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REVIEW ARTICLE

Adiposity, fatty acid composition, and delta-9 desaturase activity during growth in beef cattle

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ABSTRACT

Oleic acid (18:1n-9) is the most abundant fatty acid in bovine adipose tissue. Because most of the lipid in bovine muscle is contributed by intramuscular adipocytes, oleic acid also is the predominant fatty acid in beef. In many species, the concentration of oleic acid in adipose tissue is dictated by the average concentration of oleic acid in the diet, but in ruminant species such as beef cattle, oleic acid is hydrogenated largely to stearic acid by ruminal microorganisms. In these species, the concentration of oleic acid in adipose tissue is dependent upon the activity of Δ^9 desaturase, encoded by the stearoyl coenzyme A desaturase (SCD) gene. Expression of the SCD gene is essential for bovine preadipocyte differentiation, and desaturase gene expression and catalytic activity increase dramatically as adipose tissue mass increases after weaning. Feeding a hay-based diet to American Wagyu steers to a typical Japanese bodyweight endpoint (650 kg) markedly stimulated desaturase enzyme activity as well as the accumulation of both oleic acid and intramuscular lipid, but the increase in oleic acid and intramuscular lipid was much less in hay-fed Angus steers. Increasing the concentration of oleic acid improves the palatability and healthiness of beef, and Korean Hanwoo and Japanese Black (and American Wagyu) seem especially well adapted to accumulate oleic acid in their adipose tissue.

Key words: *adiposity, beef cattle, fatty acids, stearoyl coenzyme A desaturase.*

INTRODUCTION

Early research demonstrated that the concentration of oleic acid (18:1n-9) in beef is positively correlated with its overall palatability (Waldman *et al*. 1968; Westerling & Hedrick 1979). This may be related to fat softness, because beef lipids enriched with oleic acid have lower melting points (Smith *et al*. 1998; Wood *et al*. 2004; Chung *et al*. 2006b). There also is a growing body of information to indicate that increasing the intake of oleic acid (usually as olive or canola oil) reduces risk factors for metabolic disease in humans (Baggio *et al*. 1988; Grundy *et al*. 1988; Kris-Etherton *et al*. 2002). Oleic acid is the most abundant fatty acid in US beef (Waldman *et al*. 1968; Westerling & Hedrick 1979; St John *et al*. 1987), and it is especially elevated in beef from Japanese Black cattle (Mitsuhashi *et al*. 1988; Sturdivant *et al*. 1992; Oka *et al*. 2002) and the closely related American Wagyu (May *et al.* 1993; Chung *et al*. 2006b) and the Korean Hanwoo (Jung & Choi 2003).

In the USA, there is no economic incentive to produce beef that is higher in oleic acid. Under the US Department of Agriculture (USDA) beef grading system, carcass value is determined primarily by the abundance of marbling adipose tissue (USDA 1997). In Japan, fat softness as well as marbling abundance are important components of beef carcass quality grade (JMGA 1988). Stearic acid (18:0) is one of the main fatty acids that dictate fat hardness (Smith *et al*. 1998; Wood *et al*. 2004; Chung *et al*. 2006b), so any dietary or production factor that increases the

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conversion of stearic acid to oleic acid will increase fat softness. The enzyme responsible for the conversion of all saturated fatty acids (SFA) to their respective monounsaturated fatty acids (MUFA) is Δ^9 desaturase. This enzyme, which is encoded by the stearoyl coenzyme A desaturase (SCD) gene, also may convert *trans*-vaccenic acid (18:1*trans*-11) to its corresponding conjugated linoleic acid (CLA) isomer, 18:2cis-9,*trans*-11.

Due to the contribution of fat softness to Japanese beef quality and the importance of the Japanese market, investigators from the USA, Korea and Australia are focusing their research on the dietary modification of Δ^9 desaturase gene expression and enzyme activity. This review will address the relationship between adiposity and fatty acid composition in the adipose tissues of beef cattle raised in the USA, Australia, Japan and Korea.

