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Regulation of Fat and Fatty Acid Composition in Beef Cattle

Stephen B. Smith*, Clare A. Gill, David K. Lunt and Matthew A. Brooks
Department of Animal Science, Texas A&M University, College Station 77843-2471, USA

ABSTRACT : Fat composition of beef, taken here to mean marbling, can be manipulated by time on feed, finishing diet, and breed type. These three factors also strongly influence the fatty acid composition of beef. Both the amount of marbling and the concentration of monounsaturated fatty acids (MUFA) increase with time on feed in grain-fed and pasture-fed cattle, but much more dramatically in grain-fed cattle. High-concentrate diets stimulate the activity of adipose tissue stearoyl-CoA desaturase (SCD), which is responsible for the conversion of saturated fatty acids (SFA) to their Δ9 desaturated counterparts. Also, grain feeding causes a depression in ruminal pH, which decreases those populations of ruminal microorganisms responsible for the isomerization and hydrogenation of polyunsaturated fatty acids (PUFA). The net result of elevated SCD activity in marbling adipose tissue and depressed ruminal isomerization/hydrogenation of dietary PUFA is a large increase in MUFA in beef over time. Conversely, pasture depresses both the accumulation of marbling and SCD activity, so that even though pasture feeding increases the relative concentration of PUFA in beef, it also increases SFA at the expense of MUFA. Wagyu and Hanwoo cattle accumulate large amounts of marbling and MUFA, and Wagyu cattle appear to be less sensitive to the effects of pastures in depressing overall rates of adipogenesis and the synthesis of MUFA in adipose tissues. There are small differences in fatty acid composition of beef from *Bos indicus* and *Bos taurus* cattle, but diet and time on feed are much more important determinants of beef fat content and fatty acid composition than breed type. (**Key Words :** Adipose Tissue, Bovine, Fatty Acids, Intramuscular, Stearoyl-CoA Desaturase)

INTRODUCTION

In Japan, U.S. beef previously was considered superior to Australian beef because i) Australian producers could not produce beef as highly marbled as beef from the U.S., even in long-fed cattle; and ii) Australian cattle previously had harder fat than U.S. cattle. Japanese and Korean consumers highly value both marbling (but not excess fat trim) and soft fat, but the distinction between U.S. and Australian beef is disappearing.

The fatty acid primarily responsible for soft fat in Japanese (Wagyu) and Korean (Hanwoo) cattle is oleic acid (18:1n-9). The concentration of oleic acid also is positively correlated with overall palatability of beef (Waldman et al., 1968; Westerling and Hedrick, 1979), which may be related to fat softness. Stearic acid (18:0) is a primary determinant of fat hardness (i.e., lipid melting point; Smith et al., 1998; Wood et al., 2004; Chung et al., 2006b), so any dietary or production factor that enhances the conversion of stearic acid to oleic acid will increase fat softness.

There are three fatty desaturases in animal tissues, Δ5, Δ6, and Δ9 desaturase. Of these, only the Δ9 desaturase acts upon saturated fatty acids (SFA) to convert them to their respective monounsaturated fatty acids (MUFA). The most abundant fatty acid in beef is oleic acid (Figure 1), produced by the Δ9 desaturation of stearic acid. The Δ9 desaturase, which is encoded by the stearoyl-CoA desaturase (SCD) gene, also converts *trans*-vaccenic acid (TVA) to its corresponding conjugated linoleic acid (CLA) isomer, *cis*-9,*trans*-11 CLA (Figure 1). Approximately 5% of the total fatty acids in beef are comprised of polyunsaturated fatty acids (PUFA), by far the most abundant of which is linoleic acid. As is the case for MUFA and *cis*-9,*trans*-11 CLA, PUFA contain a double bond at the Δ9 position (Figure 1); however, this is introduced into the fatty acid structure by the plant from which the linoleic acid was derived, and is not produced by Δ9 desaturation in animal tissues.

There are three major factors that influence the fatty acid composition of beef: i) age of animal; ii) diet; and iii) breed type. Age of animal and breed type specifically affect the concentration of MUFA in beef by affecting SCD gene expression and activity, whereas diet is the sole source of the essential fatty acids, linoleic acid and α-linolenic acid.

