CARCASS CHARACTERISTICS, FATTY ACIDS, STEAROYL-COA DESATURASE GENE EXPRESSION AND SENSORY EVALUATION OF CALF-FED AND YEARLING-FED ANGUS STEERS

A Thesis

by

MATTHEW ALAN BROOKS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2007

Major Subject: Nutrition

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Approved by:

Chair of Committee,	Stephen B. Smith
Committee Members,	Guoyao Wu
	John E. Bauer
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ABSTRACT

Carcass Characteristics, Fatty Acids, Stearoyl-CoA Desaturase Gene Expression and Sensory Evaluation of Calf-fed and Yearling-fed Angus Steers. (December 2007)

Matthew Alan Brooks, B.S., Cornell University

Chair of Advisory Committee: Dr. Stephen B. Smith

There is a growing interest in documenting the effect of diet on the ability to convert saturated fatty acids (SFA) to monounsaturated fatty acids (MUFA) by modulating expression of the SCD gene. We propose that if cattle were raised to a constant body weight, their MUFA:SFA ratio will be the same regardless of being calf-fed (CF) or yearling-fed (YF). Twenty-four Angus cattle were acquired for this study. Cattle were slaughtered at weaning at 8 mo of age (SFCF, n=4), eight steers were assigned to the CF group and slaughtered at 12 mo of age (MFCF, n=4) and 16 mo of age (LFCF, n=4). Twelve cattle were assigned to the YF group and slaughtered at 12 mo of age (SFYF, n=4) 16 mo of age (MFYF, n=4) and market weight of 525 kg (LFYF, n=4). Cattle were then statistically analyzed based on time on high energy diet. Fatty acids from digesta, plasma, liver, *L. dorsi*, and s.c. and i.m. adipose tissue were all analyzed by FAME. In s.c. 18:1 and 16:1 were greatest in LFCF (41.27% and 5.58%, respectively, $P = 0.05$), and 18:0 and 16:0 did not differ between groups ($P > 0.10$). MUFA:SFA ratios of s.c. tended to be higher in LFCF animals (1.26) vs. LFYF (1.06, $P = 0.10$). However, there was no difference seen when comparing CF to YF animals ($P = 0.26$). MUFA:SFA ratio was higher in i.m. ($P = 0.03$) and also increased with age ($P < .01$). A trained sensory

panel saw no significant differences between palatability of flavor characteristics of cooked steaks from LFCF, MFYF, or LFYF ($P > 0.05$). We showed increased SCD gene expression in the LFYF (248.41 to 1528.69 SCD/GAPDH, $P = 0.01$). Expression was higher in YF ($P = 0.04$), but their initial deposits of SFA, combined with the lack of SCD expression while on pastures, prevented the MUFA:SFA ratio from increasing at a rate fast enough to change the final ratios in the animal.

DEDICATION

I dedicate this thesis and all the work that went into it to my beautiful and loving wife, Stephanie. It is her encouragement, support, commitment, love and faith in me that has kept me going every day.

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NOMENCLATURE

AHA	American Heart Association
AMSA	American Meat Science Association
AOAC	Association of Official Analytical Chemists
C/EBP	CCAAT/enhancer-binding protein
CVD	Cardiovascular disease
CLA	Conjugated Linoleic Acid
FAME	Fatty acid methyl ester/esterification
GAPDH	Glyceraldehyde 3-phosphate dehydrogenase
HDL	High density lipoprotein
i.m.	Intramuscular adipose tissue
LCFA	Long-chain fatty acid
LD	*Longissimus dorsi*
LDL	Low density lipoprotein
MeOH	Methanol; Methyl alcohol
MUFA	Monosaturated fatty acid
NMR	Nuclear Magnetic Resonance
PPAR	Peroxisome proliferator activated receptor
PUFA	Polyunsaturated fatty acid
s.c.	Subcutaneous adipose tissue
SCD	Stearoyl coenzyme A desaturase
SFA	Saturated fatty acid

SDS	Sodium dodecyl sulfate
SSC	Trisodium citrate dihydrate
TG	Triglycerides
UFA	Unsaturated fatty acids
VLDL	Very low density lipoprotein

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INTRODUCTION

With the growing interest by the beef industry in providing a healthier product, it is apparent that different feeding strategies can lead to alterations in the quality of the fatty acid composition in beef. The beef industry can optimize their management strategies to raise cattle to produce beef that is higher in monounsaturated fatty acids (MUFA) and lower in saturated fatty acids (SFA) and thus a healthier product for the general public. This will also affect fat softness, color and palatability, which leads to a more desirable product for both domestic and foreign markets.

In beef, most of the MUFA are created by the conversion of SFA in the adipose tissue of the animal. This function is regulated by the stearoyl-CoA desaturase gene (SCD, Δ^9) (Miyazaki and Ntambi, 2003; St. John et al., 1991). Difficulties with producing higher expression of SCD in *Bos taurus* cattle lie in the fact that it generally requires feeding the cattle diets that consist of high-energy corn-based feeds for longer periods of time. The cost to the producer for such diets is increasing as the demand for corn increases due to bio-ethanol production. However, there is evidence the expression of the SCD gene can also be affected by the age of the animal, in that older animals have been shown to have a higher ratio of MUFA:SFA (Chung et al., 2006). Therefore, if an animal was fed a lower-energy pasture-based diet before being placed on this high-energy corn-based diet, the SCD gene would be able to more efficiently convert MUFA to SFA and thus increase the MUFA:SFA ratio while decreasing the amount of time on the high-energy corn-based diet.

This thesis follows the style and format of the Journal of Animal Science.

A product produced with a higher MUFA:SFA ratio would be able to provide domestic consumers with a fatty acid profile that is more in-line with the recent changes in the American Heart Association (AHA) guidelines (Krauss et al., 2000). These changes call for a greater percentage of MUFA than polyunsaturated fatty acids (PUFA) and SFA. MUFA have shown to have the ability to lower low-density lipoprotein (LDL) levels without lowering high-density lipoprotein (HDL) levels (Grundy et al., 1988; Mensink and Katan, 1989). These effects show the preventative effects of MUFA towards cardiovascular disease (CVD) (Kris-Etherton et al., 2002).

Along with beneficial health effects, applications for this type of product can be applied to the Asian markets, specifically the Japanese and Korean markets. These markets put great economical value in beef that contains a softer fat with larger amounts of marbling throughout the whole muscle meats (Kim, 2003; Lin and Mori, 1991). Such a product is already produced by cattle native to those lands, and this is accomplished by long-feeding the cattle with a natural genetic disposition for expressing the SCD gene (Chung et al., 2006; Chung et al., 2007). The product of the SCD gene, stearoyl-CoA desaturase, is responsible for converting SFA to MUFA, and this consequent increase in MUFA is correlated with increased fat softness and increased muscle marbling (Chung et al., 2006; Taniguchi et al., 2004a; Wood et al., 2004). Being able to replicate the success of the Asian native cattle using the American Angus cattle would allow us to provide a premium product for Japanese and Korean markets and tap into a billion dollar industry.

This study aimed to look at several carcass characteristics, fatty acid profiles, and flavor attributes to observe differences between calf- and yearling-fed cattle. The primary goal of this study was to test whether feeding calves as yearling cattle would optimize the expression of the SCD gene and thus lead to a product with a greater MUFA:SFA ratio than can be achieved in calf-fed animals.

REVIEW OF LITERATURE

Calf-fed vs. yearling-fed systems. Conventional methods of feeding cattle are used to optimize growth and feed efficiency to help producers get the highest potential profit for their animals. Calf-feeding, putting animals on feedlots directly after weaning, allows for faster growth to provide greater turnover for the producer, but this comes at a higher price due to the cost of the concentrate feeds for the animals, which can be as great as half the cost of raising the animal. Yearling-fed cattle are designed to have longer growth times and a shortened finishing time when compared to the calf-fed animals. This allows producers with ample high-quality pasture the ability to raise the cattle to similar standards of the calf-fed cattle with a much lower cost of feed.

Recent work compared the economic efficiency and the growth traits of cattle raised on these two systems (Anderson et al., 2005). Yearling-fed cattle showed higher average daily gain (ADG) when fed to a constant weight, which has been seen in previous literature (Harris et al., 1997; Lunt and Orme, 1987). However, the yearling cattle had lower marbling grades than calf-fed animals, which is similar to what Lunt and Orme saw but contrary to the similar quality grades seen in by Harris et al. when the animals were fed to the same weight. Anderson also found lower break-even points and higher profit potential for the producer when these yearling-fed cattle were sold on a live basis. This shows that from a producer standpoint, yearling-feeding has the potential to provide them with an economic benefit.

However, the meat produced from the same cattle used by Anderson et al.(Anderson et al., 2005) were evaluated by Brewer et al. (2007), and they found the calf-fed animals

produced a product with characteristics that would be considered more desirable by the consumer. Even though the yearling-fed animals produced larger carcasses, the meat was leaner and had lower quality grade than the calf-fed animals. Tenderness and palatability of beef from the calf-fed animals was shown to be more desirable when compared to yearling-fed cattle. These sensory characteristics have consistently shown to favor beef that is calf-fed (Harris et al., 1997; Hedrick et al., 1983; Lunt and Orme, 1987). These traits have also been shown to be very influential with the consumers, and thus, when used in combination with production data, increase the potential profit for the producer if the evaluation were based on a final product and not a live weight (Umberger et al., 2002).

Differences in these findings can depend on breed of the animal and time on finishing diet. It has been well documented that Wagyu cattle will produce greater marbling scores when fed on hay-based diets (Lunt et al., 2005; May et al., 1993), and it has also been shown that animals-fed that are fed a long enough finishing diet to meet a certain backfat thickness, even after a period of being pasture-fed, will produce carcass traits and sensory characteristics indistinguishable from calf-fed animals. These attributes are usually related to the amount of time on feed and compensatory growth of backgrounded animals (Dolezal et al., 1982; Sainz and Paganini, 2004)

Digesta fatty acid metabolism. In the ruminant, the lipid component of the digesta is not only a function of the dietary fat intake but also of the microbial manipulation and production of fatty acids.

The specific microbes and controls in the rumen that facilitate biohydrogenation remain undetermined. This also is compounded by the sources of the fatty acids found in the duodenal and abomasal samples taken. Rumen protozoa, bacteria, and undegraded feed all contribute to the fatty acids being presented for absorption in the duodenum. Yet, they each provide different subsets of the fatty acid profile.

The list of specific strains of bacteria for biohydrogenation remains incomplete. The conversion of linoleic acid to stearic acid has been attributed to *Clostridium proteoclasticum* (Wallace et al., 2006). It seems that *Butyrivibrio* strains of bacteria also have a part in ruminal biohydrogenation (Fukuda et al., 2006; Vossenberg and Joblin, 2003).

Rumen protozoa have been shown to have higher vaccenic acid, CLA and palmitic acid levels than bacteria; however, the bacteria show higher stearic acid and oleic acid (Devillard et al., 2006; Or-Rashid et al., 2007; Yanez-Ruiz et al., 2006). In fact, one study showed bacteria containing values of long-chain SFA 123% greater than the values seen in protozoa (Or-Rashid et al., 2007).

Protozoal-free lambs showed higher SFA and lower MUFA and PUFA in their intramuscular (i.m.) adipose tissue, while their abomasal contents showed higher SFA and lower PUFA but similar MUFA. Protozoa could be incorporating more UFA into their phospholipids and thus protect them from biohydrogenation and allowing them to get past the rumen, protozoa are responsible for 30-50% of the UFA flowing out of the rumen and only about 10-20% of the SFA (Yanez-Ruiz et al., 2007).

Multiple studies have produced inconclusive results on the effect rumen protozoa have on biohydrogenation (Or-Rashid et al., 2007; Yanez-Ruiz et al., 2006; Yanez-Ruiz et al., 2007). However, Devillard et al. (2006) concluded protozoa do not hydrogenate stearic acid, and instead, they may preferentially accumulate CLA and vaccenic acid. Their work showed no evidence of an ability to produce SFA through either desaturation or hydrogenation.

Typical corn-based diets fed to ruminants have been shown to have high percentages of palmitic, oleic and linoleic acids (16:0, 18:1 and 18:2). They also contain low levels of stearic and palmitoleic acids (18:0 and 16:1) (Dayani et al., 2007; Duckett et al., 2002). However, measurements of fatty acid percentages entering the duodenum found very high levels of stearic acid with continuing high levels of palmitic acid, and lower percentages of oleic acid, linolenic, and palmitoleic (Chung, 2004; Duckett et al., 2002). This biohydrogenation occurring in the rumen is providing the tissues with the substrates needed for the production of more MUFA by the SCD gene. Concentrate diets could be defaunating the rumen because they lower ruminal pH. This is obvious when whole cotton seed is used (Dayani et al., 2007), which defaunates the protozoa. Protozoal defaunation is also caused by long-chain unsaturated fatty acids (UFA) and medium-chain saturated acids, which are found in cattle fed high-grain diets. This decrease in protozoal numbers could potentially lower the availability of vaccenic acid and other UFA to the cattle (Hristov et al., 2004).

Grass-based diets have lower levels of oleic and linoleic acid and consist of much higher levels of linolenic acid (Nuernberg et al., 2005). The rumen fluid from these diets

ends up having more PUFA and less SFA than corn-based diets, and those PUFA and MUFA are taken up by the protozoa. There are two things that would happen with this type of diet. The bacteria would begin to die off because high amounts of linolenic acid are inhibitory toward their growth and survival (Wallace et al., 2006), which would reduce biohydrogenation. Also, if it is true that protozoa do not have a role in biohydrogenation, they would store the PUFA preferentially and incorporate them into their phospholipids protecting them from ruminal biohydrogenation (Devillard et al., 2006). The difficulty with this is that even lower amounts of SFA are being presented to the duodenum which means less substrate is available for the tissue for use by SCD. This finding in digesta fatty acid levels has been seen in other studies looking at the difference between corn and hay based diets. The levels of PUFA did increase when compared to the corn-based diet, while at the same time, the levels of SFA decreased (Chung, 2006; Chung, 2004).

Fatty acid absorption and transport. There is no absorption of long-chain fatty acids (LCFA) between the rumen and the abomasum. Fatty acids present to the small intestine as they were in the rumen in the form of triglycerides (TG), phospholipids and free fatty acids. Pancreatic lipase from the bile releases these fatty acids, which are then packaged into micelles and absorbed into the small intestine, with the bulk of the absorption occurring in the jejunum (Bauchart, 1993). In monogastric animals, TG are packaged into the larger less dense lipoproteins called chylomicrons for transport out of the endothelial cells. However, due to the relatively low fat intake of ruminants, chylomicrons are not required, and thus are not produced and used by the ruminant in

appreciable amounts (Drackley, 2005). Instead, the TG are packaged into very low density lipoproteins (VLDL) for transport into the lymphatic system, where they will enter the blood stream via the left internal jugular or left subclavian vein (Kris-Etherton and Etherton, 1982).

Plasma fatty acids. Once in the blood stream, VLDL combines with any free nonesterified fatty acids, which travel through the plasma bound to albumin (Emery, 1979). When the VLDL and free fatty acids have reached the tissues, particularly adipose and muscle tissues, the VLDL are acted upon by lipoprotein lipase and the TG are released and hydrolyzed to be taken up, with the free fatty acids, by the cells via various receptors (Emery, 1979; Mersmann and Smith, 2005).