DELTA-9 DESATURASE GENE EXPRESSION IN BOVINE PREADIPOCYTES

Twenty years ago, Casimir and Ntambi (1996) demonstrated that Δ^9 desaturase gene expression increases immediately preceding lipid filling in murine 3T3-L1 preadipocytes. We recently demonstrated essentially identical results for bovine preadipocytes (Chung *et al*. 2006a; Fig. 1). Stromal-vascular cells were obtained by collagenase treatment of perirenal adipose tissue from mature Angus steers, plated at a density of 10^4 cells and grown to confluence. At confluence, the medium was supplemented either with insulin plus pioglitizone (a PPARγ agonist) or insulin alone. Prior to confluence, Δ^9 desaturase (SCD) mRNA was undetectable (Fig. 1), but after 7 days of exposure to insulin ± pioglitizone, Δ^9 desaturase mRNA was highly abundant.

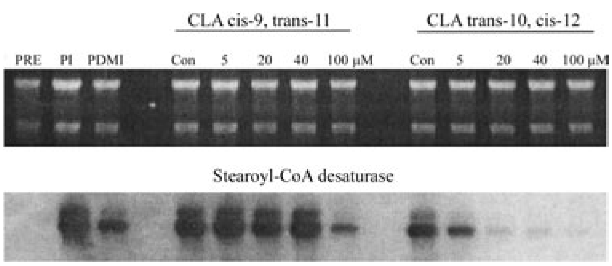

Figure 1 Stearoyl-CoA desaturase and fatty acid synthase gene expression in Angus preadipocytes at confluence, predifferentiated (PRE); differentiated in the presence of 5 μmol/L pioglitizone, 10 μg/mL insulin, and Dubelco's modified eagle medium (DMEM) (PI); or differentiated with PI plus 1 μg/mL dexamethasone (PDMI). In lanes 4–10, preadipocytes were differentiated for 7 days with PI in the presence of *cis*-9,*trans*-11or *trans*-10,*cis*-11 CLA. CLA, conjugated linoleic acid. Derived from data in Chung *et al*. (2006a).

Ntambi and coworkers have 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 the latter system, the *cis*-9,*trans*-11 CLA isomer also inhibited SCD gene expression (Choi *et al*. 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; Fig. 1). The *trans*-10,*cis*-12 isomer also strongly depressed lipid filling (not shown; 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 (not shown).

This is of considerable interest in livestock production. Feeding mixed isomers of CLA to pigs depressed adipose tissue Δ^9 desaturase activity (Smith *et al*. 2002), which caused a dramatic increase in the concentration of stearic acid and a concomitant, 10°C increase in melting point in adipose tissue lipids (King *et al*. 2004). In spite of this, several investigators, including ourselves, are working to establish production conditions that will increase the concentration of *trans*-10,*cis*-12 CLA in beef (e.g. Duckett *et al*. 2002; Archibeque *et al*. 2005). While this may reduce carcass adiposity, it also will reduce the accumulation of marbling and may increase fat hardness.

FATTY ACID COMPOSITION AND FAT HARDNESS

The fatty acid composition of beef and its associated adipose tissues (subcutaneous, seam, and marbling) has been reported in a large number of studies spanning over 40 years. Gas/liquid chromatography of fatty acid methyl ester derivatives of tissue fatty acids is the method of choice, based on its high reproducibility and relatively low cost. Many of the investigators, including ourselves (e.g. St John *et al*. 1987) originally used packed columns that were typically 15–25 m in length and provided only modest separation of the fatty acid methyl ester peaks. The primary shortcoming of these was their inability to separate the various 18-carbon MUFA. Thus, values reported for oleic acid also included significant quantities of 18:1*trans*-11 and 18:1n-7 (the latter being the elongation product of 16:1n-7, palmitoleic acid). In addition, values for palmitoleic acid may have included 17:0, and 17:1n-8 frequently was combined with other, minor peaks. Identification of the various 18-carbon MUFA, in addition to other less abundant fatty acids, was made possible by the development of the capillary columns of up to 100 m in length. Fatty acid compositions such as those reported in Table 1 now include most of the known fatty acids present in bovine adipose tissue in reasonable abundance.