* Corresponding Author: Stephen B. Smith. Tel: +1-979-845-3939, Fax: +1-979-458-2702, E-mail: sbsmith@tamu.edu

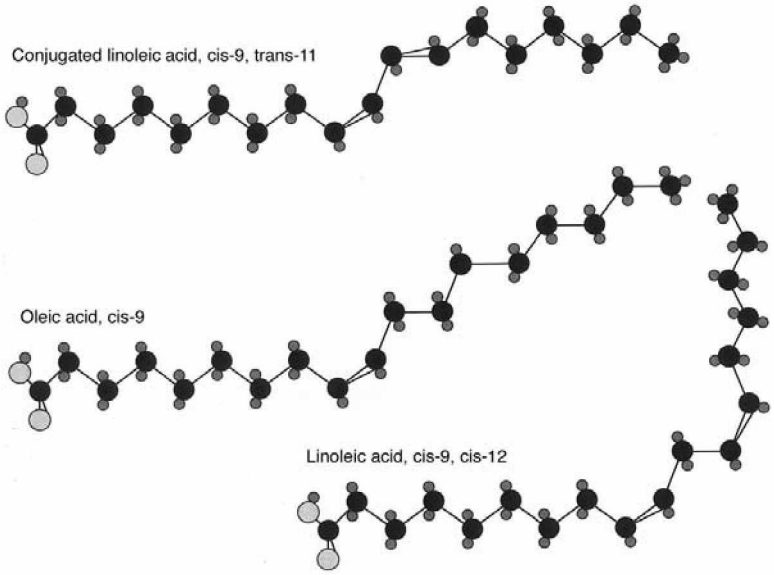

Figure 1. Structures of oleic acid, *cis*-9, *trans*-11 conjugated linoleic acid, and linoleic acid.

This review will address those factors that regulate fat composition (i.e., marbling) and fatty acid composition of beef cattle.

Changes in fatty acid composition and stearoyl-CoA desaturase activity over time

Table 1 contains data from a large number of studies that varied widely in age of cattle, breed type, and finishing diets, and indicates the large variation in fatty acid composition that can be achieved across production systems. Generally, the highest MUFA:SFA ratio was observed in the oldest cattle. It now is well established that, in neutral lipids of muscle and total adipose tissue lipids in beef cattle, there is a general elevation in MUFA and concomitant depression in SFA with increasing time on a grain-based, feedlot diet (Huerta-Leidenz et al., 1996; Malau-Aduli et al., 1997; Rule

Table 1. Fatty acid concentrations (g/100 g total fatty acids) in subcutaneous adipose tissue of steers and cows produced in the U.S., Australian crossbred cattle, Japanese Black steers, and Hanwoo steers fed under different production conditions

Item	Cattle group/diet[a]					
	Brahman	Hereford	Angus	Australian	J. Black	Hanwoo
Age (months)	54	54	16	22	27 (est.)	28
14:0	4.3	4.0	3.0	1.5	1.3	3.2
14:1n-5	3.2	2.4	1.1	0.1	1.3	1.0
16:0	22.7	26.0	27.4	24.2	24.2	27.9
16:1n-7	10.7	9.4	5.6	1.6	5.2	4.6
18:0	7.6	8.9	8.8	26.1	7.6	9.6
18:1*trans*-11	NR	NR	1.6	2.3	0.7	NR
18:1n-9	49.6	47.8	41.3	39.8	52.9	47.3
18:1n-7	NR	NR	2.0	1.0	3.0	NR
18:2n-6	4.3	1.7	1.9	1.6	2.0	4.2
18:3n-3	0.9	0.7	0.1	0.5	0.2	0.4
16:1:18:0	1.41	1.06	0.19	0.06	0.68	0.48
MUFA:SFA[c]	1.85	1.59	1.26	0.77	1.86	1.28

[a] The Brahman and Hereford cows grazed on native pasture and oats. All other cattle were fed finishing diets typical for the country in which they were produced. The age of the Japanese Black (J. Black) steers is estimated, based on typical production conditions in Japan. Data for the Brahman and Hereford cows are from Huerta-Leidenz et al. (1993); data for Angus steers are from Chung et al. (2006b); data for Australian and J. Black are from Smith et al. (1998); data for Hanwoo are from Jung and Choi (2003).

[b] NR = Not reported.

[c] MUFA = Monounsaturated fatty acids (14:1n-5, 16:1n-7, 17:1n-8, 18:1n-9, and 18:2*cis*-9,*trans*11). SFA = Saturated fatty acids (14:0, 16:0, 17:0, 18:0, and 18:1*trans*-11).