It has been shown that cattle fed hay based diets have higher levels of SFA and PUFA in their plasma. However, these levels are different from the levels seen in the digesta. In studies where plasma fatty acids were compared by diet, the levels seen in the plasma of hay-fed animals showed higher SFA and PUFA levels than in corn-fed animals, but these levels were not consistent with the levels seen in the digesta (Chung, 2006; Chung, 2004). This indicates that other factors affect plasma fatty acid composition, and may be due, in part, to the mobilization of fatty acids from various depots in the body.

Fatty acid synthesis and modification. The primary tissue of fatty acid synthesis varies depending on species. Rats and humans use the liver as the primary site of fatty acid synthesis and modification (Masoro, 1977). However, in ruminants, the primary site is in the adipose tissue (Drackley, 2005; Vernon, 1980).

Acetate, lactate and glucose are the carbon sources used for *de novo* LCFA synthesis. In adult cattle, acetate is the primary substrate for LCFA synthesis in all adipose depots with the exception of i.m., which has been shown to instead use glucose and gluconeogenic precursors such as propionate (Smith and Crouse, 1984). The process of *de novo* LCFA synthesis has been long known and well described in other reviews (Mersmann and Smith, 2005; Vernon, 1980). Briefly, acetate or glucose are used to form acetyl-coA which is then used to add two carbon units to increasing chain lengths producing palmitic acid (16:0) as the main product. Palmitic acid then has the possibility of being desaturated to palmitoleic acid (16:1) or elongated to stearic acid (18:0).

Since the liver is not the main site of fatty acid modification in the rumen, this means that the main site of desaturation of LCFA in bovine occurs in the peripheral tissues, as was shown by Gruffat et al. (2005) who found no modification of vaccenic acid to form CLA in bovine liver cells. A comparison of both liver and s.c. adipose tissue by St. John et al. (1991) was even more telling by showing rat liver and bovine s.c. adipose tissue to have similar levels of SCD activity while also showing no measurable enzyme activity in the bovine liver. This desaturation activity and its controls will be expanded upon in a later section of this review (See *RNA activity*).

Liver fatty acids. Because ruminant liver lacks lipoprotein lipase and is not a major site for de novo fatty acid synthesis, all LCFA found in the liver come from the uptake of free fatty acids in the plasma (Emery et al., 1992), and the amount of uptake by the liver is mainly dependent on the plasma concentration of the free fatty acids. However, it has also been shown that the liver's uptake of stearic acid (18:0) remains low and

variable despite high or low concentrations in the blood. This is in contrast to the uptake of oleic and palmitic acid, whose uptake shows a linear relationship to plasma concentrations (Bell, 1979). Since the liver is also not a major source of fuel from fatty acids and it has very low level of triglyceride secretion, there is a low level of fatty acid disappearance from the liver (Emery et al., 1992). This makes the fatty acid profile a function of accumulation of individual free fatty acids over time.

Muscle fatty acids. The absorption of fatty acids in the muscle is a function of the activity of lipoprotein lipase on the VLDL transporting the triglycerides through the blood. Once in the muscle, the fatty acids can be oxidized as fuel, incorporated into the phospholipid membranes of the cells, or directed to i.m. fat deposition for storage. The data available for comparison of lean muscle tissue fatty acid composition is limiting. Most studies use the whole muscle fatty acid profile as an indicator of the i.m. adipose fatty acid profile, instead of dissecting out the i.m. and measuring its fatty acid profile separately from the muscle (Noci et al., 2005). Primary fat classes were phospholipids, free fatty acids and triglycerides with triglycerides increasing as marbling increased (Hecker et al., 1975). There are many factors that can effect fat deposition in the muscle of ruminants including breed, age, gender, diet. This paper will not go into detail about all of these factors because they have been covered elsewhere (Nürnberg et al., 1998). However, we will mention that muscle lipid showed that when ruminants were pasture fed they had higher proportions of SFA than cattle fed pasture supplemented with either linseed oil or sunflower oil (Noci et al., 2005), and that PUFA:SFA ratios are generally increased in grazing steers supplemented with plant oils (Noci et al., 2007). Further, it

was found that the cholesterol concentration of muscle in ruminants is not subject to manipulation of diet or differences in breed effects (Eichhorn et al., 1986; Rule et al., 1997). Even with diets differing in forage and concentrate levels, French et al. (2000) saw no difference in fat or moisture content of the LD with animals of similar carcass weight.

Adipose tissue development. Fat accretion in ruminants is well understood to develop in the order of perirenal and omental fat, subcutaneous (s.c.) fat, and lastly i.m. fat, with the development of i.m. fat occurring late in development (Vernon, 1980). Development of individual cells requires differentiation of preadipocytes to developed adipocytes via the use of certain transcription factors. In the first stages of development, C/EBPβ activates PPARγ which is a regulator for adipocyte differentiation and development (Roh et al., 2006; Wu et al., 1995). These particular transcription factors have been shown to be regulated by free fatty acids, such as CLA (Azain, 2004). The cells then go into stages of hyperplasia and hypertrophy. During early growth stages, hyperplasia causes increases in cell numbers. This is followed by a stage of both hyperplasia and hypertrophy where the cells are beginning to fill while division begins to slow. The last stage is mainly cell hypertrophy, where the adipocytes increase in diameter and volume during lipid filling (Hood, 1982). Because i.m. fat deposits are the last to be developed, they generally do not see a very extensive hypertrophy stage before slaughter; therefore, they show smaller cell diameters but large numbers (Smith, 1995; Smith et al., 2007).

As mentioned earlier, the primary substrates of s.c. and i.m. *de novo* fatty acid synthesis are acetate and glucose, respectively (Smith and Crouse, 1984). Thus, the

relative rates of incorporation into the adipose tissue have been studied. Acetate incorporation into s.c. cells of yearling-fed steers was higher than market weight calf-fed steers of the same age. The yearling-fed cattle were still growing and had a higher capacity to deposit s.c. fat than the calf-fed at the same age. However, by the time yearling-fed cattle achieved the same body weight as the calf-fed animals, the incorporation of acetate into fatty acids had dropped to levels comparable to the calf-fed steers. This showed that the animals' deposition of fatty acids had started to decline (Smith et al., 2007).

Histology. Intramuscular fat cells develop around the outside of the muscle fiber bundle in *Bos taurus* cattle. These "islands" of cells are found in the connective tissue close to capillary beds where they can easily obtain nutrients and fatty acids from the blood (Moody and Cassens, 1968). Many times these adipose tissue depots are not visible to the naked eye, and are therefore not considered important by the market industry when factoring a quality grade for the beef (Harper and Pethick, 2004). However, these small portions of fat do factor into the overall fatty acid profile in the meat, which is important in regards to the flavor and healthfulness of the product.

Yang et al. (2006), performed extensive measurements on i.m. adipose tissue to see how cell number and volume related to marbling flecks and other areas of adipose tissue. It was found that hyperplasia had a greater effect on the amount of i.m. than hypertrophy. This indicated that, although hypertrophy via triglyceride filling and lipogenesis play a role in i.m., the larger role comes from cell division. This fits with other data that report lipogenesis to be lower in cells with smaller diameters such as i.m.

adipose tissue or in adipose of young animals (Smith, 1995). It was also observed that when looking at i.m. cell volume of calf-fed steers, yearling-fed steers raised to a constant age, or yearling-fed steers raised to a constant weight, the calf-fed steers had higher i.m. cell volume than the yearling-fed animals raised to the same age. However, by the time the yearling-fed animals reached the same body weight, the volume had caught up, but the number of cells remained the same as the calf-fed steers (Smith et al., 2007). This shows that the time on feed and body weight played some part in the animals' ability to deposit i.m. adipose tissue.

Subcutaneous fatty acids. Subcutaneous fat in beef cattle is, for the most part, considered a waste fat when discussing whole muscle meats. However, when considering processed meat products, this s.c. adipose tissue depot is widely used as added fat. Therefore, it is useful to look at the composition of s.c. adipose as a product with the possibility of being a significant part of the diet. The fatty acid composition of s.c. adipose in ruminants has been associated with the overall amount of s.c. adipose deposited. Also, the concentration of oleic acid was positively correlated with fat thickness (Duckett et al., 1993; Xie et al., 1996). This is in agreement with Link et al. (1970) who found the concentration of oleic acid and linoleic acid to increase during growth, while stearic acid decreased when fed a corn-based diet. Subcutaneous adipose tissue of corn-fed *Bos taurus* bulls was found to be higher in MUFA and lower in SFA when compared to i.m. adipose tissue (Aldai et al., 2007). This study also showed the s.c. adipose tissue concentrations of *trans*-vaccenic acid and CLA were higher than in the i.m. adipose tissue. Chung et al. (2006) found adipose tissue of corn-fed steers

contained higher concentrations of palmitoleic, trans-vaccenic, and linoleic acid, total MUFA, total PUFA, and increased MUFA:SFA ratios than adipose tissue of hay-fed steers, whereas adipose tissue of hay-fed steers contained more stearic, linolenic acid and total SFA. Oleic acid only tended to be higher in s.c. adipose tissue of corn-fed steers.

The melting point and the fatty acid composition of s.c. adipose tissue have a direct relationship which has been demonstrated in numerous studies (Leat, 1975; Tume, 2004; Wood et al., 2004). As fatty acids become more unsaturated, their melting point decreases. This is particularly true with relationship to the amount of stearic acid in the tissue. Ruminants fed corn-based diets as opposed to forage-based diets have been shown to have lower melting points and SFA levels (Smith et al., 1998; Yang et al., 1999a).

Intramuscular fatty acids. Intramuscular adipose tissue is the last fat deposit to develop during ruminant growth. Marbling has been shown to be positively correlated with carcass fatness (Huffman et al., 1990). Carter et al. (2002) demonstrated that the deposition of i.m. was accelerated once animals reached a particular body weight. The cattle from that study were raised on pasture and sent to the feedlot once they reached a predetermined body weight. The measurements showed animals on the corn based feedlot ration, once at their target body weight, had accelerated i.m. deposition. Increased marbling has also been found to be negatively associated with concentrations of stearic acid, linoleic acid and total PUFA (Xie et al., 1996). This is in agreement with studies showing i.m. fat remains more saturated than s.c. fat (Yang et al., 1999a). French

et al. (2003) compared the fatty acid profiles of i.m. adipose tissue from cattle fed a combination of concentrate and grass based diet. Diets with low grass and high concentrates showed lower concentrations of palmitic and stearic acid with greater proportions of palmitoleic and oleic acid compared to a diet with high grass and low concentrates. They also showed that supplementing concentrates with high grass allowance, did not affect the MUFA:SFA ratio; however, when high concentrates were supplemented with low and medium grass allowance, there was an increased MUFA:SFA ratio. When these diets were compared to the exclusively concentrate fed animals, they all had lower i.m. concentrations and lower MUFA:SFA ratios.

RNA activity. Leat (1975) originally saw the differences between rumen digesta, hydrogenation, and the tissue deposit of MUFA. He noticed the highly saturated rumen contents did not match up with the tissue deposition of oleic and palmitoleic acids. He further realized that this deposition of MUFA increased with age after weaning, even though the diet did not change. At the time, the specific desaturase activity in the tissues was not studied, but the research community would soon come to realize its' importance. Since that study the enzyme stearoyl CoA desaturase (SCD) was discovered to be responsible for this alteration of SFA into MUFA after deposition in the tissues (Miyazaki and Ntambi, 2003; Smith et al., 2006).

It previously has been established that, in beef cattle, adipose tissue has greater stearoyl-CoA desaturase (SCD) enzyme activity than any other tissue (Chang et al., 1992; St. John et al., 1991). As stated earlier, the liver is not a site of fatty acid modification in the ruminant, thus no SCD activity has been found in their liver (St. John

et al., 1991). It was demonstrated that i.m. adipose tissue has approximately 50% of the SCD activity of s.c. adipose tissue in feedlot cattle (Archibeque et al., 2005). High SCD activity contributes to adipose tissue development, so adipose tissue from cattle with more finish usually has more SCD enzyme activity and, therefore, a higher concentration of oleic acid (May et al., 1993; Smith et al., 2006).

Until recently, SCD activity and oleic acid content changes have been attributed to either carcass weight or time on feed. Only now is the greater effect that age of the cattle has on these changes being fully appreciated. Previous studies have demonstrated that the concentration of oleic acid in adipose tissue increases during growth (Clemens et al., 1973; Huerta-Leidenz et al., 1996; Leat, 1975; Rule et al., 1997). Correspondingly, it was demonstrated that the increase in oleic acid was caused by a dramatic increase in SCD gene expression between weaning and slaughter (Martin et al., 1999). In a comparison of Angus and American Wagyu steers fed to the Japanese endpoint (650 kg), a higher concentration of oleic acid was observed in the Angus adipose tissue than what had been previously seen suggesting that SCD enzyme activity continued to increase past the typical U.S. slaughter weight (May et al., 1993) (Table 2). At the other extreme, fat trim from Angus steers fed a corn-based diet to 470 kg contained an unusually low concentration of oleic acid (33.6%), and the MUFA:SFA ratio (0.73) was one of the lowest ever observed in corn-fed steers (Archibeque et al., 2005).

These changes are also dependent on diet. It has been shown that in *Bos taurus* cattle SCD gene expression is greater when they are fed corn based diets as opposed to hay based diets (Chung et al., 2007). This is not true when pasture based diets are compared

to grain diets with whole cottonseed as their main grain. In this case, whole cottonseed appears to depress desaturase activity, due to its' content of cyclopropenoid fatty acids (Martin et al., 1999; Yang et al., 1999b). Other inhibitors of SCD include PUFA such as linoleic, linolenic acid, and CLA (Azain, 2004; Lee et al., 2005; Ntambi et al., 2004). This would mean that pasture based diets, where these fatty acids show a lower rate of rumen biohydrogenation and thus a greater passage rate, would lead to depressed SCD activity. Another possible inhibitor of the SCD gene that is found in grass and forage based diets is vitamin A (Kawachi, 2006). This vitamin has been shown to depress the SCD activity by repressing the PPARγ transcriptional factor, and diets containing grasses are high in the carotenoid precursors of vitamin A (Siebert et al., 2003).

Monounsaturated fatty acids. Monounsaturated fatty acids (primarily oleic acid) constitute 35 to 45% of the total fatty acids in U.S. beef (Archibeque et al., 2005; Gilbert et al., 2003; St. John et al., 1991; Sturdivant et al., 1992). Our research has focused on understanding the variation in MUFA in beef from feedlot cattle, and our most recent investigations suggest that the practice of calf-feeding, which results in cattle being slaughtered at a youthful age, leads to a reduction in MUFA.

These data indicate the importance of finishing cattle on a grain-based diet for increasing the amount of oleic acid in beef, and provide additional evidence that age of the steers very strongly dictates the concentration of oleic acid in fat trim.

Our laboratory recently completed an investigation documenting the fatty acid composition of adipose tissues from Angus steers fed corn- or hay-based diets to 525 kg (U.S. endpoint) or 650 kg (Japanese endpoint) (Chung et al., 2006; Chung et al., 2007).

The beef from some of these animals was used in the human study described in Table 1. The concentration of oleic acid, hence the MUFA:SFA ratio, increased markedly with live weight in the s.c. adipose tissue of Angus steers, and was highest in the long-fed (Japanese endpoint) steers fed the corn-based diet (Table 2).