Adipose tissue fatty acids typically become less saturated between weaning and slaughter in cattle that are fed a grain-based diet (Table 1; Huerta-Leidenz *et al*. 1996; Chung *et al*. 2006b). The MUFA : SFA ratio increases from 0.66 to 0.86 between weaning and 16 months of age, primarily due to an increase in oleic acid. There was no increase in the MUFA : SFA ratio in cattle fed hay-based diets; small decreases in myristic (14:0) and palmitic acid (16:0) are offset by reciprocal increases in stearic acid (18:0). The lesser MUFA : SFA ratio in the hay-fed steers, relative to corn-fed steers, suggests that some component of the hay diet caused a depression in Δ^9 desaturase activity. This was demonstrated recently in sheep fed concentrate- and forage-based diets (Daniel *et al*. 2004). There was a greater accumulation of oleic acid and a higher ratio of SCD to acetyl-CoA carboxylase mRNA in the adipose tissue of concentrated-fed sheep than in forage-fed sheep.

Wood *et al*. (2004) demonstrated the positive correlation between lipid melting points and the percentage of stearic acid in lamb subcutaneous adipose tissue. A more recent study (Chung *et al*. 2006b) provided additional support for the strong relationship between stearic acid and slip points in bovine adipose tissue (Fig. 2). Variation in fatty acid saturation dictates fat firmness, which in turn affects the economics of meat processing and the consumer acceptance of meat (Perry *et al*. 1998). Smith *et al*. (1998) demonstrated large increases in melting points (estimated as slip points) as the percentage of stearic acid increased in subcutaneous adipose tissue lipids in cattle raised in Japan and Australia. Adipose tissue lipids from Japanese Black cattle raised in Japan contained less than 8% stearic acid, with an average slip point of 22.8°C (Table 1). Mitsuhashi *et al*. (1988) previously reported that, in Japanese Black cattle, the melting point of adipose tissue lipids decreased from 35.5°C in 14-month-old steers to 21.2°C in 28-month-old steers, and suggested that melting point may be controlled by Δ^9 desaturase. Adipose tissue lipids of other breed types raised in Australia contained over 25% stearic acid, with an average slip point of 45.1°C (Smith *et al*. 1998).

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

Item	Cattle group/diet†					
	Angus/weaned‡	Angus/corn§	Angus/hay§	Australian¶	Japanese Black¶	Hanwoo††
Age (months)	8	16	20	22	27 (est.)	28
14:0	5.9	3.9	3.7	1.5	1.3	3.2
14:1n-5	1.4	1.1	0.9	0.1	1.3	1.0
16:0	31.8	29.2	30.7	24.2	24.2	27.9
16:1n-7	2.7	3.1	2.5	1.6	5.2	4.6
17:0	1.6	0.5	1.0	1.3	0.4	0.7
17:1n-8	0.8	0.3	0.4	0.1	1.1	NR
18:0	18.3	17.1	22.0	26.1	7.6	9.6
18:1*trans*-11	3.6	2.1	2.6	2.3	0.7	NR
18:1n-9	32.9	39.8	34.6	39.8	52.9	47.3
18:1n-7	0.8	0.7	0.8	1.0	3.0	NR
18:2n-6	0.9	2.7	1.7	1.6	2.0	4.2
18:3n-3	0.4	0.0	0.3	0.5	0.2	0.4
18:2*ci*-9,*trans*-11	0.8	0.3	0.4	NR	NR	NR
18:2*trans*-10,*cis*-12	0.2	0.1	0.1	NR	NR	NR
16:1:18:0	0.17	0.19	0.11	0.06	0.68	0.48
MUFA : SFA	0.66	0.86	0.66	0.77	1.86	1.28

†The Angus and Hanwoo steers were weaned at 8 months of age. The age of the Japanese Black steers is estimated, based on typical production conditions in Japan. ‡Data are unpublished data. §Data are from Chung *et al*. (2006b). ¶Data are from Smith *et al*. (1998). ††Data are from Jung and Choi (2003). est., estimated; MUFA, monounsaturated fatty acids (14:1n-5, 16:1n-7, 17:1n-8, 18:1n-9 and 18:2*cis*-9,*trans*-11); NR, not reported; SFA , saturated fatty acids (14:0, 16:0, 17:0, 18:0 and 18:1*trans*-11).