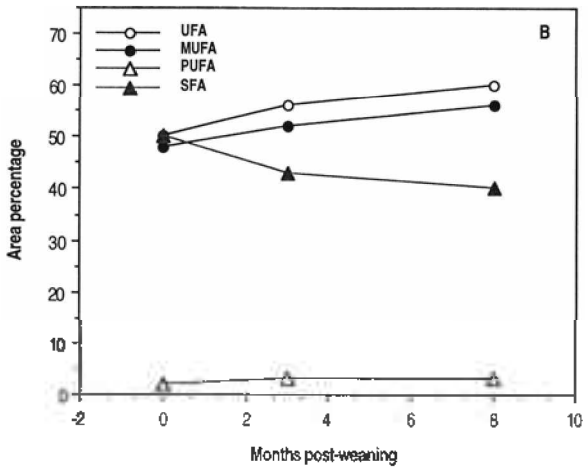

Figure 2. Changes in SFA, MUFA, and PUFA over time in subcutaneous adipose tissue from Brahman and Hereford steers (data pooled across breed type). Adapted from Huerta-Leidenz et al. (1996).

et al., 1997; Chung et al., 2006b; Figure 2). It appears likely that some portion of the increase in MUFA over time in subcutaneous adipose tissue is due to an increase in SCD gene expression and concomitant catalytic activity in corn-fed steers (Chung et al., 2007; Jiang et al., 2008; Duckett et al., 2009). Pasture or hay feeding strongly depresses SCD gene expression (Chung et al., 2007; Duckett et al., 2009), resulting in an elevation in SFA in beef. Pasture or hay feeding also causes a depression in marbling scores, even when cattle are taken to the same body weight (Lunt et al., 2005).

The concentration of intramuscular lipid (primarily from marbling adipose tissue) in longissimus muscle can be as low as 2% in beef from steers fed for the U.S. market, to over 30% in Japanese Black or American Wagyu cattle fed for the Japanese market (Lunt et al., 1993, 2005; Zembayashi 1994; Zembayashi et al., 1999; Smith et al., 2001). As intramuscular lipid accumulates, there is a concomitant elevation in the concentration of oleic acid, from a low of 30% to over 50% of total adipose tissue fatty acids (Figure 3; data M. A. Brooks and S. B. Smith, unpublished and Chung et al., 2006b). These and other data from our laboratory have indicated a significant correlation between amount of intramuscular lipid and the concentration of MUFA in beef. However, this relationship is significant only when data from long-fed cattle are included to provide sufficient variation in intramuscular lipid. The increase in intramuscular lipid in beef is the result of marbling adipocyte hypertrophy. In Angus steers grazing on native pasture to 12 months of age, marbling adipocytes contain little lipid and are barely visible (Figure 4), and the MUFA:SFA ratio in beef from these calves is only 0.83. After the steers had been fed a corn-based finishing diet for an additional 4 months, there was marked increase in

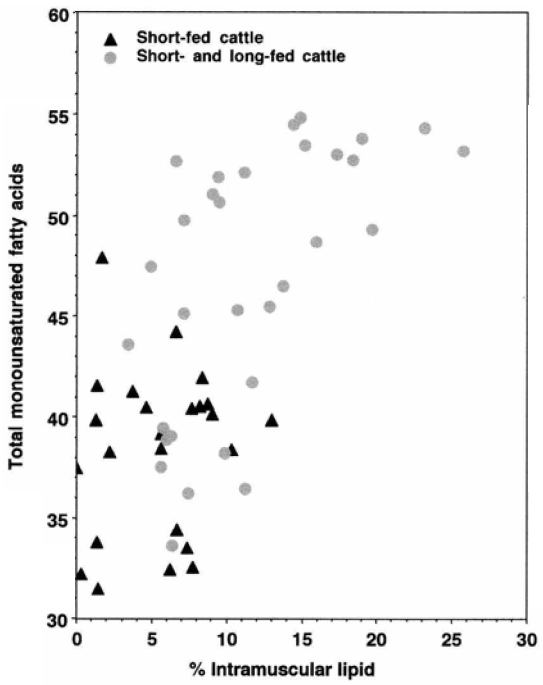

Figure 3. Relationship between the percentage intramuscular lipid and total MUFA in *M. longissimus dorsi* and Angus and Wagyu steers fed a corn-based finishing diet to 16 months of age (short-fed) or fed either a corn-based or hay-based diet to over 20 months of age (long-fed). The data labeled Short-fed are from M. A. Brooks and S. B. Smith (unpublished data), data labeled Short- and long-fed are from Chung et al. (2006b).

marbling adipocyte volume and the MUFA:SFA increased to 1.04. We conclude that, as marbling adipocytes increase in size, there is a concomitant increase in intracellular MUFA, due primarily to large increases in oleic acid.