Health benefits of monounsaturated fatty acids. The MUFA:SFA ratio was studied due to the healthful aspects of MUFA enriched products. An elevated MUFA:SFA ratio has been associated with decreased low-density lipoprotein (LDL) levels and a decreased risk of cardiovascular disease (CVD) (Berry et al., 1992; Grundy et al., 1988).

Cardiovascular disease (CVD) has become the leading cause of death in the United States, and research into the healthfulness of the different fats in the diet has shown many benefits of oleic acid. Some studies have shown that diets high in polyunsaturated fatty acids (PUFA) have cholesterol-lowering effects and diets high in saturated fatty acids (SFA) show cholesterol raising effects, but the diets with elevated monounsaturated fatty acids (MUFA) showed little or no effect on serum cholesterol (Hegsted et al., 1993; Keys et al., 1965). However, other studies showed that diets high in MUFA will lower total and LDL-cholesterol while maintaining the levels of HDL-cholesterol (Berry et al., 1992; Grundy et al., 1988).

Lopez-Miranda et al. (2006) reviews the benefits associated with what is being termed the "Mediterranean Diet," which consists of a high inclusion of olive oil in food preparation. Olive oil is known to contain oleic acid as its primary fat, and the health aspects of the diet have been related to that particular MUFA. They discuss the fact that one of the possible reasons for the onset of arteriosclerosis is the oxidative modification

of LDL. LDL particles rich in MUFA are shown to be more resistant to this modification than LDL rich in PUFA. They also reviewed papers that showed that when dietary SFA was replaced with MUFA, the diet with the higher MUFA showed less platelet aggregation in the arterial walls.

The American Heart Association has taken note of these studies and has since altered their recommendations from a low to no-fat diet to a diet with about 25 to 30% of calories coming from fat with emphasis on the greater portion of these coming from MUFA and PUFA (SFA < 7%, PUFA ≤ 10%, MUFA ≤ 10%) for normal adults (Krauss et al., 2000), while the National Cholesterol Education Program raises the amount of MUFA to up to 20% (Cleeman, 2001).

We recently conducted a pilot study that demonstrated significant differences in the LDL:HDL ratios of men (n = 10) consuming ground beef patties with MUFA:SFA ratios of 0.82 and 1.34 (beef from hay-fed and long-fed Angus steers, described below), and 1.38 (beef from Wagyu steers). The men consumed five, 115-g ground beef patties per wk for 5 wk. Ground beef with the lowest MUFA:SFA ratio reduced VLDL cholesterol, whereas beef with the higher MUFA:SFA ratios sufficiently reduced LDL cholesterol and increased HDL cholesterol to cause a significant decrease in the LDL:HDL ratio (Table 1). These results provide additional justification for U.S. cattle feeders to produce beef that is enriched with oleic acid.

Sensory and marketing. In a review by Muir et al. (1998), the differences between grain- and forage-fed animals are looked at across several different studies. Overall it was seen that when animals are fed to equal weights or fat covers, diet was not a factor

when assessing tenderness, juiciness, or flavor using a sensory panel; however, there is a weak correlation between juiciness and marbling score. It was also noted in this review that it has been observed that the largest differences in flavor were seen between cattle slaughtered coming directly off a concentrate diet and those coming directly off pasture. This was associated with the higher SFA and n-3 fatty acids of pasture, versus the higher MUFA and n-6 fatty acids from concentrate diets. Westerling & Hendrick (1979) showed that fatty acid composition does affect the sensory attributes. They showed that positive sensory panel scores were associated with higher levels of oleic acid found in grass-fed beef, while lower scores were seen with the higher SFA, mainly stearic and palmitic acid, found in grass-fed beef. This was also seen by Dryden and Marchello (1970), who saw a positive correlation of palatability and levels of oleic acid. Yet, the beef flavor intensity has been shown to not be affected by the amount of i.m. as indicated by the quality grade (Wheeler et al., 1994).

There is also the visual aspect to consider when marketing these meat products. Yellow fat is an undesirable trait in market products. This is more so true when considering foreign markets where fat color is so highly prized. The color of the fat is due to carotenoids in diet. These carotenoids are higher in pasture-fed animals due to the high levels inherently found in plant products. These fat soluble substances are laid down in the fat as they are absorbed from the diet, providing the fat with the distinctive yellow color found in grass-fed beef (Kerth et al., 2007). This also means the longer an animal remains on this grass based diet, the more yellow the fat will become (Moon et al., 2006). This increased level of carotenoids is also an indication of increased levels of

vitamin A in the animals. Vitamin A, as stated previously, inhibits the SCD gene (Siebert et al., 2003). Therefore, diets higher in vitamin A not only have more yellow in the fat; they also will have less desaturase activity and harder fat. Fat color was shown to improve with true grain-fed diets lacking any grass silage or pasture (Kerth et al., 2007; Muir et al., 1998).

In a recent study looking at consumer preference, it was shown that the U.S. consumer is willing to pay a premium for corn-fed beef as opposed to grass-fed beef at auction. However, this data is based on animals that were strictly corn-fed or strictly grass-fed (Sitz et al., 2005; Umberger et al., 2002). All carcass and sensory data available show that cattle backgrounded on pasture and finished on corn diets showed sensory traits and aspects similar to those found in truly corn-fed animals depending on the amount of time spent on the finishing diet (Harris et al., 1997; Kerth et al., 2007).

Foreign market. Japan and Korea grading systems have developed to reflect the carcass characteristics valued by their consumers (Dubeski et al., 1997; Kim, 2003; Lin and Mori, 1991). These markets prize highly marbled beef with soft fat. Before the Japan and Korea borders were closed to U.S. beef due to the BSE outbreak, they encompassed a billion dollar market for U.S. beef exports. Now that the ban has been lifted, there is the potential for great economic benefit to U.S. producers if they can provide a product that is highly marbled with soft fat. It has been shown that increasing the MUFA levels in beef will decrease the slip point and thus produce softer, and in this case, more desirable fat (Chung et al., 2006; Taniguchi et al., 2004b; Wood et al., 2004).

Australian beef producers, a large exporter of beef to the Japanese market, generally produce harder fat and have lower oleic acid levels in their fat trim when compared to U.S. produced beef (Smith et al., 1998; Yang et al., 1999a). Due to its softer fat and greater amounts of marbling, the United States beef is more highly valued by the Japanese market than Australian beef and is worth 50% more per ton. Now that the Japanese market has reopened its borders to United States beef producers, this country has a chance at getting into a multi-billion dollar market if they can provide a quality product.

METHODOLOGY

Animals and diet. Twenty-four Angus steers were purchased as calves at weaning (approximately 8 mo of age; 210kg) and transported to either the Texas A&M University Research Center at McGregor (20 steers) or to the Rosenthal Meat Science and Technology Center at the Texas A&M University College Station campus (4 steers). The 4 steer calves taken directly to the Rosenthal Center were slaughtered and samples collected as described below to provide baseline data.

Coastal Bermuda grass hay containing 9.5 % crude protein was fed free choice for 8 d after the steers were transported to McGregor. Eight of the steer calves transported to McGregor (calf-fed) were then adapted to a high-corn finishing diet (designed to achieve 1.36 kg/d) over a 2-wk period. The diet contained 48 %ground corn, 20 % ground sorghum, 15 % cottonseed hulls, 7.5 % molasses, 0.96 % limestone, 0.56 % trace mineral salt, and 0.08 % vitamin premix (Table 3). The calf-fed steers were fed the corn-based diet until 12 mo of age (4 steers; 370 kg) or 16 mo of age (4 steers; 525 kg), at which times they were transported to College Station, slaughtered, and samples collected.

The remaining 12 steers housed at McGregor (yearling-fed) were fed Bermuda grass hay and allowed to graze on native central Texas and/or oat pasture, supplemented with the corn-based diet (Table 3) to achieve 0.90 kg/d. When the steers reached 12 mo of age, 4 steers were transported to the College Station campus, slaughtered, and samples collected. The remaining 8 steers were adapted over a 2-wk period to the same corn-based finishing diet being fed to the calf group. At 16 mo of age (terminal age for the

calf-fed group), 4 steers were transported to the College Station campus, slaughtered, and samples collected. The final 4 steers were transported to College Station at 525 kg (terminal weight for the calf-fed group; approximately 18 mo of age).

Sample collection. The steers in each time-on-feed group were slaughtered on two consecutive days. Upon exsanguination blood was collected and taken to the lab to be spun down to obtain the plasma fraction. Immediately following removal of the hide, a section of the *Longissimus dorsi* (LD) muscle and overlying s.c. adipose tissue from the 5th to 8th thoracic rib section was removed from the carcass. Samples were taken from the lower lobe of the liver, and samples of digesta were obtained from the duodenal side of the pyloric sphincter. In the lab, samples of i.m. adipose tissues and fat-free LD were dissected from the rib section for the analysis of fatty acids along with the s.c. adipose tissue, plasma, and digesta as described below. Samples for fatty acid analysis were stored at -20°C to minimize oxidation of fatty acids. Adipose tissue, liver and muscle samples were snap-frozen in liquid nitrogen and stored at 94°C to preserve the samples for RNA analysis as described below. Twenty-four to forty-eight hours after slaughter a steak from the 13th rib area was obtained from each steer and frozen at -20°C and later used for histology. From the 16 mo and 18 mo old cattle, three more steaks from the below the 12th rib were taken from the carcass half of each animal for sensory analysis by a trained sensory panel.

Total lipid extraction. Total lipids were extracted by a modification of the method of Folch et al.(1957), modified as described by Archibeque et al.(2005). Approximately 1 g of closely trimmed LD, 1 g of liver, 5 mL of plasma, 2 g of digesta, and 100 mg each of

s.c. and i.m. adipose tissues were homogenized with 5.0 mL of chloroform:methanol (2:1, vol/vol). For adipose tissue, liver and muscle, homogenization was done using a Brinkmann Polytron Homogenizer (Brinkmann Instruments, Westbury, NY), while digesta and plasma were vortexed for homogenization. After homogenization, 10 mL of additional chloroform:methanol was added to the sample for a final volume of 15 mL, which was then left to sit at room temperature for 30 to 60 min for lipid extraction. The samples were vacuum filtrated through a sintered glass filter funnel and through Whatman GF/C filters (Whatman Ltd., Maidstone, England) into a clean test tube which contained 8 mL of KCl (0.74%, wt/vol). The sample was then vortexed and allowed to sit for 2 h to allow for phase separation. The upper phase was then discarded, and the lower phase was transferred into a clean test tube and evaporated to dryness at 60°C under nitrogen. The remaining liquid was the total extracted lipid which could then be used for fatty acid analysis or, in the case of s.c. tissue, slip point determination.

Fatty acid analysis. Fatty acid methyl esters (FAME) were prepared as described by Morrison and Smith (1964). The total extracted lipid obtained from the procedure described above had 1 mL of 0.5 N KOH in MeOH and put into a 70°C water bath for 10 min. Then, 1 mL of boron trifluoride (BF_3) (14% , wt/vol) was added to the sample which was then flushed with nitrogen, loosely capped, and place back into the 70°C water bath for 30 min The samples were removed from the bath and allowed to cool before 2 mL of HPLC grade hexane and 2 mL of saturated NaCl were added to the samples and vortexed. This produced two distinct phases of which the upper phase was extracted off and transferred to a clean test tube with 800 mg of Na_2SO_4 to remove any

moisture from the sample. Two milliliters were added to the tube with the saturated NaCl and vortexed. The upper layer was again pipetted off into the tube with Na_2SO_4. The sample was vortexed and the liquid from the test tube was then transferred to a scintillation vial. One milliliter of HPLC grade hexane was used to wash the Na_2SO_4. This final volume was transferred to the scintillation vial to give a final volume of 5 mL of sample in the scintillation vial. The sample was then evaporated to dryness at 60°C under nitrogen and finally reconstituted with HPLC grade hexane and analyzed using a Varian gas chromatograph (model CP-3800 fixed with a CP-8200 autosampler, Varian Inc., Walnut Creek, CA) (Smith et al., 2002). Separation of FAME was accomplished on a fused silica capillary column CP-Sil88 [100 m x 0.25 mm (i.d.)] (Chrompack Inc., Middleburg, The Netherlands), with helium as the carrier gas (flow rate = 1.2 mL/min). After 32 min at 180°C, oven temperature was increased at 20°C/min to 225°C and held for 13.75 min Total run time was 48 min Injector and detector temperatures were at 270°C and 300°C, respectively. Individual FAME was quantified as a percentage of total FAME analyzed. This equipment can accurately measure all fatty acids normally occurring in beef lean and fat trim, including isomers of conjugated linoleic acid and the omega-3 fatty acids.

Slip points. Melting points of the s.c. adipose tissue lipids were approximated by determining slip points (Smith et al., 1998). After heating the total extracted lipid to approximately 45°C, the lipids were drawn 1 cm into glass capillary tubes and frozen at 20°C. After freezing, the capillary tubes were suspended vertically in a chilled water bath with the portion of the tube containing the lipid submerged in the water. The water

bath was heated at 2°C/min with constant stirring. Temperature of the water was monitored with a Type K thermocouple (model KTSS-HH, Omega Engineering, Inc., Stamford, CT) attached to a digital thermometer (model 91100-50, Cole-Parmer Instrument Co., Vernon Hills, IL). Slip point is defined as the temperature at which the lipid moves up the capillary tube.

Fats and moistures. Lean muscle moisture and fat percentage was determined from ground samples of 5th to 8th thoracic rib section by use of CEM SMART system (microwaving drying system manufactured by CEM Corp., Matthews, NC) and SMART Trac (NMR system manufactured by CEM Corp., Matthews, NC) as outlined by Keeton et al.(2003). Briefly, a sample of LD was ground to a fine paste using a commercial food processor. Approximately, 4 g of sample was transferred and spread onto a tared CEM sample pad using a Teflon-coated spatula. Then a second tared CEM sample pad was placed on top of the sample in a sandwich-like fashion. The sample was then placed inside the microwaving drying system. (AOAC, 2007) After this part of the procedure, the dried pads with sample were taken out and rolled in SMART Trac Film. The rolled sample was placed into a CEM Trac Tube and compressed. This sleeve with sample was then placed into the NMR chamber for analysis.

Cholesterol concentrations. Cholesterol concentrations of the muscle samples were analyzed as described (Rule et al., 2002; Rule et al., 1997) using gas chromatography. One hundred grams of LD was freeze-dried and homogenized in a home-style electric grinder. Cholesterol was extracted with 3 mL of ethanol per 100 mg of dried tissue. The lipids were saponified by the addition of 1 mL of 33% (wt/vol) KOH and heating for 60

min in an 80 to 90°C water bath. Stigmasterol was used as the internal standard to quantify the total cholesterol. Cholesterol was isolated on an HP-1, fused capillary column [30 m x 0.322 mm x 1.00 μm] (VWR International, West Chester, PA) with an initial column temperature of 250°C and a detector and injector temperature of 300°C. Helium was the carrier gas with a 1:3 split ratio. The run time for this sample was about 5 to 6 min.