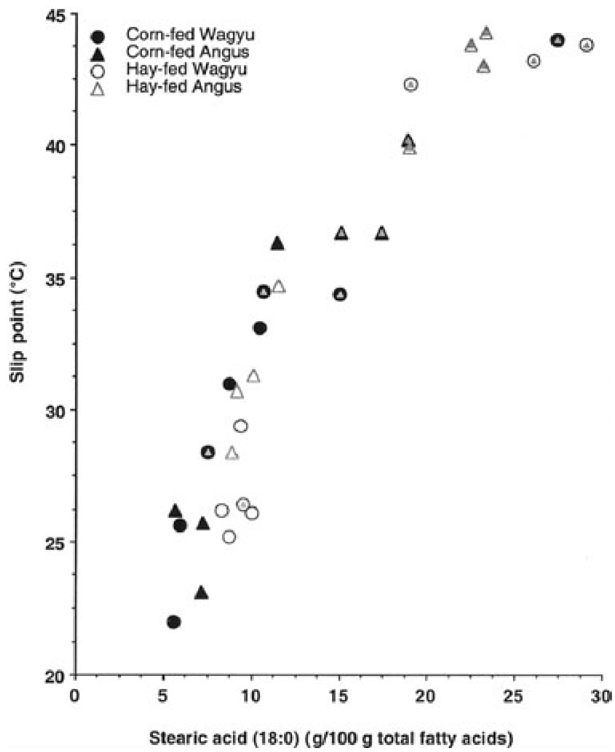

Figure 2 Slip points as a function of the concentration of stearic acid (18:0) in subcutaneous adipose tissue of Angus and Wagyu steers fed corn-based or hay-based diets to US or Japanese endpoints. Symbols for the cattle raised to the US endpoint contain shaded triangles. Reproduced with permission from Chung *et al*. (2006b).

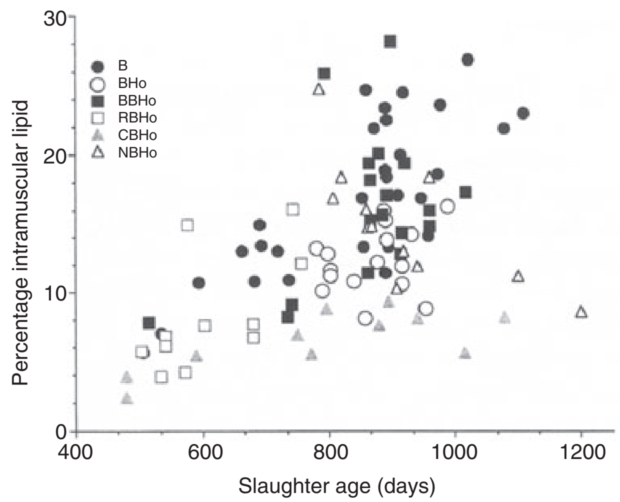

Figure 3 Percentage of intramuscular lipid as a function of slaughter age. B, Japanese Black; BBHo, Japanese Black × Japanese Black/Holstein; BHo, Japanese Black × Holstein; CBHo, Charolais × Japanese Black/Holstein; NBHo, Japanese Shorthorn × Japanese Black/Holstein; RBHo, Japanese Brown × Japanese Black/Holstein. Reproduced with permission from Zembayashi *et al*. (1999).

These particular Australian cattle had been fed a grain-based diet (which did not include corn), supplemented with 10% whole cottonseed; it has been suggested that sterculic acid contained in the whole cottonseed depressed Δ^9 desaturase activity (Page *et al*. 1997; Smith *et al*. 1998; Yang *et al*. 1999). However, long-fed cattle under Australian production systems now produce adipose tissue lipid with stearic acid concentrations of 8–10% (R.K. Tume, unpubl. data, 2006).

FATTY ACID COMPOSITION OF BEEF AT DIFFERENT STAGES OF GROWTH

A MUFA : SFA ratio of nearly 1.2 can be achieved in Angus steers fed a hay-based diet for 16 months past weaning to 24 months of age (Table 1; Chung *et al*. 2006b). However, cattle fed in Australia in excess of 400 days achieved a MUFA : SFA ratio of only 0.77, and stearic acid was markedly elevated in their adipose tissue lipids (Smith *et al*. 1998). Japanese Black cattle fed roughage/grain diets can attain MUFA : SFA ratios approaching 2:1 (Table 1; Sturdivant *et al*. 1992; May *et al*. 1993; Zembayashi *et al*. 1995; Chung *et al*. 2006b).