In many species, the concentration of oleic acid in adipose tissue reflects the average concentration of oleic acid in the diet (St. John et al., 1987), but in ruminant species such as beef cattle, oleic acid is hydrogenated largely to stearic acid by ruminal microorganisms (Ekeren et al., 1992). Research from the 1990s demonstrated that bovine adipose tissue had considerably higher SCD catalytic activity (St. John et al., 1991; Chang et al., 1992) and gene expression (Cameron et al., 1994) than muscle, liver, or intestinal mucosa. Archibeque et al. (2005) similarly demonstrated that subcutaneous adipose tissue had approximately twice the SCD catalytic activity of marbling adipose tissue, which is consistent with a higher concentration of MUFA in subcutaneous than in marbling adipose tissue (Sturdivant et al., 1992; May et al., 1993).

SCD gene expression increases after weaning in subcutaneous adipose tissue of steers fed a corn-based finishing diet (Martin et al., 1999), and elevations in SCD activity persist even after SCD gene expression begins to decline (Chung et al., 2007; Figure 5). Similarly, Lee et al. (2005) observed peak SCD mRNA at 12 months of age in

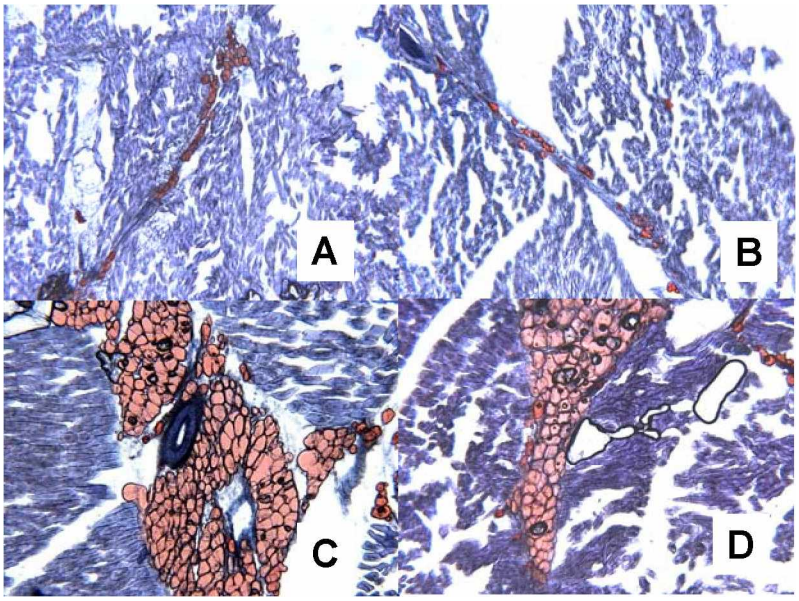

Figure 4. Marbling adipocyte development from the *M. longissimus dorsi* of Angus steers at 12 months (top) and 16 months of age (bottom). Cells were stained with Oil Red O to stain adipocyte cells and hematoxylin solution according to Mayer and bluing solution for nuclei. Steers were backgrounded to 12 months of age on native pasture (A and B) and then fed a corn-based finishing diet from 12 to 16 months of age (C and D). White areas are due to separation of the tissue due to freeze/thaw damage.

muscle from Hanwoo steers. The rate of *de novo* fatty acid biosynthesis increases gradually after weaning in adipose tissue of steers, but lags behind the elevation in desaturase gene expression (Martin et al., 1999). These data suggest that SCD activity is essential for subsequent development of lipogenic capacity of subcutaneous adipose tissue in growing steers. These whole-animal results are consistent with the cell culture data, in that SCD gene expression is highly expressed during adipocyte differentiation.

Casimir and Ntambi (1996) demonstrated that SCD gene expression increased immediately preceding lipid filling in murine 3T3-L1 preadipocytes, and we have demonstrated essentially identical results for bovine preadipocytes (Chung et al., 2006a; Figure 6). Stromal-