Preparation and analysis of RNA. Total RNA was isolated from adipose and liver tissue samples in Tri® Reagent (Sigma Chemical Co., St. Louis, MO) per the manufactures instructions, which is essentially an improved version of the guanidine thiocyanate-phenol-chloroform extraction method reviewed in the literature (Chomczynski and Mackey, 1995; Chomczynski and Sacchi, 1987). Approximately 400 to 500 mg of adipose tissue or 100 to 200 mg of liver was placed into 50-mL centrifuge tubes and homogenized with 2.5 mL or 2.0 mL of Tri® Reagent, respectively. At this point, the adipose tissue had an extra centrifugation step for 15 min at 23,700 x g at 4°C, after which the clear upper phase was transferred into a new set of 50-mL centrifuge tubes. Both liver and adipose were allowed to sit at room temperature for 5 min The samples had 100 μL of chloroform added to them for every 500 μL of Tri® Reagent originally used on the sample (500 μL chloroform for adipose, 400 μL chloroform for liver). The samples were vortexed for 1 min each and again left to sit for 5 min at room temperature. The samples were then centrifuged for 15 min at 23,700 x g at 4°C, which caused separation of the samples into three distinct phases: a lower, red phenol-chloroform phase (protein and DNA), a white interphase (protein and DNA), and a

colorless upper aqueous phase (RNA). The upper aqueous phase was transferred into a new set of 50-mL centrifuge tubes which included 0.5 mL of isopropyl alcohol per 1 mL of Tri® Reagent (1.25 mL isopropyl alcohol for adipose, 1 mL isopropyl alcohol for liver). For adipose tissue, 1.5 μL of Ethachinmate (Wako Chemicals USA, Inc., Richmond, VA) was added to help visual the pellet after the next centrifugation step. The sample was vortexed briefly, allowed to sit at room temperature for 10 min, and then centrifuged for 30 min for liver tissue and over 1 h for adipose tissue at 23,700 x g at 4°C. The supernate was discarded, leaving the gel-like RNA pellet in the tube. The tubes were washed with 500 μL of 75% ethanol and the pellet and wash were transferred to 1.5-mL microcentrifuge tubes. Samples were centrifuged with a table-top centrifuge for 5 min at 13,400 x g at 4°C. The 50-mL centrifuge tubes were washed with 700 μL of 75% ethanol. After the centrifugation, the supernate was decanted and the second wash from the 50-mL centrifuge tubes was added to the microcentrifuge tubes, which were then centrifuged again for 5 min at 13,400 x g at 4°C. Lastly, the samples had the supernate decanted, the samples were centrifuged for 10 sec at 13,400 x g at 4°C, and a pipette was used to remove most of the remaining liquid. These samples were stored at -80°C.

Yield and purity were determined by measurement of absorbance at 260λ and 280λ. Samples were reconstituted with diethylpyrocarbonate (DEPC) H_2O, and 2 μL of each reconstituted sample was added to 48 μL of DEPC H_2O. This sample was analyzed by UV spectrometry using a Varian spectrophotometer at 260λ, 280λ, and 320λ for nucleic

acids, protein and background, respectively. The purity was calculated by dividing the nucleic acid content by the protein content after both were corrected for the background.

RNA integrity was evaluated using a Northern gel electrophoresis. One microgram of each sample was added to a tube containing 10 μL of RNA Loading mix consisting of ethidium bromide and bromophenol-blue. The samples were then loaded into an agarose gel and run for over 30 min.

For slot blot analysis of SCD and GAPDH, an mRNA sample concentration of 2 μg/10 μL was incubated at 68 to 70°C for 15 min in a pre-mix of the following solutions: 20 μL of formamide, 7 μL of formaldehyde (37% solution), and 2 μL of 20x trisodium citrate dihydrate (SSC). Samples were chilled on ice and 80 μL of 20x SSC were added. The RNA was applied to a positively charged nucleic acid transfer membrane, Amersham Hybond-N+ (GE Healthcare Biosciences Corp., Piscataway, NJ) in the slots of a commercial slot blot apparatus (Schleicher & Schuell). The membranes were prehybridized in 48% 5x SSC, 0.02% sodium dodecyl sulfate solution (SDS), 50% formamide, 2% Blocking Solution [10% (wt/vol) Blocking Reagent (DIG gel Shift Kit #16, Roche Applied Chemicals, Indianapolis, IN), maleic acid buffer], 0.1% sodium N-lauroylsarcosine solution at 68°C for more than 30 min.

Bovine SCD and GAPDH radio-labeled RNA probes prepared using the DIG RNA Labeling Kit (SP6/T7) were generously provided by the Kyoto University, Kyoto, Japan. The probes were hybridized to the membranes at 68°C for 16 h.

Rinsed membranes for all probes were placed with Kodak X-AR5 x-ray film (Eastman Kodak, Rochester, NY) 1 to 10 h. After auto radiography, slot blots were

scanned using an LKB 2202 Ultroscan Laser Densitometer (Bromma, Sweden), and the intensities of the bands were determined. The densities of the SCD mRNA bands were normalized by GAPDH mRNA.

Sensory evaluation. The steaks sampled for sensory evaluation were individually vacuum packaged and aged for 14 d, after which they were stored at -40°C until evaluated. Steaks were randomly assigned numbers and were subjected to sensory evaluation by an 8-member expert, descriptive attribute sensory panel as defined by ASMA (1995), Meildaard et al. (1991), and Civille and Lyon (1996). Panelists evaluated each sample's attributes using the Spectrum Universal Scale (Meilgaard, 1991) where 0 = none or the absence of the attribute and 15 = extremely intense. Training sessions using reference samples to anchor the panelists and samples from the study were conducted.

On days of testing, the samples had raw weight recorded and were thermocoupled in a geometric center of the thickest portion of each using copper constant wire attached to a digital thermometer (model 91100-50, Cole-Parmer Instrument Co., Vernon Hills, IL). Samples were cooked on an electric Hamilton-Beach grill to an internal temperature 72°C. Cooked weight and time were recorded and samples were cut into 3-cm cubes. Two cubes of sample were then immediately served to the trained meat descriptive attribute sensory panel. Before sample testing began, panelists conducted a warm-up sample to standardize and calibrate the panelists each testing day. Panelists were seated in individual booths that were separated from the sample preparation area. Samples were evaluated under red incandescent lights to reduce the visual appearance on sensory

attributes. Panelists were allowed to cleanse their palette using salt-less saltine crackers and double distilled deionized water.

Histology. Steaks taken for histology were frozen and stored at -20°C. Frozen sections from the steak were cut into 1-cm cubes and sectioned to 10-µm sections using an AO Reichert Model 975C HISTOSTAT Cryostat Microtome (AO Reichert Scientific Instruments, Buffalo, NY). The cubes were fixed in neutral buffered formalin (37%) and then mounted with Tissue-Tek® O.C.T. compound (Sakura Finetek USA, Torrance, CA) Sections were then affixed to VWR microslides superfrost® plus (VWR International, West Chester, PA) and taken through a serial staining process of Oil Red O to stain adipocyte cells and hematoxylin solution according to Mayer (Sigma-Aldrich, St. Louis, MO) for nuclei as described by Preece (1972). Samples were photographed by an Olympus Vanox-S (Olympus America, Inc., Center Valley, PA) using the Scion Visicapture program (Scion Corp., Fredrick, MD) with an objective lens magnification of 4X and an ocular lens magnification of 10X to give a total 40X magnification.

Statistical analysis. All statistical analyses were performed by using SAS® version 9.1.2 (SAS Institute Inc., Cary, NC). Fatty acid composition of s.c. and i.m. adipose tissues, LD, liver, plasma, digesta, and slip points of s.c. lipids were compared by PROC MIXED evaluating the effects of Feeding Group (yearling-fed, calf-fed), Time on high-energy (corn) diet (short-fed, medium-fed, and long-fed) and the interaction of Group x Time. The $P < 0.05$ probability level was established for statistical significance. Sensory characteristics were compared by PROC GLM evaluating the differences in means of the

long-fed yearling-fed group, medium-fed calf-fed group and long-fed calf-fed group. The $P < 0.05$ probability level was established for statistical significance.

RESULTS

Carcass characteristics. The data from the animals shows that all carcass characteristics increased with age (Table 4). Yield grade showed a significant difference between calf-fed and yearling-fed groups ($P = 0.4$). Yield grades also showed a tendency to increase at a greater rate in calf-fed steers than in yearling-fed steers (time x group interaction $P = 0.8$). There was a significant time x group interaction for slaughter and carcass weights ($P < 0.01$). The slaughter and carcass weights showed medium-fed yearling-fed, long-fed calf-fed and long-fed yearling-fed groups were all similar, but these groups were higher than all of the other time on feed groups (Table 4).

Longissimus dorsi and subcutaneous adipose tissue characteristics. The percent moisture in the *Longissimus dorsi* (LD) muscle decreased as the time on feed increased ($P < 0.01$). There also was a significant time x group interaction for percent LD lipid ($P = 0.01$). The percentage i.m. lipid of fat of the calf-fed animals was less than the yearling-fed animals at the short-fed point; however, it showed a consistent rise throughout the study. The yearling-fed cattle showed a similar increase to the calf-fed animals between the short- and medium-fed time points, but this increase then leveled off and was thus lower than the calf-fed animals by the long-fed time points (Table 5).

The slip point temperatures of the s.c. adipose tissue significantly decreased for all animals as time on feed increased ($P < 0.01$), while the concentration of cholesterol in the animals only showed a tendency to decrease with time ($P = 0.06$). Stearoyl CoA desaturase gene expression of the s.c. adipose tissue had separate significant effects for both time on feed ($P < 0.01$) and between yearling and calf-fed groups ($P = 0.04$). All

animals at the medium-fed and long-fed stages showed the greatest mean expression of the SCD gene, whereas the short-fed animals had a very low mean SCD expression. Also, the mean SCD expression of the yearling-fed group had a higher expression than the calf-fed group overall. Yet the SCD expression did not show a time x group interaction ($P = 0.19$) (Table 4). However, visual inspection of the changes in temporal SCD gene expression (Figure 4 and 5) shows that the yearling-fed animals had higher expressions at later ages than calf-fed animals, and they continued to increase in expression with increasing age, whereas the calf-fed animals had already begun to decline in expression by their final slaughter weight. (Table 5)

Fatty acid composition of subcutaneous adipose tissue. The s.c. adipose tissue from the cattle showed significant time on feed effects for the 16:0 (palmitic, $P = 0.02$), 18:0 (stearic, $P < 0.01$), and 20:1 ($P < 0.01$) fatty acids, and the MUFA:SFA ratio ($P < 0.01$). However, whereas 20:1 and the MUFA:SFA ratio means increased with time, the stearic acid decreased and the palmitic acid decreased and then rebounded slightly.

There were many significant time x group interactions for s.c. adipose tissue. Myristic acid (14:0) was shown to decrease in the initial 4 mo of feeding of the calf-fed group when they were no longer milk-fed animals, however, after that time the concentration of myristic acid no longer increased. The yearling-fed cattle had relatively constant levels of myristic acid through the entire study (3.71%-3.02%, $P < 0.01$). Palmitoleic (16:1), oleic (18:1n-9) and linoleic (18:2n-6) acids all showed yearling-feeding and calf-feeding increased fatty acid levels as the time on feed increased ($P = 0.05, 0.05, 0.01$, respectively). The yearlings showed an increase in 20:0 and 18:2 *cis*-9

trans-11 conjugated linoleic acid (CLA), which reached a plateau between the medium- and long-fed times on feed ($P < 0.01$, $P = 0.01$, respectively). However, the calf-fed cattle levels of the same fatty acids decreased between the short-fed and medium-fed times, but then began to rebound slightly by the long-fed time on feed. The yearling-fed group *trans*-vaccenic acid (18:1 *trans*-11) increased between the short-fed and medium-fed group and decreased to the long-fed group, but the calf-fed group levels decreased between the short- and medium-fed groups and then leveled off by the end of the study ($P <0.01$). Alternately, *cis*-vaccenic acid (18:1 *cis*-11) increased in a linear fashion for the calf-fed cattle, whereas in the yearling-fed cattle there was an increase between the short- and medium-fed groups which then leveled off by the long-fed group ($P < 0.01$). Linolenic acid saw a decline in calf-fed cattle between the short- and medium-fed groups, but a slight increase was seen during the last four months on feed. The yearling-fed cattle showed a gradual decline in linolenic acid, but the levels maintained a relatively close range (0.15%-0.09%, $P < 0.01$) (Table 6).

Fatty acid composition of intramuscular adipose tissue. Intramuscular adipose tissue showed significant time on feed effects for palmitic (16:1, $P = 0.01$), oleic (18:1 n-9, $P < 0.01$), cis-vaccenic (18:1 cis 11, $P < 0.01$), and linolenic (18:2 n-6, $P < 0.01$) acids. In the palmitic, oleic and cis-vaccenic acids, the short-fed groups were the lowest with a rise occurring before the medium fed time point, which remained stable until the end of the study. However, the linolenic acid only increased over time.

The MUFA:SFA ratio of i.m. adipose tissue had separate time on feed and group effects, but showed no time x group interaction. This ratio showed an increase from

short-fed to medium-fed time points, which then leveled off ($P < 0.01$); however, the calf-fed group had higher ratios than the yearling-fed group ($P = 0.03$).

There were many significant time x group interactions for i.m. adipose tissue. Stearic acid (18:0) was unique among these fatty acids. It showed about a 2% decrease with time in the calf-fed group (18.99%-17.17%), while the yearling-fed group's concentration decreased from the short-fed to the medium-fed time points and rebounded slightly by the end of the study ($P = 0.02$). Calf-fed group concentrations of 18:1 *trans* 11, 20:0, 18:3 n-3, 18:2 *trans* 10 *cis* 12, 20:1 all showed a drastic initial decrease from the short-fed to medium fed time points followed by a rebound between the medium-fed and long-fed time points. The yearling-fed group showed either an increase during each time period (18:2 *trans* 10 *cis* 12, 20:0, 20:1; $P \leq 0.05$), an increase and then plateau (18:3 n-3, $P < 0.01$), or an initial increase and followed by a decrease (18:1 *trans* 11, $P < 0.01$) (Table 7).

Fatty acid composition of the longissimus dorsi. In the LD muscle, the concentration of 20:1 was significantly higher in the calf-fed group than the yearling-fed group, which was almost devoid of the fatty acid in this tissue ($P = 0.02$). Significant differences with time on feed were shown in percentage of palmitic acid (16:0), which increased with time ($P < 0.01$); *cis*-vaccenic acid (18:1 *cis*-11), which rose between the short- and medium-fed time points, but returned to a similar level by the long-fed time point ($P = <0.01$); and *trans*-vaccenic acids (18:1 *trans*-11), which declined from the short- to long-fed time points ($P = 0.01$).