The Japanese Wagyu breed types share a common ancestry with the Korean Hanwoo. About 6000 years ago, cattle that originated in China migrated into the Korean peninsula, after which they were brought to Japan. The cattle originally were brown or black; Koreans selected for cattle with brown coats, whereas both black and brown cattle lines of the original (native) cattle persist in Japan (S. Takeda, pers. comm., 2006). Because Japanese Wagyu and Korean Hanwoo cattle share a common ancestry, they both exhibit high MUFA : SFA ratios in their muscle and adipose tissues (Table 1; Jung & Choi 2003). In both countries, cattle are fed to 28–30 months of age to over 600 kg bodyweight. How much of the greater MUFA : SFA ratio in Japanese and Korean cattle is due to breed type (i.e. genetic) differences in SCD gene expression, and how much is caused by their larger bodyweights and/or extensive time on feed?

The concentration of intramuscular lipid in longissimus muscle can be as low as 3% in beef from steers fed for the US market, to over 30% in Japanese Black or American Wagyu cattle fed for the Japanese market (Fig. 3; Lunt *et al*. 1993, 2005; Zembayashi 1994;

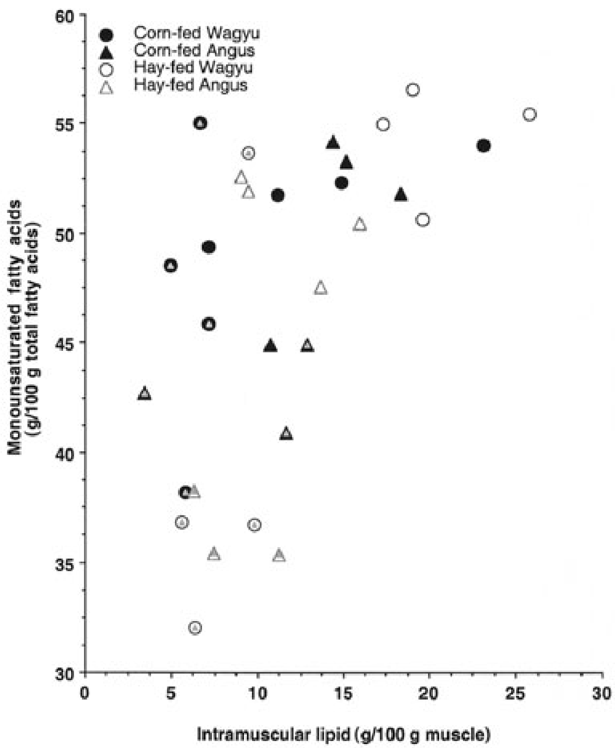

Figure 4 Relationship between total monounsaturated fatty acids in subcutaneous adipose tissue and percentage intramuscular lipid in longissimus muscle from Wagyu and Angus steers fed corn-based or hay-based diets to US or Japanese endpoints. Symbols for the cattle raised to the US endpoint contain shaded triangles. Overall: $y = 0.75x + 38.3$; $R^2 = 0.338$; $P < 0.01$. Derived from data in Lunt *et al*. (2005) and Chung *et al*. (2006b).