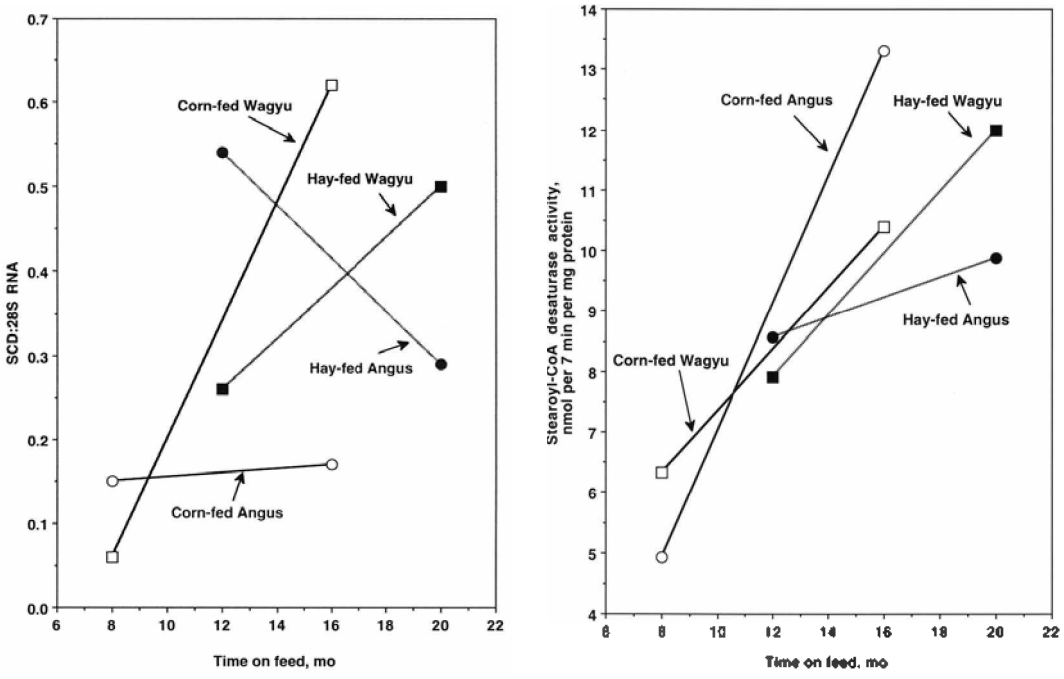

Figure 5. Stearoyl-CoA desaturase (SCD) gene expression (left) and catalytic activity (right) in subcutaneous adipose tissue of Angus and Wagyu steers fed corn- or hay-based diets. Adapted from Chung et al. (2007).

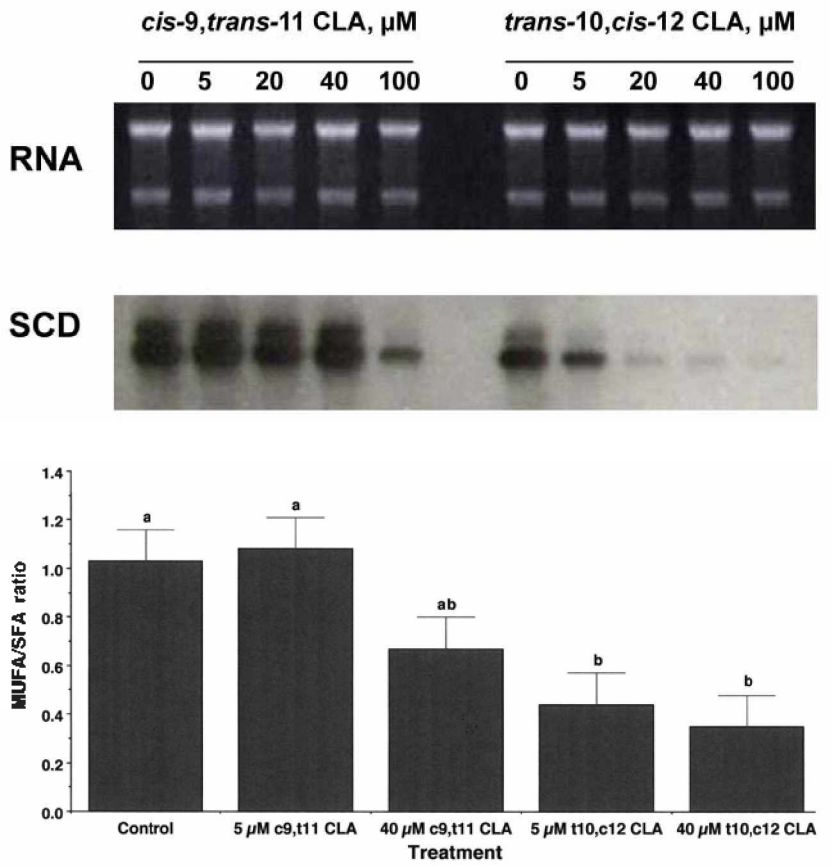

Figure 6. Stearoyl-CoA desaturase (SCD) gene expression (top) and the MUFA:SFA ratio (bottom) in bovine perirenal preadipocytes. Preadipocytes were differentiated in the presence of 5 μM pioglitizone, 10 μg/ml insulin, and DMEM. RNA from differentiated adipocytes was extracted after 7 d of treatment with differentiation medium, followed by 3 d of treatment with CLA. Reprinted with permission from Chung et al. (2006a).

vascular cells were obtained by collagenase treatment of perirenal adipose tissue from mature Angus steers, were plated at a density of 10^4 cells, and were grown to confluence. At confluence, the medium was supplemented either with insulin plus pioglitizone (a PPARγ agonist) or insulin alone. Prior to confluence, SCD mRNA was undetectable, but after 7 d of exposure to insulin plus pioglitizone, SCD mRNA was highly abundant.