The interaction of time x group was shown to be significant in both myristic acid (14:0) and myristoleic acid (14:1). The calf-fed group's concentration of myristic acid increased over time, while the yearling-fed concentrations increase initially between the short- and medium-fed time points, but then declined to levels similar to the short-fed time point by the end ($P < 0.01$). Although the concentrations of myristic acid were greater than 0.7% and the levels of myristoleic acid were lower than 0.6%, the pattern shown with the myristic acid were similar to the myristoleic acid. However the myristoleic acid concentration of the calf-fed group remained relatively steady between short- and medium-fed time points, and the concentration of the long-fed time point in the yearling-fed group dropped slightly below the levels of the short-fed time point ($P < 0.01$). Time x group interaction effects were also seen in stearic acid (18:0), oleic acid (18:1 n-9), linoleic acid (18:2 n-6), and linolenic acid (18:3 n-3). The concentration of stearic acid in the calf-fed group was similar between the short- and medium-fed time points (16.32% and 16.06%, respectively); however, they then dropped down to 13.06% by the long-fed time point. Whereas, the yearling-fed animals had an initial drop from 18.73% at the short-fed time point to 13.06% at the medium-fed time point followed by an increase to 16.55% by the long-fed time point ($P < 0.01$). The oleic acid concentration of the yearling-fed group steadily increased over time from 30.22% to 40.55%. Yet, the calf-fed group concentration increased from 28.01% to 42.56% from the short- and medium-fed time points and then declined to a final concentration of 38.19% by the end of the study ($P = 0.01$). This concentration is similar to the final long-fed yearling-fed group. The linoleic acid of the yearling-fed cattle remained steady

between the first two time points, but these concentrations decreased by the long-fed time point. Conversely, the calf-fed group concentration dropped between the short- and medium-fed time points, but the concentrations then increased by the long-fed time point to a level parallel to the yearling-fed animals ($P = 0.05$). The concentration of linolenic acid in the short-fed calf-fed group were much higher than the yearling-fed animals at the same time point, 1.7% as opposed to 0.54%; however, the other time points had concentrations which were essentially zero for both calf- and yearling-fed animals ($P = 0.01$).

The MUFA:SFA ratio tended to be lower in the short-fed time point than in the medium-fed and long-fed time points, which were both similar in concentration ($P = 0.06$). (Table 8)

Fatty acid composition of liver tissue. With the liver fatty acids, there was a significant group effect for 16:0, 18:1 n-9 and 20:1. Each of these fatty acids displayed higher levels in the calf-fed group than in the yearling-fed group ($P \leq 0.03$). Gadoleic acid (20:1) also showed a separate effect with time on feed, as did *cis*-vaccenic acid (18:1 *cis*-11). The levels of gadoleic acid declined with time on feed ($P < 0.01$); while the *cis*-vaccenic acid showed similar concentrations in the short- and medium-fed time points which then declined by the end of the study ($P = 0.05$).

There were several fatty acids which exhibited significant time x group interaction. Myristic acid (14:0) steadily declined in the yearling-fed group; however, myristic acid concentration in the calf-fed group declined and leveled-off by the long-fed group ($P < 0.01$). The calf-fed group showed a similar pattern with myristoleic acid (14:1), even

though the actual concentrations were lower than the myristic acid. The yearling-fed group's myristoleic acid levels also declined between the short- and medium-fed time points, but, unlike the myristic acid, the concentrations leveled off between the medium- and long-fed time points ($P < 0.01$). Interestingly, palmitoleic acid (16:1) and stearic acid (18:0) showed opposing patterns. Whereas the oleic acid concentrations of the calf-fed group decreased between the short- and medium-fed time points followed by an increase by the long-fed time points; the concentration of stearic acid increased during the first period and then decreased by the long-fed time points. Conversely, whereas the oleic acid concentrations in the yearling-fed cattle increased slightly during the first period and then decreased by the long-fed time points, the stearic acid levels decreased slightly between the short- and medium-fed time points and then increased by the long-fed time points ($P = 0.03$, oleic acid; $P < 0.01$, stearic acid). The concentration of *trans*-vaccenic acid (18:1 *trans*-11) dropped from 2.14% in the short-fed time point to 0.59% in the long-fed calf-fed group, but the yearling-fed group's level of *trans*-vaccenic acid remained steady between the short-fed and medium-fed time points before declining at long-fed time point ($P < 0.01$). Linoleic acid (18:2 n-6) of both the calf- and yearling-fed groups increased in concentration and had similar finishing points for the long-fed time points (10.34%, 10.27%, respectively). However, the starting point of the yearling-fed group was higher than the calf-fed group (8.92% vs. 5.61%, $P = 0.01$). The levels of arachidic acid (20:0) for the both the calf- and yearling-fed groups started at 0.06%, but the yearling-fed group showed no 20:0 for the remained of the study. The calf-fed animals showed a drop to 0.05% by the medium-fed time point, but then their

concentration of 20:0 also dropped to zero by the long-fed time point ($P = 0.05$). Linolenic acid (18:3 n-3) started with higher concentrations in the calf-fed group than in the yearling-fed group (1.78% vs. 0.89%), but these concentrations dropped to similar values by the medium-fed time point and remained there until the end of the study ($P < 0.01$). The levels of *cis*-9, *trans*-11 CLA increased steadily 0% to 0.28% in the calf-fed group, but the yearling-fed group increased from 0.02% to 0.31% and then dropped to 0.25% by the long-fed time point ($P < 0.01$). The MUFA:SFA ratio of the calf-fed group remained consistently higher than the yearling-fed group at each time point. The calf-fed group ratio ranged between 0.43 and 0.38, while the yearling-fed group ratio remained between 0.32 and 0.37. (Table 9)

Fatty acid composition of plasma. The plasma fraction of linoleic acid (18:2 n-6) had separate time on feed and group effects with no significant interactions. Linoleic acid increased over time in both groups ($P < 0.01$). While separately, the yearling-fed group had overall higher values than the calf-fed group ($P = 0.03$).

The time x group interaction was seen in several of the plasma fatty acids. Palmitic acid concentrations had completely opposing patterns between groups. The short-fed yearling-fed group started a lower concentration than the calf-fed group (7.94% vs. 12.84%). Then the yearling-fed group's concentration increased while the calf-fed group's concentration decreased causing the yearling-fed group to have higher concentrations than the calf-fed group at the medium-fed time point (12.66% vs. 9.78%). This was then reversed to concentrations similar to those at the start of the study for both the yearling- and calf-fed groups at the long-fed time point (8.67% vs. 11.7%,

respectively; $P < 0.01$). A similar effect was seen for palmitoleic acid (16:1), with the exception that the concentrations for the long-fed time point were lower at the long-fed time point than the short- and medium-fed time points for both respective groups ($P < 0.01$). Stearic acid (18:0) levels in the yearling-fed group started lower than the calf-fed group, but the yearling-fed group increased linearly over time at levels consistently higher than the calf-fed group throughout the rest of the study. The calf-fed group concentrations remained stable between the short- and medium-fed time points, but they then increased between the medium and long-fed animals at a similar rate to the yearling-fed group ($P = 0.02$). *Trans*-vaccenic acid (18:1 *trans*-11) had a pattern similar between groups with the yearling-fed group concentrations rising to a peak at the medium-fed time point and then falling to a concentration similar to the starting point by the end of the study. The calf-fed group concentrations of *trans*-vaccenic acid started at a high concentration and dropped to zero by the end of the study. Both oleic acid (18:1 n-9) and *cis*-vaccenic acid (18:1 *cis*-11) had identical patterns in the plasma. The yearling-fed group's concentration of these fatty acids started low at the short-fed time point, while the calf-fed group concentration started high. Then by the medium-fed time point the yearling-fed group's concentrations increased while the calf-fed group's concentrations decreased. However at the long-fed time point, the yearling-fed group's concentrations decreased and the calf-fed group's concentrations increased finishing with the calf-fed and yearling-fed concentrations at similar points ($P < 0.01$). The values of linolenic acid (18:3 n-3) started with concentrations higher in the calf-fed group than the yearling-fed group (7.63% vs. 2.29%), but both groups dropped to essentially zero

values for the rest of the study ($P < 0.01$). The same is true with the calf-fed group in regards to *cis*-9, *trans*-11 CLA (18:2 *cis*-9, *trans*-11); however, the yearling-fed group concentrations were zero throughout the whole study ($P < 0.01$). The MUFA:SFA ratio of the yearling-fed group remained stable through the study (0.39 to 0.45), whereas, the calf-fed group started higher (0.69) and dropped to a ratios similar to the yearling-fed animals at the medium-fed and long-fed time points (around 0.40; $P < 0.01$) (Table 10).

Fatty acid composition of digesta. Many of the fatty acids from digesta did not show any significant differences due to time on feed, group or the time x group interaction. Time on feed was a significant effect for myristic acid (14:0), linoleic acid (18:2 n-6), arachidic acid (20:0), linolenic acid (18:3 n-3), and *cis*-9, *trans*-11 CLA (18:2 *cis*-9, *trans*-11). Myristic acid concentration was lowest at the short-fed time point and then peaked at the medium-fed point before dropping down again by the long-fed time point ($P = 0.03$). Both linoleic and *cis*-9, *trans*-11 CLA concentrations increased with time ($P < 0.01$), and arachidic acid and linolenic acid had higher concentrations at the short-fed time point, dropped down at the medium-fed time point and remained steady through to the end of the study ($P < 0.01$).

A significant time x group interaction was seen with myristoleic acid (14:1), palmitic acid (16:0), and *trans*-vaccenic acid (18:1 *trans*-11). Myristoleic acid was higher in the yearling-fed group than the cattle-fed group at the short-fed time period. The yearling-fed group remained at this concentration throughout the study, while the calf-fed group rose to meet similar levels of the yearling-fed group at the medium-fed time point. The calf-fed group concentration then continued to rise past the yearling-fed group by the

end of the study ($P = 0.05$). Palmitic acid levels in the calf-fed animals rose steadily from the short-fed to the long-fed time points, while the yearling-fed cattle rose between the short-fed and medium-fed time points and then dropped back to similar starting levels by the long-fed group ($P < 0.01$). *Trans*-vaccenic acid levels in the calf-fed animals remained steady between the short-fed and medium-fed time points and then dropped down slightly by the long-fed time points. Whereas, the yearling-fed group remained at concentrations higher than the calf-fed group throughout the study, but these concentration increased between the short-fed and medium-fed time points before declining to concentrations lower than the short-fed time point ($P = 0.04$). MUFA:SFA ratios did not show any significant differences or trends for digesta during this study ($P > 0.25$) (Table 11).

Histology. Under visual inspection the histological sections of the LD tissue of cattle from each different treatment show development of marbling adipose tissue with varying treatment and age. The short-fed calf-fed group (baseline) and short-fed yearling-fed group marbling development had small sparse adipose cells that were beginning to develop around the fasciculus (Figure 1). These sections show there was no appreciable marbling development before weaning in the calf-fed group or in the time the yearling-fed group was on pasture.

The cattle from the medium-fed time points (12 mo of age) started to develop what the industry term as “flecks” of marbling (Figure 2). At this point, these flecks are still not visible to the naked eye; however, the calf-fed group show fewer cells taking up a similarly area on the section as the yearling-fed group. Meaning, the yearling-fed group

have a greater amount of cells with smaller volumes than the calf-fed group. This visual difference can again be seen in the older animal, where a similar area of adipose tissue is shown to have greater numbers of smaller cells in the yearling-fed group than in the calf-fed group (Figure 3).

DISCUSSION

First it must be noted that during the study period for these animals, the yearling-fed animals were supplemented with the high energy (corn) diet. This was due to the drought conditions being experienced in this area and the lack of high quality pasture. The animals were supplemented only to make sure they were obtaining the desired gain of 0.9 kg/day. This could have provided a confounding factor for the carcass characteristics and fatty acid profiles of the animals. However, it would appear that it had very little, if any effect on the SCD gene expression data.

It must also be noted that for the purposes of this study, 18:1 *trans*-vaccenic acid was used to calculate total SFA due to its similar health effects and mainly due to its use as a substrate for the SCD enzyme activity. Under the same reasoning, 18:2 *cis*-9, *trans*-11 CLA was used to calculate MUFA because it is a product of the SCD enzyme activity.

The data from this study show that calf-fed and yearling-fed animals fed to the same market weight and age differ very little in their carcass composition and characteristics between groups at the same time on feed endpoints. The differences seen in the weights of our animals are due to the fact that the yearling-fed cattle were heavier when they were switched to the high energy diets. Once on these diets, carcass growth was linear until the last endpoint when the yearling cattle were slaughtered at market weight. Contrary to Lunt and Orme (1987) and Anderson et al. (2005), our cattle displayed similar marbling scores when fed to this constant body weight. These data are similar to those seen by Harris et al. (1997). These data also show that marbling essentially did not begin to accumulate to a large degree in the yearling-fed cattle until after they were

switched to the corn based diet. This holds true with other data comparing quality of corn-fed vs. grass-fed *Bos taurus* animals (Chung et al., 2006). Although the exact mechanisms are not known for this effect, some have attributed this to the negative effects of high vitamin A and PUFA content found in pasture and grass-based diets can have on the genetic expression required for the development of i.m. adipose cells (Bindon, 2004; Chung, 2006; Siebert et al., 2003; Yang et al., 1999b).

In evaluating time on feed of a finishing diet, Duckett et al. (1993) observed that as carcass weight and time on feed increased, the fat levels continued to increase while the moisture levels inversely decreased. However, their study differed from ours in that all of their animals were pasture-fed from weaning age and spent twice the time on pasture than the cattle in our study. Still, they were able to show a rise in muscle lipid and drop in muscle moisture that was comparable in magnitude, if not actual numerical value, to what was seen in our study. They were also able to demonstrate that levels of total lipids in s.c. and i.m. will reach a plateau similar to what was seen in our data with the yearling-fed cattle. Although not reflected in the called marbling score, the percentage of lipid did not differ between groups at different times on feed. The consistent rise in lipid in the muscle is to be expected in the calf-fed animals that began i.m. adipocyte hyperplasia early and, by market weight, were most likely in the stage of adipocyte hypertrophy. However, due to the backgrounding of the yearling cattle, the i.m. adipocytes were still in the stage of hyperplasia and were just beginning the state of hypertrophy by the time they reached market weight. This is in agreement with the histological sections taken from the animals, which showed many large cells at market

weight in the calf-fed group but many more cells of smaller size in the yearling-fed cattle at market weight. If allowed to grow older, the cells in the yearling-fed animals could have fully reached the hypertrophy stage of adipocyte development and potentially had higher lipid percentages and marbling scores.

The sensory traits followed suit with the carcass characteristics and showed no significant differences between the flavor or palatability of steaks from the calf-fed group or yearling groups fed to either the same age or body weight. These steaks were all from animals with similar marbling scores and backfat thicknesses, and, as has been shown previously, animals fed for similar times on feed will produce indistinguishable sensory characteristics (Dolezal et al., 1982; Sainz and Paganini, 2004).

Pre-weaned ruminants function like a monogastric and they deposit LCFA from milk fat into the adipose tissue for storage (Drackley, 2005). Our short-fed calf-fed group represent weaned calves whose rumen has just become fully developed. Thus, any fat deposited before this point would represent only dietary fat and *de novo* synthesis in the tissues. Also, we demonstrated the lack of SCD expression of cattle at weaning age, and therefore, there is no conversion of SFA to MUFA up to this point. Milk from pasture-fed beef cows is rich in palmitic, stearic acid, and oleic acid (Lake et al., 2007). This would explain why these are the three predominant fatty acids in the adipose tissue; however, palmitic and oleic are the highest of these three fatty acids. What is interesting is that we saw the concentration of oleic acid in the i.m., LD, and s.c. was the lower for the short-fed calf-fed group than in any other group for each respective tissue. Once the SCD gene expression was increased after being put on the corn-based diet, the value of

oleic acid began to increase in the s.c. and i.m., while the concentration of palmitic acid remained relatively constant. This is so because the deposition of palmitic acid does come from dietary fatty acids, but in the tissues its concentrations are regulated by *de novo* synthesis. This is evidenced in our study by low digesta and plasma concentrations, but high concentrations found in the tissues, and by the fact that the levels remained relatively constant throughout the study for both groups.