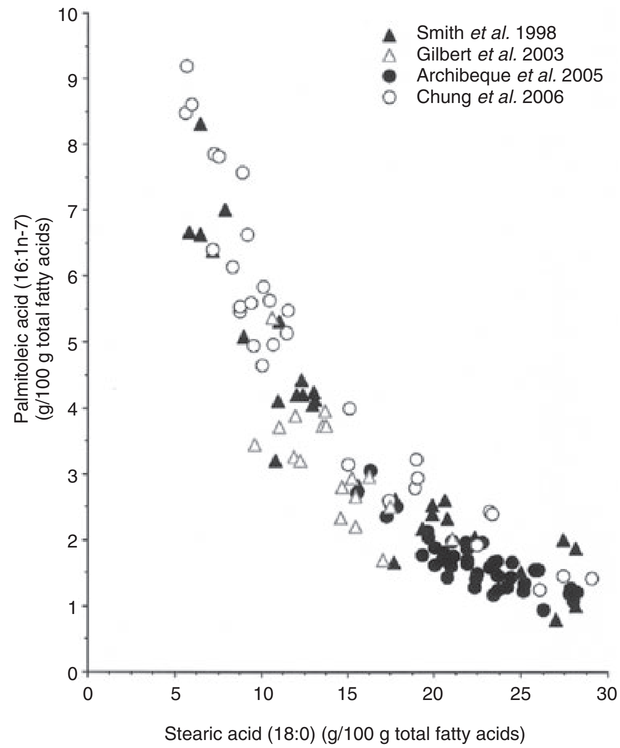

Figure 5 Relationship between stearic acid (18:0) and palmitoleic acid (16:1n-7) in subcutaneous adipose tissue lipids of cattle raised in Australia and Japan (Smith *et al*. 1998) or in the USA (Gilbert *et al*. 2003; Archibeque *et al*. 2005; Chung *et al*. 2006b). The cattle raised in Australia were crossbred Murray Grey, Angus and Grey Brahman steers fed a grain-based diet for a minimum of 400 days, whereas those raised in Japan were Murray Grey and Japanese Black fed for approximately 570 days. The cattle raised in the USA were Brangus (Gilbert *et al*. 2003), Angus (Archibeque *et al*. 2005; Chung *et al*. 2006b), or American Wagyu (Chung *et al*. 2006b).

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 more than 50% of total adipose tissue fatty acids (Table 1 and Fig. 4; Chung *et al*. 2006b).

Data taken from a number of studies indicate that there is a strong, negative correlation between palmitoleic acid (16:1n-7) and stearic acid (Smith *et al*. 1998; Gilbert *et al*. 2003; Archibeque *et al*. 2005; Chung *et al*. 2006b; Fig. 5). In these studies, samples were collected from a variety of breed types fed diets varying widely in concentrates and roughage, and the cattle were sampled between 14 and approximately 30 months of age. It is remarkable that such a strong relationship occurs between palmitoleic acid and stearic acid, regardless of breed type, diet, or age. Because palmitoleic acid occurs at sparingly low levels in the diet, its concentration in adipose tissue is dictated primarily by the activity of Δ^9 desaturase. The high, negative correlation between palmitoleic acid and stearic acid further suggested that the concentration of stearic acid also is determined by the activity of Δ^9 desaturase, rather than by the diet.

CHANGES IN ADIPOSE TISSUE Δ^9 DESATURASE GENE EXPRESSION/ ACTIVITY DURING GROWTH

In many species, the concentration of oleic acid in adipose tissue reflects the average concentration of oleic acid in the diet, but in ruminant species such as beef cattle, oleic acid is hydrogenated largely to stearic acid by ruminal microorganisms (Ekeren *et al*. 1992). As is the case for palmitoleic acid, the concentration of oleic acid in bovine adipose tissue is dependent upon the activity of Δ^9 desaturase.

Research from the 1990s demonstrated that bovine adipose tissue had considerably higher Δ^9 desaturase enzyme activity (St John *et al.* 1991; Chang *et al.* 1992) and gene expression (Cameron *et al.* 1994) than muscle, liver, or intestinal mucosa. This was confirmed by Archibeque *et al.* (2005), who also demonstrated that subcutaneous adipose tissue had approximately twice the Δ^9 desaturase catalytic activity of intramuscular adipose tissue. This was consistent with a higher concentration of MUFA in subcutaneous tissue than in intramuscular adipose tissue (Archibeque *et al.* 2005).

Expression of the Δ^9 desaturase gene increased profoundly between weaning and 12 months of age in subcutaneous adipose tissue of Angus steers (Martin *et al.* 1999; Fig. 6). Similarly, Lee *et al.* (2005) observed peak SCD mRNA at 12 months of age in muscle from Hanwoo steers. The rate of *de novo* fatty acid biosynthesis increased gradually in the adipose tissue of Angus steers, but lagged behind the elevation in desaturase gene expression (Martin *et al.* 1999). These data suggest that desaturase activity is essential for the subsequent development of lipogenic capacity of subcutaneous adipose tissue in growing steers. These whole-animal results are consistent with the cell culture data presented above, in that desaturase gene expression was highly expressed during adipocyte differentiation.