Ntambi and coworkers demonstrated that the *trans*-10,*cis*-12 isomer of CLA strongly depresses SCD gene expression in hepatic and human breast cancer cell lines (Choi et al., 2001, 2002). In our bovine preadipocyte cell line, *trans*-10,*cis*-12 CLA nearly abolished SCD gene expression, whereas *cis*-9,*trans*-11 CLA was without effect except at the highest concentrations (Chung et al., 2006a). The *trans*-10,*cis*-12 isomer also strongly depressed lipid filling (Chung et al., 2006a). Consistent with reduction in SCD gene expression, *trans*-10,*cis*-12 CLA reduced the MUFA:SFA ratio for lipids from treated bovine adipocytes (Figure 6).

The depression of SCD gene expression by *trans*-10,*cis*-12 CLA is unusual in light of the fact that this CLA isomer is a product of rumen fermentation, and its accumulation would effectively block the conversion of TVA (a primary product of ruminal fermentation) to *cis*-9,*trans*-11 CLA. From a production standpoint, clearly any production practice that profoundly increases the formation and absorption of *trans*-10,*cis*-12 CLA from the digestive system will depress adipogenesis (including intramuscular adipose tissue development), and will cause adipose tissue lipids to become more saturated and contain less *cis*-9,*trans*-11 CLA.

Diet effects on fat and fatty acid composition

Changes in the ruminal environment in response to grain feeding also may contribute to the increase in MUFA in cattle fed high-grain diets. Kucek et al. (2001) demonstrated that increasing dietary forage increased duodenal flow of stearic acid and α-linolenic acid, but decreased the duodenal flow of oleic and linoleic acid. Protozoa contain high levels of TVA and palmitic acid (Devillard et al., 2006; Or-Rashid et al., 2007), and feeding a high-corn diet could lower rumen pH sufficiently to decrease protozoal populations. A prolonged reduction in

Table 2. Selected fatty acids (g/100 g total fatty acids) in marbling adipose tissue and digesta of steers fed a corn-based finishing diet from weaning, or grazed on native pasture and then fed a corn-based finishing diet

Item	Cattle group/diet[a]					
	Calves	Corn-fed	Corn-fed	Pasture	Pasture/corn	Pasture/corn
Age, months	8	12	16	12	16	18
Subcutaneous adipose tissue						
18:0	19.0	18.0	17.2	25.1	16.5	19.9
18:1*trans*-11	3.76	1.60	2.20	1.75	3.67	2.56
18:1n-9	30.7	38.4	37.6	30.7	36.2	37.2
18:2n-6	1.24	1.67	2.24	1.65	1.58	1.99
18:3n-3	0.62	0.05	0.08	0.00	0.14	0.13
18:2*cis*-9,*trans*-11	0.34	0.15	0.28	0.00	0.36	0.27
MUFA:SFA	0.66	0.86	0.84	0.56	0.80	0.79
Digesta						
18:0	34.8	33.5	29.6	42.1	34.5	25.9
18:1*trans*-11	1.61	1.60	0.91	2.54	3.60	1.91
18:1n-9	12.3	13.5	13.6	10.5	13.6	12.2
18:2n-6	7.1	10.6	16.1	9.1	11.2	15.1
18:3n-3	2.69	0.20	0.39	0.69	0.17	0.27
18:2*cis*-9,*trans*-11	0.00	0.00	0.27	0.00	0.08	0.17
MUFA:SFA	0.30	0.29	0.32	0.20	0.26	0.25

[a] All steers were weaned at 8 months of age. The corn-fed steers immediately were adapted to a corn/sorghum finishing diet and were sampled at 12 and 16 months of age. The pasture-fed steers grazed native pasture until 12 months of age, were adapted to the same corn/sorghum finishing diet, and were sampled at 16 and 18 months of age. The corn-fed steers at 16 months of age were the same body weight and had the same fat thickness over the 12th rib and USDA marbling scores as the pasture/corn steers at 18 months of age.

rumen pH also could cause reductions in the population of bacteria responsible for rumen biohydrogenation (Vossenberg and Joblin, 2003; Fukuda et al., 2006; Wallace et al., 2006).