It is interesting to note the fact that linoleic acid was the predominant circulating fatty acid throughout the study, and these levels increased with the yearling-fed group always showing higher values than the calf-fed animals. However, the reasoning for this is unclear at this time.

In the developed rumen, higher roughage diet produces more acetic acid, while high concentrate diet produces more proprionic acid from the rumen at the expense of acetic acid (Bell, 1979). Since i.m. uses glucose as the main substrate for de novo fatty acid synthesis (Rhoades et al., 2007; Smith and Crouse, 1984), perhaps the greater concentrate diet adds to greater proprionate, which contributes to higher glucose levels for i.m. de novo fatty acid synthesis and less acetate for s.c. de novo fatty acid synthesis. Conversely, the high roughage diet allows for more acetate, which is why the s.c. fat will continue to grow to meet similar backfat thickness while not improving in quality grade. Once switched over to a concentrate diet from a roughage diet, the ratios change and marbling begins to develop, but is unable to catch up before weight and backfat thickness reach market standards. This could explain why the i.m. fat had not reached a state of hypertrophy until after the animals were switched to the corn-based diet.

Further, Smith et al. (2007) found that acetate incorporation into s.c. cells of yearling-fed steers was higher than market weight calf-fed steers of the same age. The yearling-fed cattle were still growing and had a higher capacity to deposit s.c. fat than the calf-fed at the same age. However, by the time yearling-fed cattle got the same body weight as the calf-fed animals, the incorporation of acetate into fatty acids had dropped to levels comparable to the calf-fed steers. This indicated the animals' deposition of fatty acids had started to decline. Showing a plateau reached at market weight of the yearling-fed cattle's ability for de novo fatty acid synthesis. This could explain why we did not see higher rates of MUFA:SFA ratios in our yearling-fed animals at market weight. Due to the animals' lack of ability to provide enough de novo SFA substrate to keep up with the SCD gene activity, the MUFA:SFA ratio did not vary from the calf-fed animals at the same weight.

The digesta of these animals showed higher levels of *trans*-vaccenic acid and palmitic acid in the short-fed and medium-fed endpoints for the yearling-fed group. Since protozoa have been shown to contain higher levels of both of these products (Devillard et al., 2006; Or-Rashid et al., 2007), feeding a high energy concentrate diet will produce an inhospitable acidic environment for the protozoa causing their population to decrease. When prolonged, this could also cause bacterial populations to decrease. Bacteria have been shown to be responsible for rumen biohydrogenation (Fukuda et al., 2006; Vossenberg and Joblin, 2003; Wallace et al., 2006); therefore, as their populations decrease, the substrates for these reactions, linoleic acid and CLA, would begin to increase while the products, stearic acid and *trans*-vaccenic acid, would

decrease. This is precisely what is seen within our animals. In the digesta, the levels of linoleic acid and CLA significantly increased with time on feed, and at the same time, there was a numeric decrease in stearic acid. Because of this, at a time when SCD gene expression is higher in the older cattle the levels of SFA passing out of the rumen would be predicted to be lower and thus providing less substrate for the enzyme. However, all through the study the levels of MUFA, palmitoleic, and oleic acid remained at similar levels. The increase in concentration of palmitic and linoleic acids and the steady-state of oleic acid can also be partially attributed to the higher concentrations of these fatty acids found in corn-based diets (Dayani et al., 2007; Duckett et al., 2002). Conversely, the low levels of palmitoleic acid and numerically decreasing level of stearic acid are due to the low levels also found in this diet. This diet, combined with the decreasing protozoal and bacterial populations, would explain what was observed in our study.

The manipulation of the MUFA:SFA ratio in these Angus steers proved to be more difficult than just increasing the age of the cattle before switching it to a high energy diet. The SCD gene expression was greater in the yearling-fed cattle, which were older at the time the gene expression was stimulated. This shows that they had a greater capacity to produce the enzyme capable of desaturating fatty acids to provide a healthier MUFA. This increase was higher than the levels seen in all calf-fed animals, and continued to increase even by the point of market weight. Conversely, the calf-fed animals' expression peaked at the medium-fed endpoint. This leaves the question of why there was a decline in expression for the calf-fed animals once they reached market weight. It would suggest that they reached a plateau after 8 months on feed. However,

we cannot confirm this in the yearling-fed animals because they reached market weight at only 5 months. Even with this high expression of the yearling-fed animals, a concomitant increase in MUFA:SFA ratio of s.c. adipose tissue was not seen. We suggest that this is due to the initial deposit of SFA while the animal was on pasture. This accumulated a core of SFA during the beginning hyperplasia and hypertrophy stages that remained in the adipocyte. Although more MUFA may have been produced and deposited later in the adipocyte, the initial SFA brought the ratio down in the final product. This study thus demonstrated that, although gene expression was greater in yearling-fed cattle than calf-fed animals at market weight, the MUFA:SFA ratio was not able to surpass the calf-fed animals.

This field requires further investigation if we are to provide a product which meets the health guidelines set down by the AHA and also meets demands of the Japanese and Korean markets. Now that it has been demonstrated that greater expression of the SCD gene is capable in older animals, we need to devise a way to utilize this expression to provide us with the desired results.

CONCLUSIONS

In summary, increasing the oleic acid and other MUFA in beef is hindered by the fact that the optimization of these fatty acids is a multifaceted issue. The ideal diet to produce these results is not as straightforward as the amount of time on a pasture or feedlot ration. Each of these separate diets affects the products from the rumen and expression of the genes in a different manner. With all of this, the breed and age of the animal are also major factors which affect the results. In our study, we demonstrated that yearling-fed animals provided a comparable end-product to that of the calf-fed animals. However, the yearling-fed animals were not able to surpass the MUFA:SFA ratio seen in the calf-fed animals as we had hypothesized. We were able to show an increase in SCD gene expression in the long-fed yearling-fed cattle, but their initial deposits of SFA combined with the lack of SCD expression while on pastures, prevented the MUFA:SFA ratio from increasing at a rate fast enough to change the final ratios in the animal. Further investigation into this field is required if we want to be able to improve the healthfulness our beef products, and in turn, increase its marketability to the consumer.

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APPENDIX

Table 1. Plasma values of mildly hypercholesterolemic men fed ground beef from hay-fed steers, ground beef from corn-fed steers, or ground beef containing Wagyu fat trim.

Item	Baseline	Hay-fed Angus ground beef	Long-fed Angus ground beef	Wagyu/s.c.[x] ground beef	SE
n	10	5	5	10	
VLDL- Cholesterol	30.1[ab]	17.1[b]	34.3[a]	31.36[ab]	2.92
HDL-Cholesterol	38.2	38.2	42.7	40.1	0.73
LDL-Cholesterol	138.6	159.5	142.3	142.5	3.18
LDL:HDL ratio	3.64[a]	4.19[a]	3.35[b]	3.58[b]	0.06

[x] Ground beef produced with Wagyu s.c. fat trim.
[ab] Means within a row with different superscripts differ ($P < 0.05$).

Table 2. Carcass and cellular characteristics of Angus steers fed corn or hay-based diets for 8, 12, 16, or 20 mo.

	Endpoint/diet[a]						
	U.S. endpoint		Japanese endpoint			P-values	
Item	8 mo/corn	12 mo/hay	16 mo/corn	20 mo/hay	SE	Diet	Endpoint
Carcass data							
Carcass weight, kg	323.4	307.7	407.8	403.0	14.5	0.59	0.01
Marbling score[b]	673.3	580.0	802.5	672.5	45.4	0.24	0.24
Adjusted fat thickness, cm	1.44	1.30	2.51	1.90	0.18	0.23	0.01
Subcutaneous fatty acids[c]							
18:0	16.1	20.4	7.25	9.11	1.51	0.01	0.001
18:1*n*-9	37.5	32.1	41.7	39.8	1.14	0.01	0.01
MUFA:SFA ratio	0.91	0.72	1.42	1.22	0.22	0.01	0.0.1

[a] Data are means for 4 steers per endpoint and diet group.
[b] A = 100; B = 200; C = 300; D = 400; E = 500.
[c] g/100 g total fatty acids

Table 3. Ingredients and chemical composition of the high-energy (corn) diet.

Item	Diet Analysis
Ground milo	20.00
Ground corn	48.05
Cottonseed meal	6.00
Cottonseed hulls	15.00
Molasses	7.50
Limestone	0.96
Trace mineralized salt[a]	0.56
Dicalcium phosphate	0.23
Potassium chloride	0.16
Zinc oxide	0.01
Ammonium sulphate	0.25
Vitamin premix[b]	0.08
R-1500[c]	1.20
Total Percentages	100.00
Nutritional composition[d]	
Dry matter, %	89.13
Crude Protein, %	11.16
NEm (Mcal/kg)	1.81
NEg (Mcal/kg)	1.19
Acid detergent fiber, %	14.12
Calcium, %	0.52
Phosphorus, %	0.36

[a] Trace mineralized salt: NaCl, 98%; Zn, 0.35%; Mn 0.28%; Fe, 0.175%; Cu, 0.035%; I, 0.007%; Co, 0.0007%.

[b] Vitamin Premix: vitamin A, 2,200,000 IU/kg; vitamin D, 1,100,000 IU/kg; vitamin E, 2,200 IU/kg.

[c] R-1500: 1.65g monensin sodium (Rumensin) per kg.

[d] Percentage of dry matter. Calculated values based on NRC (1996).

Table 4. Carcass characteristics of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[c]
Slaughter Wt., kg	175.09[z]	297.78[y]	376.37[x]	514.26[w]	488.18[w]	503.83[w]	16.89	<0.01	<0.01	<0.01
Carcass Wt., kg	103.08[z]	172.71[y]	219.99[x]	292.00[w]	314.00[w]	317.63[w]	10.69	<0.01	<0.01	<0.01
Marbling[d]	200.00	272.50	452.50	422.50	455.50	492.50	25.50	<0.01	0.21	0.15
Quality grade[e]	250.00	262.50	400.00	387.50	400.00	425.00	15.02	<0.01	0.50	0.46
Actual Fat Thickness, cm	0.17	0.25	1.14	1.43	1.71	1.59	0.13	<0.01	0.46	0.31
Adjusted Fat Thickness, cm	0.17	0.32	1.30	1.46	1.84	1.68	0.12	<0.01	0.62	0.34
Ribeye area, cm^2	47.90	49.19	66.13	76.13	75.81	75.16	0.45	<0.01	0.15	0.17
KPH, %	1.30	1.67	3.08	3.34	4.10	3.53	0.36	<0.01	0.93	0.37
Yield Grade	1.16	1.82	2.35	2.61	3.19	3.10	0.16	<0.01	0.04	0.08

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] Practically Devoid = 100; Trace = 200; Slight = 300; Small = 400; Modest = 500; Moderate = 600; Slightly Abundant = 700; Moderately Abundant = 800; Abundant = 900.

[e] Standard = 200; Select = 300; Choice = 400; Prime = 500.

Table 5. Percentage moisture and lipid, cholesterol concentration of *L. dorsi* muscle tissue and slip points and stearoyl-CoA desaturase gene expression of subcutaneous adipose tissue of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[c]
% Moisture	75.78	74.39	70.81	71.33	69.40	70.46	0.80	<0.01	0.92	0.29
% Lipid	0.79[z]	1.62[z]	5.13[y]	7.00[x]	9.98[w]	7.75[wx]	0.64	<0.01	0.76	0.01
Cholesterol, mg/100g	82.29	70.94	76.32	68.12	73.96	70.21	4.82	0.06	0.57	0.73
Slip points, °C	41.00	43.13	39.15	39.60	34.53	36.48	1.16	<0.01	0.13	0.73
Stearoyl-CoA Desaturase[d]	4.99	248.41	576.06	1180.45	138.91	1528.69	311.75	<0.01	0.04	0.19

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] Reported as gene expression (SCD/GAPDH)

Table 6. Subcutaneous adipose tissue % fatty acid composition of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[x]
14:0	5.34^{x}	3.34^{y}	3.16^{y}	3.71^{y}	3.02^{y}	3.19^{y}	0.29	<0.01	0.08	<0.01
14:1n-5	1.31	0.94	1.04	1.43	1.74	1.28	0.18	0.12	0.33	0.06
16:0	28.59	29.85	26.08	26.97	27.43	27.32	0.93	0.02	0.38	0.75
16:1n-7	2.43^{z}	3.60^{yz}	3.57^{yz}	4.23^{xy}	5.58^{wx}	4.23^{wy}	0.51	<0.01	0.70	0.05
18:0	16.49	18.79	14.71	11.84	8.79	12.01	1.67	<0.01	0.52	0.17
18:1trans-11	3.19^{xz}	1.70^{y}	1.48^{y}	3.78^{x}	1.60^{y}	2.19^{yz}	0.42	0.19	0.21	<0.01
18:1n-9	29.62^{y}	33.33^{y}	40.30^{xz}	37.37^{z}	41.27^{x}	39.86^{xz}	1.32	<0.01	0.85	0.05
18:1cis-11	0.64^{z}	0.96^{z}	1.50^{y}	1.48^{y}	2.01^{x}	1.45^{y}	0.12	<0.01	0.37	<0.01
18:2n-6	0.81^{z}	1.52^{x}	1.61^{yx}	1.59^{wx}	1.93^{wy}	1.83^{wx}	0.14	<0.01	0.10	0.01
20:0	0.26^{x}	0.00^{y}	0.00^{y}	0.07^{z}	0.04^{yz}	0.07^{yz}	0.03	<0.01	0.02	<0.01
18:3n-3	0.39^{x}	0.15^{y}	0.02^{z}	0.11^{yz}	0.06^{yz}	0.09yz	0.04	<0.01	0.25	<0.01
18:2cis-9,trans-11	0.54^{x}	0.00^{y}	0.20^{xy}	0.47^{x}	0.36^{xy}	0.46^{x}	0.13	0.55	0.59	0.01
18:2trans-10,cis-12	0.24	0.00	0.13	0.11	0.09	0.08	0.06	0.79	0.08	0.10
20:1	0.09	0.00	0.17	0.24	0.30	0.22	0.04	<0.01	0.26	0.07
MUFA:SFA[d]	0.65	0.73	1.04	0.98	1.26	1.06	0.06	<0.01	0.26	0.10

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] MUFA:SFA = (14:1 + 16:1 +18:1cis-9 + 18:1cis-11 + 18:2cis-9,trans-11, 20:1)/(14:0 + 16:0 + 18:0 + 18:1trans-11 + 20:0).