There was a large increase in subcutaneous adipocyte volume between birth and weaning (Fig. 6) although *de novo* fatty acid biosynthesis remained depressed. Both phenomena are caused by the intake of milk fat in the preweaned calves. During this time, there was no significant change in Δ^9 desaturase gene expression. Between the period of 7.5 and 12 months of age, the calves of Martin *et al.* (1999) were moved to native pasture. As a result of this postweaning reduction in energy intake, there was a depression in the adipocyte volume, but desaturase gene expression increased markedly. These results indicate that desaturase gene expression was independent (at least to some degree) of energy intake, and may be more dependent on the postweaning weight or age of the steers.

A recent study demonstrated the interaction between diet and time on feed for Δ^9 desaturase catalytic activity in cattle raised to US or Japanese endpoints (Fig. 7; Chung *et al.* 2005; Lunt *et al.* 2005). The cattle were fed either a hay-based diet, supplemented

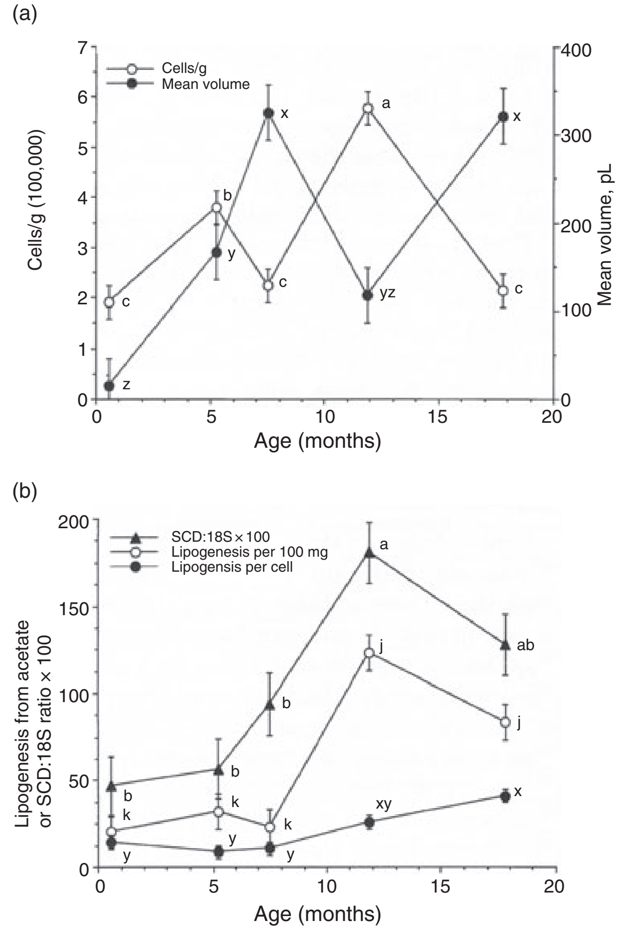

Figure 6 Changes in cellularity, lipogenesis and stearoyl coenzyme A desaturase (SCD) gene expression during growth in preweaning (2.5 weeks to 7.5 months) and postweaning Angus steers. (a) Mean values for number of adipocytes per gram of adipose tissue and adipocyte volumes. (b) Lipogenesis and SCD gene expression. Overall standard errors of the means are affixed to the symbols for each item. [abcjkxyz]Values within a measurement with the same superscripts were not different ($P > 0.05$). Reproduced with permission from Martin *et al.* (1999).

with corn to provide 0.9 kg/day average daily gain; or a corn-based diet, which provided 1.36 kg/day average daily gain. The cattle were raised to a constant bodyweight within endpoint, such that steers raised to the US endpoint (8 and 12 months on feed) were sampled at 490 kg live weight and steers raised to the Japanese endpoint (16 and 20 months on feed) were sampled at an average weight of 625 kg (Lunt *et al.* 2005). The corn-fed Angus steers fed to the Japanese endpoint were excessively fat, with 2.51 cm fat thickness over the 12th thoracic rib, whereas the corn-fed Wagyu

