peak concentration and the area under the curve of serum GH in heifers. Thus, the effect of feed restriction on the plasma GH levels may differ by the durations of restriction.

In conclusion, we have shown that a high growth rate (1.0 kg/day) during the early fattening period increased the rib thickness, and a moderate low growth rate (0.6 kg/day) during the early fattening period increased the fat content of longissimus muscle. The present results also suggest that Japanese Black steers with genotype A have higher plasma GH concentration and lower serum IGF-I concentration than those with genotype B.

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REFERENCES

- Association of Official Analytical Chemists (AOAC). 1990. *Official Methods of Analysis*, 15th edn. AOAC, Arlington, VA.
- Bishop MD, Simmen RCM, Simmen FA, Davis ME. 1989. The relationship of insulin-like growth factor-I with postweaning performance in Angus beef cattle. *Journal of Animal Science* **67**, 2872–2880.
- Blum JW, Schnyder W, Kunz PL, Blom AK, Bickel H, Schurch A. 1985. Reduced and compensatory growth: Endocrine and metabolic changes during food restriction and refeeding in steers. *Journal of Nutrition* **115**, 417–424.
- Chikuni K, Fukumoto Y, Tanabe R, Muroya S, Ozawa S. 1997. A simple method for genotyping the bovine growth hormone gene. *Animal Genetics* **28**, 230–232.
- Chikuni K, Nagatsuma T, Tabata T, Monma M, Saito M, Ozawa S, Ozutsumi K. 1994. Genetic variants of the growth hormone gene in Japanese cattle. *Animal Science and Technology* **65**, 340–346.
- Chikuni K, Terada F, Kageyama S, Koishikawa T, Kato S, Ozutsumi K. 1991. Identification of DNA sequence variants for amino acid residue 127 of bovine growth hormone using the polymerase chain reaction method. *Animal Science and Technology* **62**, 660–666.
- Coleman SW, Evans BC, Guenther JJ. 1993. Body and carcass composition of Angus and Charolais steers as affected by age and nutrition. *Journal of Animal Science* **71**, 86–95.
- Dalke BS, Roeder RA, Kasser TR, Veenhuizen JJ, Hunt CW, Hinman DD, Schelling GT. 1992. Dose–response effects of recombinant bovine somatotropin implants on feedlot performance in steers. *Journal of Animal Science* **70**, 2130–2137.
- Ellenberger MA, Johnson DE, Carstens GE, Hossner KL, Holland MD, Nett TM, Nockels CF. 1989. Endocrine and metabolic changes during altered growth rates in beef cattle. *Journal of Animal Science* **67**, 1446–1454.
- Fraker PJ, Speck JC Jr. 1978. Protein and cell membrane iodinations with a sparingly soluble chloroamide, 1,3,4,6-tetrachloro-3a,6a-diphenylglycol uril. *Biochemical and Biophysical Research Communications* **28**, 849–857.
- Gatford KL, Fletcher TP, Clarke IJ, Owens PC, Quinn KJ, Walton PE, Grant PA, Hosking BJ, Egan AR, Ponnampalam EN. 1996. Sexual dimorphism of circulating somatotropin, insulin-like growth factor I and II, insulin-like growth factor binding proteins, and insulin: Relationships to growth rate and carcass characteristics in growing lambs. *Journal of Animal Science* **74**, 1314–1325.
- Hall JB, Staigmiller RB, Bellows RA, Short RE, Moseley WM, Bellows SE. 1995. Body composition and metabolic profiles associated with puberty in beef heifers. *Journal of Animal Science* **73**, 3409–3420.
- Hayden JM, Williams JE, Collier RJ. 1993. Plasma growth hormone, insulin-like growth factor, insulin, and thyroid hormone association with body protein and fat accretion in steers undergoing compensatory gain after dietary energy restriction. *Journal of Animal Science* **71**, 3327–3338.
- Henricks DM, Jenkins TC, Ward JR, Krishnan CS, Grimes L. 1994. Endocrine responses and body composition changes during feed restriction and realimentation in young bulls. *Journal of Animal Science* **72**, 2289–2297.
- Hornick JL, Van Eenaeme C, Diez M, Minet V, Istasse L. 1998. Different periods of feed restriction before compensatory growth in Belgian Blue bulls: II. Plasma metabolites and hormones. *Journal of Animal Science* **76**, 260–271.
- Japan Meat Grading Association (JMGA). 1988. *New Beef Carcass Grading Standards*. Japan Meat Grading Association, Tokyo, Japan.
- Loerch SC, Fluharty FL. 1998. Effects of programming intake on performance and carcass characteristics of feedlot cattle. *Journal of Animal Science* **76**, 371–377.
- Lucy MC, Hauser SD, Eppard PJ, Krivi GG, Clark JH, Bauman DE, Collier RJ. 1993. Variants of somatotropin in cattle: Gene frequencies in major dairy breeds and associated milk production. *Domestic Animal Endocrinology* **10**, 325–333.
- Matsuzaki M, Sato T, Shiba N, Hara S, Tsuneishi E, Yamaguchi T. 2001. Effects of restricted concentrate feeding during the early growing phase on growth performance, carcass characteristics and the somatotrophic axis in Holstein steers. *Animal Science Journal* **72**, 483–493.
- Mitsuhashi T, Mitsumoto M, Ozawa S. 1997. The effects of sire, roughage feeding condition and concentrate composition on the growth rate and carcass composition of the Japanese Black steers. *Animal Science and Technology* **68**, 403–413.
- Oka A, Iwaki F, Dohgo T, Ohtagaki S, Noda M, Shiozaki T, Endoh O, Ozaki M. 2002. Genetic effects on fatty acid composition of carcass fat of Japanese Black Wagyu steers. *Journal of Animal Science* **80**, 1005–1011.
- Ozawa S, Mitsuhashi T, Mitsumoto M, Matsumoto S, Itoh N, Itagaki K, Kohno Y, Dohgo T. 2000. The characteristics of muscle fiber types of longissimus thoracis muscle and their influences on the quantity and quality of meat from Japanese Black steers. *Meat Science* **54**, 65–70.