Chung et al. (2006b) similarly demonstrated that the duodenal concentrations of stearic acid and TVA decreased, and linoleic acid and *cis*-9,*trans*-11 CLA increased, with increasing time on a corn-based, finishing diet. Thus, after some period of time on a corn-based, finishing diet, there is an apparent depression in the isomerization of linoleic acid to *cis*-9,*trans*-11 CLA as well as a decrease in the hydrogenation of *cis*-9,*trans*-11 CLA to TVA and hence to stearic acid. These changes in duodenal fatty acid concentrations are reflected in tissue fatty acid compositions (Chung et al., 2006b).

A recent study has provided similar results (Table 2). At 12 months of age, the concentration of stearic acid was lower, and oleic acid was concomitantly higher, in marbling adipose tissue of steers fed a corn-based diet for 4 months than in steers that had grazed native pasture for 4 months. SCD gene expression was virtually undetectable in adipose tissue of both weaned calves and in pasture-fed steers, but was highly expressed in adipose tissue of corn-fed steers (Figure 7), so differences in SCD activity between corn-fed and pasture-fed steers certainly contributed to differences in beef fatty acid composition. The concentration of α-linolenic acid was twofold higher in the digesta of the pasture-fed steers than in the corn-fed steers, and was higher in beef by 16 months of age in the pasture-fed steers. Waters et al. (2009) reported that SCD gene expression was

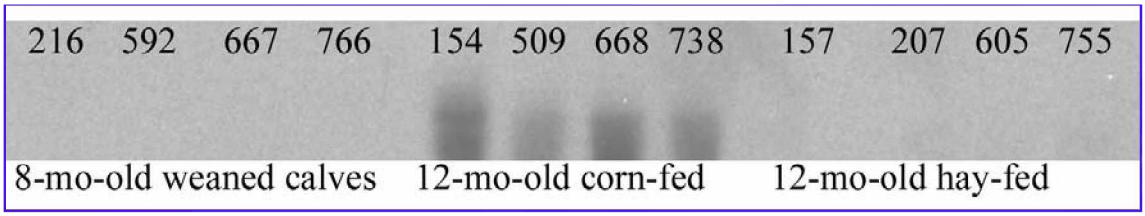

Figure 7. Northern blot of SCD mRNA from weaned Angus calf steers. Angus steers weaned at 8 months of age and then fed a corn-based finishing diet for 4 months (12-mo-old corn-fed) and Angus steers weaned at 8 months of age and then allowed to graze native pasture for 4 months (12-mo-old hay-fed). Numbers over lanes are individual animal numbers (M. A. Brooks and S. B. Smith, unpublished data).

Table 3. Fatty acid concentrations (g/100 g total fatty acids) of subcutaneous adipose tissues of 3/4 Angus progeny (n = 96) and 3/4 Brahman progeny (n = 103)

Item	Progeny[a]		SE	p-value
	3/4 Angus	3/4 Brahman		
Age, months	13	13		
14:0	3.03	3.01	0.06	0.85
14:1n-5	1.01	0.99	0.03	0.67
16:0	24.8	23.8	0.20	0.007
16:1n-7	3.81	3.59	0.06	0.08
18:0	13.4	13.6	0.27	0.67
18:1n-9	50.9	51.1	0.26	0.63
18:2n-6	2.75	3.46	0.18	0.04
18:3n-3	0.70	0.75	0.02	0.16
16:1:18:0	0.30	0.29	0.01	0.62
MUFA:SFA[b]	1.35	1.37	0.18	0.62

[a] Data are from S.B. Smith, C. Gill, S.K. Davis, J. Taylor, and D. K. Lunt (unpublished). Progeny were an equal mixture of steers and heifers produced by crossing Angus or Brahman bulls on Angus×Brahman or Brahman×Angus F1 cows, or by crossing Angus× Brahman or Brahman×Angus F1 bulls on Angus or Brahman cows. All possible progeny types are represented in approximately equal proportions.

[b] Monounsaturated:saturated fatty acid ratio = (14:1n-5+16:1n-7+18:1n-9)/(14:0+16:0+18:0).

depressed by supplementation of n-3 fatty acids (as fish oil) to bulls, and pasture feeding may similarly depress SCD gene expression by increasing the absorption of α-linolenic acid.