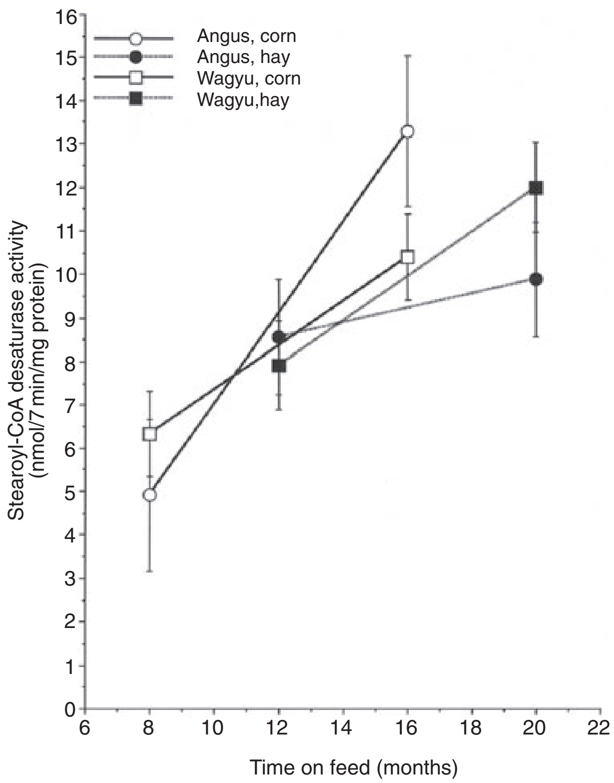

Figure 7 Changes in stearoyl-CoA desaturase (Δ^9 desaturase) enzyme activity with time on feed in subcutaneous adipose tissue of Angus and Wagyu steers fed either a corn-based diet or a hay-based diet. There was a significant endpoint ($P = 0.01$) effect for desaturase activity, and there tended to be significant diet × endpoint ($P = 0.08$) and breed × diet × endpoint ($P = 0.08$) effects. Desaturase activity increased between the US and Japanese endpoints, but not in hay-fed Angus steers. Pooled standard errors for the diet–endpoint interaction are attached to the symbols. Derived from data in Chung *et al*. (2005).

steers fed to the Japanese endpoint were considerably leaner, with only 1.53 cm fat thickness over the 12th rib (Lunt *et al*. 2005).

Desaturase enzyme activity increased in adipose tissue with time on feed in all but the hay-fed Angus steers (Fig. 7). The pattern change of desaturase enzyme activity over time was reflected in the final MUFA : SFA ratios for adipose tissue samples from the corn-fed Wagyu and Angus steers and hay-fed Wagyu and Angus steers (1.40, 1.39, 1.41, and 1.18, respectively; Chung *et al*. 2006b). Marbling scores and subcutaneous fat thickness at the 12th thoracic vertebrae also were strongly depressed in the Angus steers fed hay to the Japanese endpoint (Lunt *et al*. 2005). It was concluded from these studies that American Wagyu steers perform as well on a high roughage (hay/corn) diet as they do on a low roughage, corn-based diet; Angus steers do not. The study of Martin *et al*. (1999) measured desaturase gene expression only up to 18 months of age. The data in Figure 7 indicate that desaturase activity continued to increase up to 24 months of age in corn-fed steers, and up to 28 months of age in hay-fed Wagyu steers.

CONCLUSION

A wide variation in the fatty acid composition of adipose tissue from grain-fed cattle, which markedly influences the hardness of the fat in their beef, has been observed across a number of countries. In the USA, adipose tissue accumulates monounsaturated fatty acids, which coincides with an increase in Δ^9 desaturase gene expression and catalytic activity. This is exaggerated in Korean Hanwoo and Japanese Black (and American Wagyu) cattle, which not only have a greater genetic tendency to produce more monounsaturated fatty acids, but which are also fed for longer periods of time. Conversely, in those instances in which Australian beef cattle were fed grain-based diets containing significant levels of whole cottonseed for extended periods of time, the adipose tissue exhibited depressed Δ^9 desaturase activity and unusually high concentrations of stearic acid.

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