- Preston RL, Bartle SJ, Kasser TR, Day JW, Veenhuizen JJ, Baile CA. 1995. Comparative effectiveness of somatotropin and anabolic steroids in feedlot steers. *Journal of Animal Science* **73**, 1038–1047.
- Radcliff RP, VandeHaar MJ, Kobayashi Y, Sharma BK, Tucker HA, Lucy MC. 2004. Effect of dietary energy and somatotropin on components of the somatotrophic axis in Holstein heifers. *Journal of Dairy Science* **87**, 1229–1235.
- Rausch MI, Tripp MW, Govoni KE, Zang W, Weber WJ, Crooker BA, Hoagland TA, Zinn SA. 2002. The influence of level of feeding on growth and serum insulin-like growth factor I and insulin-like growth factor-binding proteins in growing beef cattle supplemented with somatotropin. *Journal of Animal Science* **80**, 94–100.
- Sainz RD, De la Torre F, Oltjen JW. 1995. Compensatory growth and carcass quality in growth-restricted and refed beef steers. *Journal of Animal Science* **73**, 2971–2979.
- Satoh H, Ujiie S, Onodera S, Oda S. 1991. Correlation between carcass characteristics and plasma insulin-like growth factor-I level in Japanese Black beef cattle. *Animal Science and Technology* **62**, 774–776.
- Schlee P, Graml R, Rottmann O, Pirchner F. 1994a. Influence of growth-hormone genotypes on breeding values of Simmental bulls. *Journal of Animal Breeding and Genetics* **111**, 253–256.
- Schlee P, Graml R, Schallenberger E, Schams D, Rottmann O, Olbrich-Bludau A, Pirchner F. 1994b. Growth hormone and insulin-like growth factor I concentrations in bulls of various growth hormone genotypes. *Theoretical and Applied Genetics* **88**, 497–500.
- Schwarz FJ, Schams D, Röpke R, Kirchgessner M, Kögel J, Matzke P. 1993. Effects of somatotropin treatment on growth performance, carcass traits, and the endocrine system in finishing beef heifers. *Journal of Animal Science* **71**, 2721–2731.
- Sørensen P, Grochowska R, Holm L, Henryon M, Løvendahl P. 2002. Polymorphism in the bovine growth hormone gene affects endocrine release in dairy calves. *Journal of Dairy Science* **85**, 1887–1893.
- Stick DA, Davis ME, Loerch SC, Simmen RCM. 1998. Relationship between blood serum insulin-like growth factor I concentration and postweaning feed efficiency of crossbred cattle at three levels of dietary intake. *Journal of Animal Science* **76**, 498–505.
- Therkildsen M, Melchior Larsen L, Vestergaard M. 2002. Influence of growth rate and muscle type on muscle fibre type characteristics, protein synthesis capacity and activity of the calpain system in Friesian calves. *Animal Science* **74**, 243–251.
- Veldhuis JD, Johnson ML. 1986. Cluster analysis: A simple, versatile, and robust algorithm for endocrine pulse detection. *American Journal of Physiology* **250**, E486–E493.
- Vestergaard M, Purup S, Frystyk J, Lovendahl P, Sørensen MT, Riis PM, Flint DJ, Sejrsen K. 2003. Effects of growth hormone and feeding level on endocrine measurements, hormone receptors, muscle growth and performance of prepubertal heifers. *Journal of Animal Science* **81**, 2189–2198.
- Wertz AE, Berger LL, Faulkner DB, Nash TG. 2001. Intake restriction strategies and sources of energy and protein during the growing period affect nutrient disappearance, feedlot performance, and carcass characteristics of crossbred heifers. *Journal of Animal Science* **79**, 1598–1610.
- Yambayamba ESK, Price MA, Foxcroft GR. 1996. Hormonal status, metabolic changes, and resting metabolic rate in beef heifers undergoing compensatory growth. *Journal of Animal Science* **74**, 57–69.
- Zembayashi M. 1993. Comparison of carcass tissue production of steers among pure breeds and crosses. *Animal Science and Technology* **64**, 149–155.
- Zembayashi M, Nabeta H, Mototsuji T. 1988. Effects of breeds and nutritional planes on intramuscular lipid deposition of fattening steers. *Japanese Journal of Zootechnical Science* **59**, 39–48.