There also were marked differences in digesta fatty acids at 12 months of age between corn- and pasture-fed steers. As in marbling adipose tissue, digesta stearic acid was much higher in the 12-months-old steers that had grazed pasture than in corn-fed steers (Table 2). This difference disappeared after the pasture-fed steers were adapted to the corn-based diet, because the concentration of stearic acid decreased over time on the corn-based diet. Conversely, the concentration of linoleic acid increased over time on the corn-based diet. These data provide additional evidence that grain-based diets alter ruminal microflora, which ultimately may impact the fatty acid composition of beef.

Although pasture feeding increases the relative proportion of n-3 PUFA in beef, it also decreases the total amount of lipid (e.g., Lunt et al., 2005). The net effect is that pasture feeding increases n-3 PUFA by only milligram amounts in beef, but decreases MUFA by gram quantities. Thus, this fat is harder and may be less healthful than beef from concentrate-fed cattle.

Breed type effects on fat and fatty acid composition

The data in Table 1 suggest that breed types differ in their ability to accumulate MUFA in their adipose tissues. Huerta-Leidenz et al. (1993, 1996) reported that subcutaneous adipose tissue from Brahman cows and steers contain a greater proportion of MUFA, and less SFA, than adipose tissue from Hereford steers when the cattle are raised under identical production systems. Malau-Aduli et al. (1997, 1998) reported differences in muscle and adipose tissue lipids of Jersey and Limousin cattle, and Pitchford et al. (2002) subsequently provided estimates of genetic parameters for fatty acids using the complete set of fat traits from the Australian Southern Crossbreeding Project. These reports provided additional support for a genetic basis in the variation in fatty acid composition in beef. Taylor et al. (1998) identified a quantitative trait locus for saturated and monounsaturated fatty acid composition of subcutaneous fat located at 18 centimorgans from the centromere on bovine chromosome BTA19. Adipose tissue of steers that were homozygous for Angus alleles at that locus possessed 2.4% less stearic acid and 3.7% more oleic acid than steers that were homozygous for Brahman alleles at that locus. These earlier studies demonstrated that there were breed type differences in fatty acid composition between *Bos indicus* and *Bos taurus* cattle. However, whereas Huerta-Leidenz et al. (1993, 1996) indicated that adipose tissues from *Bos indicus* cattle were less saturated than those from *Bos taurus* cattle, the opposite was reported by Taylor et al. (1998). Using the same base population as Taylor et al. (1998), we observed that subcutaneous adipose tissue of 3/4 Brahman progeny contained less palmitic acid than 3/4 Angus progeny from Angus and Brahman backcrosses, but there was no differences between progeny groups in MUFA:SFA ratios (Table 3). Interpretation of studies like these is confounded by the relatively small differences in individual fatty acids between *Bos indicus* and *Bos taurus* breed types, as well as large variation in production conditions and carcass characteristics across studies. For example, in all of the studies cited above, beef

from *Bos indicus* cattle contained less intramuscular lipid than the *Bos taurus* cattle, and the marbling adipocytes of the *Bos indicus* cattle were likely in an earlier stage of differentiation than those of the *Bos taurus* cattle.

Much larger differences have been reported between Japanese Black and Korean cattle, as compared to cattle produced in the U.S. (Sturdivant et al., 1992; May et al., 1993; Chung et al., 2006b; Table 1). Japanese Wagyu and Korean Hanwoo cattle share a common ancestry, and they both exhibit high MUFA:SFA ratios in their muscle and adipose tissues (Jung and Choi, 2003). In both Japan and Korea, cattle are fed to 28 to 30 months of age and over 600 kg body weight. It appears that the greater marbling and total MUFA in beef from Japanese and Korean cattle is due to breed type (i.e., genetic) differences in SCD gene expression, as well as their extensive time on feed.

CONCLUSIONS

Wide variation in the amount of intramuscular lipid (i.e., marbling) and fatty acid composition of beef from grain-fed cattle has been observed across a number of countries. In the U.S., Japan, and Korea, monounsaturated fatty acids accumulate in adipose tissue in cattle fed high-concentrate, finishing diets. This coincides with an increase in SCD gene expression and/or catalytic activity, which is exaggerated in Korean Hanwoo and Japanese Black cattle. These cattle not only have a greater genetic tendency to produce more MUFA, but also are fed for longer periods of time. When cattle graze pastures or are fed hay, their beef contains less marbling, much less monounsaturated fatty acids, but contains slightly more n-3 polyunsaturated fatty acids. Additionally, any production practice that elevates *trans*-10,*cis*-12 conjugated linoleic acid in bovine adipose tissue likely will reduce intramuscular adipose tissue development. Of the three factors that influence beef total fat and fatty acid composition, age, diet, and breed type, breed type has the smallest effect.

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