Table 7. Intramuscular adipose tissue % fatty acid composition of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[x]
14:0	3.13	3.40	3.18	3.25	2.95	2.55	0.34	0.28	0.94	0.60
14:1n-5	0.75	0.64	0.68	0.74	0.68	0.50	0.09	0.36	0.33	0.43
16:0	26.23	30.69	27.51	28.30	28.04	26.61	1.16	0.62	0.19	0.06
16:1n-7	1.84	1.93	2.57	2.79	2.37	1.96	0.24	0.01	0.86	0.39
18:0	18.99[y]	25.08[x]	18.00[y]	16.54[y]	17.17[y]	19.94[y]	1.23	<0.01	0.02	0.02
18:1trans-11	3.76[x]	1.75[y]	1.60[y]	3.67[x]	2.20[y]	2.56[y]	0.34	0.53	0.62	<0.01
18:1n-9	30.67	30.65	38.39	36.17	37.59	37.20	1.18	<0.01	0.37	0.61
18:1cis-11	0.89	0.83	1.14	1.06	1.05	0.92	0.06	<0.01	0.07	0.81
18:2n-6	1.24	1.65	1.67	1.58	2.24	1.99	0.14	<0.01	0.82	0.06
20:0	0.28[w]	0.00[z]	0.01[yz]	0.10[xy]	0.10[xy]	0.12[x]	0.03	0.07	0.05	<0.01
18:3n-3	0.62[w]	0.00[x]	0.05[xz]	0.14[y]	0.08[yz]	0.13[y]	0.02	<0.01	<0.01	<0.01
18:2cis-9,trans-11	0.34	0.00	0.15	0.36	0.28	0.27	0.15	0.75	0.71	0.19
18:2trans-10,cis-12	0.16[x]	0.00[y]	0.00[y]	0.05[yz]	0.08[z]	0.08[z]	0.02	0.06	0.08	<0.01
20:1	0.14[x]	0.00[y]	0.10[x]	0.13[x]	0.17[x]	0.15[x]	0.03	0.06	0.15	0.05
MUFA:SFA[d]	0.66	0.56	0.86	0.80	0.84	0.79	0.04	<0.01	0.03	0.76

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] MUFA:SFA = (14:1 + 16:1 +18:1cis-9 + 18:1cis-11 + 18:2cis-9,trans-11, 20:1)/(14:0 + 16:0 + 18:0 + 18:1trans-11 + 20:0).

Table 8. *Longissimus dorsi* lean muscle tissue % fatty acid composition of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[x]
14:0	0.90^{y}	0.75^{y}	1.25^{y}	2.00^{x}	1.90^{x}	1.09^{y}	0.21	<0.01	0.69	<0.01
14:1n-5	0.30^{z}	0.20^{yz}	0.27^{yz}	0.54^{x}	0.55^{x}	0.10^{y}	0.06	0.07	0.09	<0.01
16:0	17.76	19.17	24.53	25.83	27.46	24.64	1.40	<0.01	0.97	0.25
16:1n-7	1.47	1.52	2.95	5.69	3.14	2.25	1.11	0.06	0.49	0.26
18:0	16.32^{y}	18.73^{x}	16.06^{y}	13.06^{z}	13.52^{z}	16.55^{xy}	0.87	<0.01	0.26	<0.01
18:1trans-11	2.12	1.71	0.86	1.75	0.54	0.77	0.37	0.01	0.44	0.24
18:1n-9	28.01^{w}	30.22^{w}	42.56^{x}	36.23^{y}	38.19^{yz}	40.55^{xz}	1.45	<0.01	0.62	0.01
18:1cis-11	1.37	1.47	1.98	1.74	1.52	1.40	0.11	<0.01	0.36	0.29
18:2n-6	6.50^{x}	5.98^{x}	2.48^{y}	5.91^{x}	4.91^{x}	5.01^{x}	0.80	0.06	0.12	0.05
20:0	0.16	0.04	0.02	0.00	0.00	0.00	0.03	0.06	0.26	0.57
18:3n-3	1.70^{x}	0.54^{y}	0.03^{z}	0.00^{z}	0.00^{z}	0.00^{z}	0.10	<0.01	<0.01	<0.01
18:2cis-9,trans-11	6.95	0.00	0.00	0.00	0.08	0.05	2.61	0.33	0.28	0.33
18:2trans-10,cis-12	0.09	0.00	0.08	0.00	0.00	0.00	0.04	0.46	0.09	0.46
20:1	0.06	0.00	0.22	0.00	0.14	0.05	0.06	0.42	0.02	0.41
MUFA:SFA[d]	1.01	0.83	1.13	1.04	1.01	1.03	0.07	0.06	0.18	0.39

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] MUFA:SFA = (14:1 + 16:1 +18:1cis-9 + 18:1cis-11 + 18:2cis-9,trans-11, 20:1)/(14:0 + 16:0 + 18:0 + 18:1trans-11 + 20:0).

Table 9. Liver tissue % fatty acid composition of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[x]
14:0	1.61^{x}	0.70^{y}	0.51^{y}	0.48^{y}	0.59^{y}	0.36^{y}	0.13	<0.01	<0.01	<0.01
14:1n-5	0.47^{x}	0.25^{y}	0.15^{z}	0.13^{z}	0.21^{y}	0.15^{z}	0.03	<0.01	<0.01	<0.01
16:0	16.09	13.79	13.10	13.43	15.18	12.03	0.77	0.10	0.01	0.09
16:1n-7	1.17^{x}	0.68^{yz}	0.75^{yz}	0.73^{yz}	0.88^{y}	0.58^{z}	0.08	0.06	<0.01	0.03
18:0	22.43^{z}	26.80^{y}	27.08^{wy}	25.75^{xy}	24.26^{xz}	28.37^{x}	0.66	0.02	<0.01	<0.01
18:1trans-11	2.14^{w}	1.21^{x}	0.96^{xy}	1.21^{xy}	0.59^{z}	0.86^{yz}	0.12	<0.01	0.19	<0.01
18:1n-9	15.08	11.41	13.51	12.58	13.70	12.13	0.61	0.86	<0.01	0.09
18:1cis-11	1.35	1.17	1.22	1.31	1.03	1.15	0.08	0.05	0.86	0.13
18:2n-6	5.61^{z}	8.92^{y}	9.32^{wy}	10.75^{wx}	10.34^{xy}	10.27^{xy}	0.54	<0.01	<0.01	0.01
20:0	0.06^{x}	0.06^{x}	0.05^{x}	0.00^{y}	0.00^{y}	0.00^{y}	0.01	<0.01	0.12	0.05
18:3n-3	1.78^{x}	0.89^{y}	0.22^{z}	0.26^{z}	0.21^{z}	0.22^{z}	0.11	<0.01	<0.01	<0.01
18:2cis-9,trans-11	0.00^{z}	0.02^{z}	0.12^{y}	0.31^{x}	0.28^{x}	0.25^{x}	0.03	<0.01	0.02	<0.01
18:2trans-10,cis-12	0.00	0.02	0.04	0.00	0.00	0.00	0.01	0.24	0.40	0.06
20:1	0.14	0.10	0.11	0.05	0.05	0.00	0.03	<0.01	0.03	0.95
MUFA:SFA[d]	0.43^{w}	0.32^{x}	0.38^{yz}	0.37^{yz}	0.40^{wy}	0.34^{xz}	0.02	0.93	<0.01	0.01

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] MUFA:SFA = (14:1 + 16:1 +18:1cis-9 + 18:1cis-11 + 18:2cis-9,trans-11, 20:1)/(14:0 + 16:0 + 18:0 + 18:1trans-11 + 20:0).

Table 10. Plasma % fatty acid composition of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[x]
14:0	0.23	0.16	0.22	0.29	0.15	0.10	0.07	0.23	0.79	0.57
14:1n-5	0.15	0.08	0.15	0.06	0.11	0.00	0.06	0.55	0.06	0.91
16:0	12.84^{x}	7.94^{y}	9.78^{yz}	12.66^{x}	11.70^{xz}	8.67^{y}	0.75	0.36	0.01	<0.01
16:1n-7	1.29^{w}	0.43^{xz}	0.60^{xy}	0.86^{y}	0.50^{x}	0.22^{z}	0.10	<0.01	<0.01	<0.01
18:0	16.41^{yz}	14.09^{z}	16.00^{z}	18.67^{xy}	19.89^{wx}	22.08^{x}	0.89	<0.01	0.25	0.02
18:1trans-11	0.70^{x}	0.10^{y}	0.15^{yz}	0.48^{xz}	0.00^{y}	0.10^{y}	0.13	0.04	0.61	<0.01
18:1n-9	18.03^{w}	7.58^{x}	9.23^{xz}	12.67^{y}	10.78^{yz}	11.35^{yz}	0.82	0.06	<0.01	<0.01
18:1cis-11	1.15^{x}	0.50^{y}	0.62^{yz}	0.87^{z}	0.70^{yz}	0.68^{yz}	0.10	0.38	0.08	<0.01
18:2n-6	21.96	28.37	31.68	34.15	35.74	37.00	1.80	<0.01	0.03	0.34
20:0	0.06	0.00	0.00	0.00	0.00	0.00	0.03	0.38	0.33	0.38
18:3n-3	7.63^{x}	2.29^{y}	0.29^{z}	0.00^{z}	0.00^{z}	0.10^{z}	0.27	<0.01	<0.01	<0.01
18:2cis-9,trans-11	0.39^{x}	0.00^{y}	0.00^{y}	0.00^{y}	0.00^{y}	0.00^{y}	0.06	0.01	<0.01	<0.01
18:2trans-10,cis-12	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-
20:1	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-
MUFA:SFA[d]	0.69^{x}	0.39^{y}	0.41^{y}	0.45^{y}	0.38^{y}	0.40^{y}	0.03	<0.01	<0.01	<0.01

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] MUFA:SFA = (14:1 + 16:1 +18:1cis-9 + 18:1cis-11 + 18:2cis-9,trans-11, 20:1)/(14:0 + 16:0 + 18:0 + 18:1trans-11 + 20:0).

Table 11. Digesta % fatty acid composition of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Time on Feed/Feeding Group types									
	Short-fed[a]		Medium-fed[a]		Long-fed[a]			*P-values*		
Item	C[b]	Y[b]	C[b]	Y[b]	C[b]	Y[b]	SE	Time	Group	TxG[x]
14:0	0.03	0.47	0.57	0.89	0.44	0.44	0.17	0.03	0.08	0.42
14:1n-5	0.03[y]	0.31[x]	0.30[x]	0.29[x]	0.34[x]	0.30[x]	0.07	0.10	0.22	0.05
16:0	10.54[z]	18.23[y]	17.49[y]	24.25[x]	22.56[wx]	20.22[wy]	1.33	<0.01	<0.01	<0.01
16:1n-7	0.30	0.54	0.65	0.93	0.80	0.62	0.18	0.11	0.43	0.37
18:0	34.75	42.08	33.52	34.51	29.55	25.89	5.36	0.54	0.27	0.81
18:1trans-11	1.61[yz]	2.54[xz]	1.60[yz]	3.60[x]	0.91[y]	1.91[yz]	0.49	0.07	<0.01	0.04
18:1n-9	12.30	10.51	13.52	13.57	13.62	12.16	2.32	0.64	0.58	0.91
18:1cis-11	0.62	0.99	0.91	1.18	1.04	1.07	0.18	0.30	0.14	0.60
18:2n-6	7.06	9.09	10.63	11.24	16.05	15.14	1.86	<0.01	0.70	0.73
20:0	1.13	0.45	0.29	0.15	0.21	0.20	0.17	<0.01	0.06	0.16
18:3n-3	2.69	0.69	0.20	0.17	0.39	0.27	0.50	0.01	0.09	0.11
18:2cis-9,trans-11	0.00	0.00	0.00	0.08	0.27	0.17	0.06	<0.01	0.86	0.33
18:2trans-10,cis-12	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-
20:1	0.03	0.00	0.04	0.00	0.00	0.00	0.02	0.60	0.17	0.60
MUFA:SFA	0.30	0.20	0.29	0.26	0.32	0.25	0.06	0.82	0.20	0.87

[wxyz] Means within the same row with different superscripts are different ($P \leq 0.05$).

[a] Short-fed = 0 mo on high energy (corn) diet; Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet. Data are means for 4 steers per time on feed and diet group.

[b] C = calf-fed; Y = yearling-fed.

[c] Time x group interaction.

[d] MUFA:SFA = (14:1 + 16:1 +18:1cis-9 + 18:1cis-11 + 18:2cis-9,trans-11, 20:1)/(14:0 + 16:0 + 18:0 + 18:1trans-11 + 20:0).

Table 12. Sensory attributes of *Longissimus dorsi* of calf-fed and yearling-fed Angus steers at different times on high-energy (corn) diets.

	Medium-Fed[ab]	Long-fed[ab]			
Sensory Attribute	Yearling-fed (n=4)	Calf-fed (n=4)	Yearling-fed (n=4)	RMSE[c]	*P-value*
Juiciness	5.7	5.8	6.2	0.37	0.07
Muscle Fiber Tenderness	6.5	6.6	6.6	0.48	0.81
Connective Tissue	7.4	7.5	7.5	0.31	0.81
Overall Tenderness	6.4	6.6	6.5	0.48	0.70
Overall Flavor Intensity	5.6	5.7	5.7	0.33	0.66
Cooked Beef Lean	4.8	4.8	4.8	0.43	0.97
Cooked Beef Fat	0.9	1.2	1.3	0.37	0.13
Serum	1.1	1.1	1.2	0.34	0.76
Livery	0.1	0.1	0.1	0.09	0.28
Grassy	0.5	0.6	0.5	0.48	0.82
Salt	1.1	1.2	1.1	0.26	0.93
Bitter	1.8	1.7	1.9	0.28	0.66
Metal	2.1	2.1	2.1	0.27	0.91
Chemical Burn	<0.1	0.0	<0.1	0.06	0.59
Acid	1.4	1.4	1.3	0.27	0.66
Browned	0.5	0.4	0.3	0.40	0.58
Fishy	0.0	0.0	<0.1	0.04	0.38
Cowy	0.0	<0.1	0.0	0.04	0.38
Sour	1.3	1.1	1.1	0.36	0.59

[a] Medium-fed = 4 mo on high energy (corn) diet; Long-fed = 8 mo (calf-fed) and 5 mo (yearling-fed) on high energy (corn) diet

[b] Data are means for 4 steaks per time on feed and diet group. 0 = none or the absence of the attribute and 15 = extremely intense

[c] Root Mean Square Error

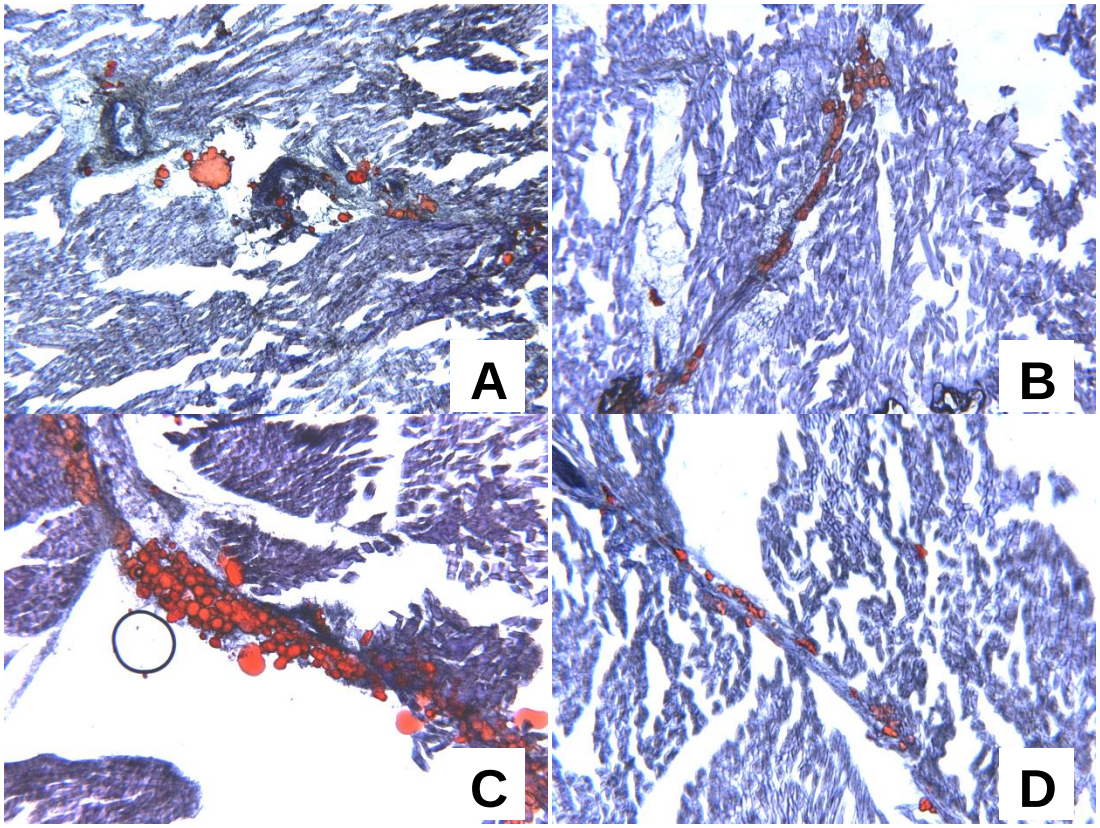

Figure 1. Intramuscular adipocyte development from the *Longissimus dorsi* of Angus steers at 0 days on a high-corn diet (short-fed). Cells were stained with Oil Red O to stain adipocyte cells and hematoxylin solution according to Mayer and bluing solution for nuclei. Calf-fed (baseline) cattle slaughtered at weaning-age (A and B). Yearling-fed cattle slaughtered at 12 mo of age (C and D). White areas are due to separation of the tissue due to freeze/thaw damage.

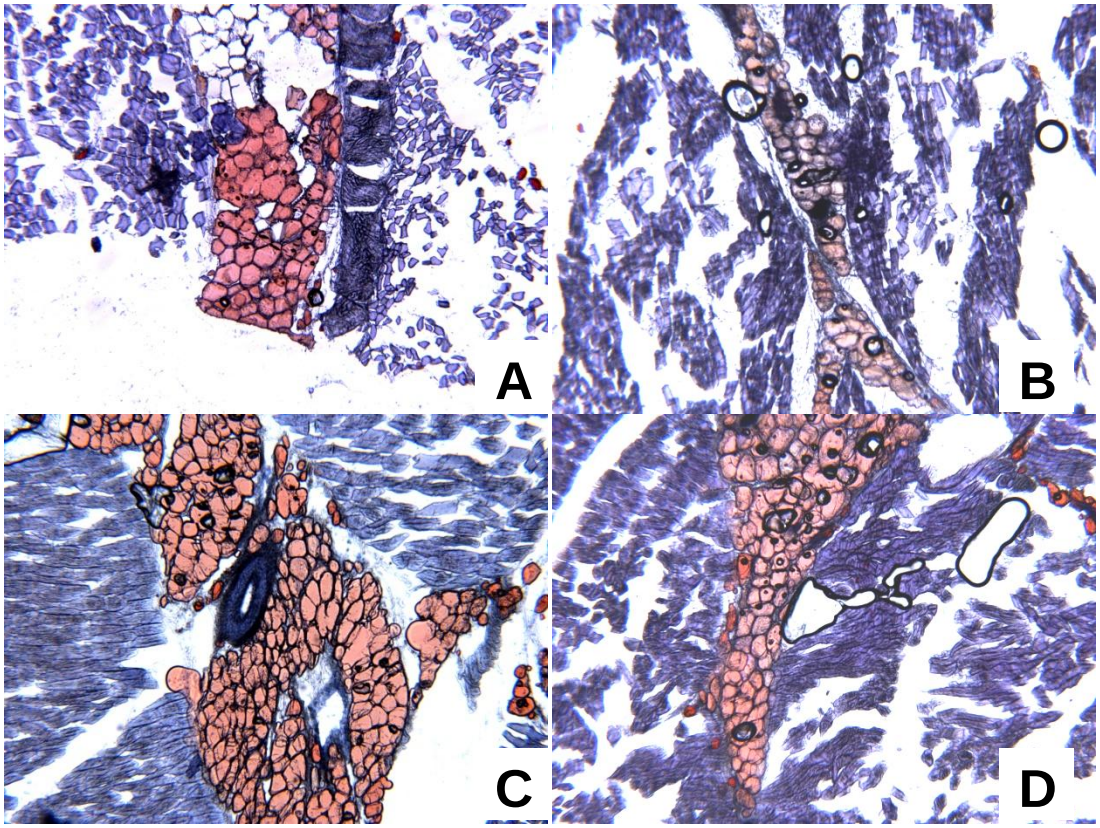

Figure 2. Intramuscular adipocyte development from the *Longissimus dorsi* of Angus steers at 4 mo on a high-corn diet (medium-fed). Cells were stained with Oil Red O to stain adipocyte cells and hematoxylin solution according to Mayer and bluing solution for nuclei. Calf-fed cattle slaughtered at 12 mo of age (A and B). Yearling-fed cattle slaughtered at 16 mo of age (C and D). White areas are due to separation of the tissue due to freeze/thaw damage.

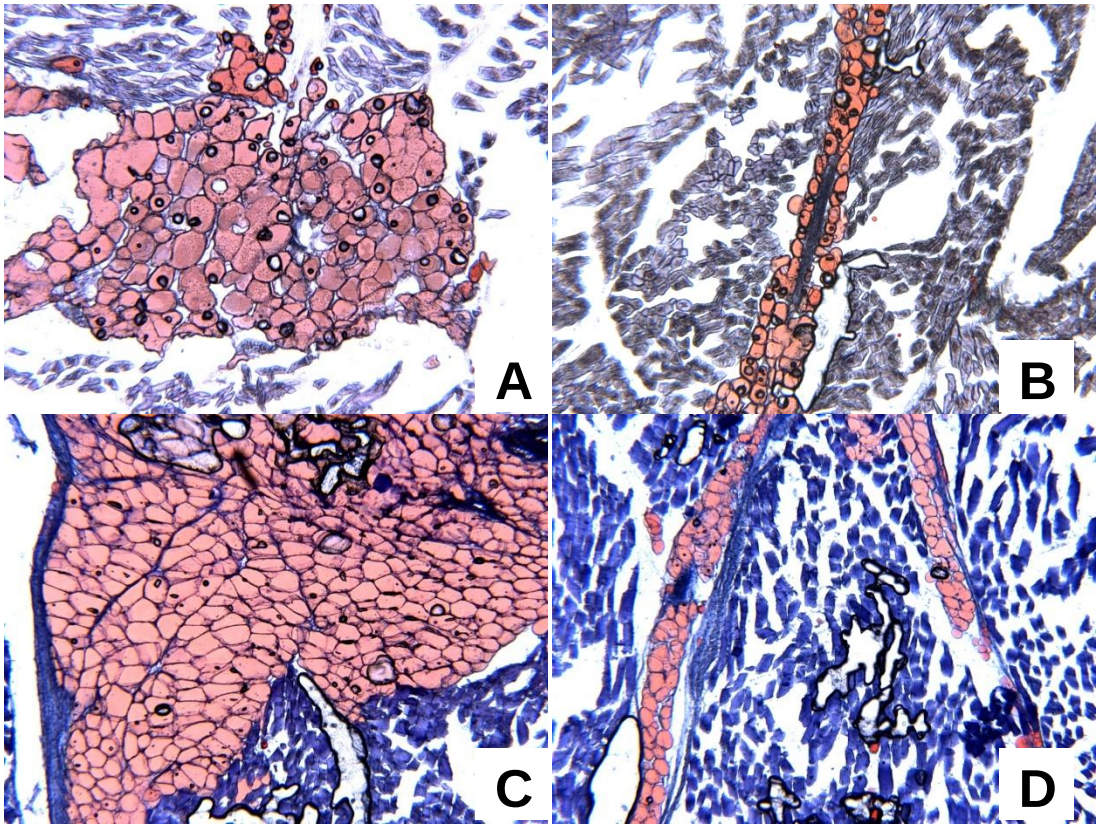

Figure 3. Intramuscular adipocyte development from the *Longissimus dorsi* of Angus steers at 8 mo (top) and 5 mo (bottom) on a high-corn diet (long-fed). Cells were stained with Oil Red O to stain adipocyte cells and hematoxylin solution according to Mayer and bluing solution for nuclei. Calf-fed cattle slaughtered at 16 mo of age (A and B). Yearling-fed cattle slaughtered at 17 mo of age (C and D). White areas are due to separation of the tissue due to freeze/thaw damage.

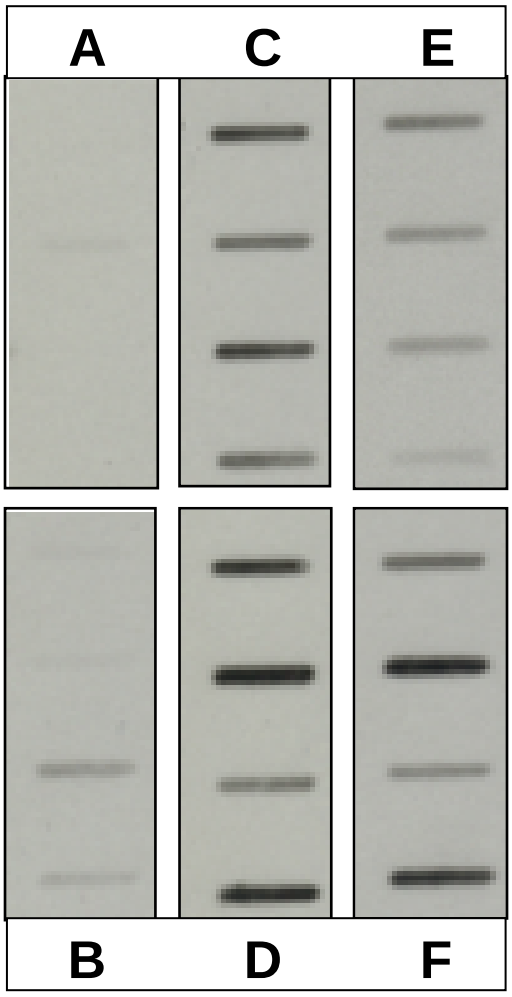

Figure 4. SCD mRNA expression of subcutaneous adipose tissue in individual Angus Steers. Cattle fed on a high-corn diet for 0 days (A and B): Baseline cattle slaughtered at weaning-age (A). Yearling-fed cattle slaughtered at 12 mo of age (B). Cattle fed on a high-corn diet for 4 mo (C and D): Calf-fed cattle slaughtered at 12 mo of age (C). Yearling-fed cattle slaughtered at 16 mo of age (D). Cattle fed on a high-corn diet for 8 mo or 5 mo (A and B, respectively): Calf-fed cattle slaughtered at 16 mo of age (E). Yearling-fed cattle slaughtered at 17 mo of age (F).

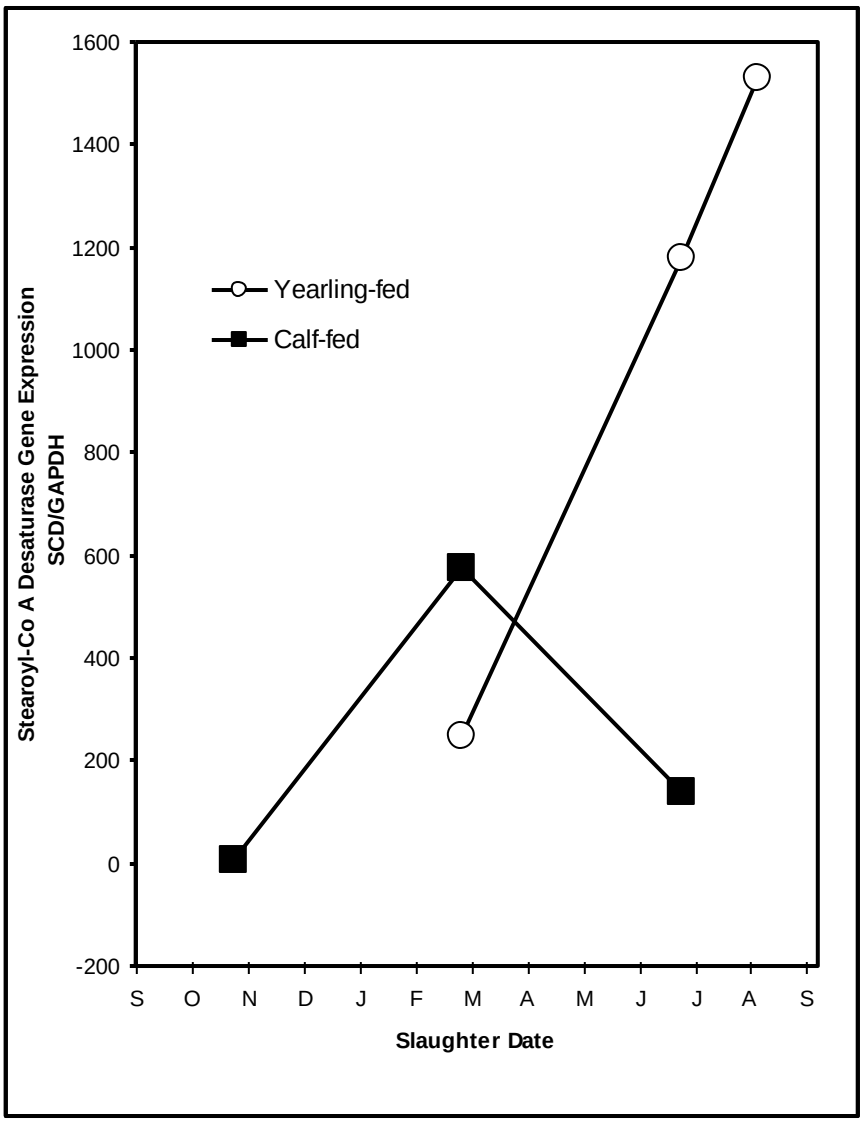

Figure 5. Temporal changes in stearoyl-CoA desaturase activity in s.c. adipose tissue of calf-fed and yearling-fed Angus steer.

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Matthew Brooks was born in Anderson, SC in 1981, and grew up in the town of Pendleton, SC. He is the son of Jeffrey Brooks and Elizabeth Brooks. He has one brother, Captain Robert Brooks, USAF. In August of 2005, Matthew married Stephanie Renee Bush, NCC, LPC. Stephanie graduated with her Bachelor of Arts in Psychology from Baylor University, and she went on to get her Master of Science in Counseling from Texas A&M University, Commerce.

Matthew graduated from Cornell University in 2003 with a Bachelor of Science in Animal Science. After spending two years working at the Fort Worth Zoological Association in their Nutrition department, he began his master's program at Texas A&M University in August of 2005 as a graduate student in the Intercollegiate Faculty of Nutrition. He conducted his research under the direction of Dr. Stephen B. Smith and received his M.S. in Nutrition in December 2007.

Matthew is an Eagle Scout and is a member of the American Society of Animal Scientists, the Nutritional Advisory Group, the Comparative Nutrition Society, Phi Kappa Phi and Alpha Zeta.

He will continue his education by pursuing his Ph.D. at the University of Missouri studying ruminant nutrition under Dr. Monty Kerley.