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The effect of selection for intramuscular fat on fatty acid composition in Duroc pigs

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The effect of selection for intramuscular fat on fatty acid composition in Duroc pigs

by

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DEDICATION

I would like to dedicate this thesis to my beautiful and loving wife Karen and our two children, Garrett, and Gage. You have all truly impacted my life in a positive manner and were my inspiration toward completing this great journey. Striving to make you proud has always brought great joy to my life. To my parents, thank you for your unwavering support; your guidance and love is something I hope to echo to my children in the future. I love you all.

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CHAPTER 1.

GENERAL INTRODUCTION

Intensive selection for increased has caused consumer acceptance issues to arise, as a result of decreased meat quality, in the U. S. swine industry. Quality characteristics that play an integral role in consumer acceptance, such as intramuscular fat (IMF), have decreased as breeders have intensely selected for increased leanness (Barton-Gade, 1990; Cameron et al., 1990). The role of IMF is of particular interest in pigs because of its role in eating quality and overall consumer acceptance (NPPC, 1995). Efforts to improve meat quality have been an objective of producers, processors, and researchers.

Selection for increased quantity of IMF in purebred Duroc pigs is possible (Schwab et al., 2009) and can be accurately measured in the live animal (Newcom et al., 2002; Newcom et al., 2003). The ideal concentration of IMF has been estimated to be between 2 and 3% (Bejerholm and Barton-Gade, 1986; DeVol et al., 1988; Barton-Gade, 1990). Because IMF is influential in determining flavor and juiciness (Hodgson et al., 1991; Huff-Lonergan et al., 2002), this trait has become important in the genetic improvement of fresh pork quality.

The main impact on pork quality, due to selection for increased percent lean in pigs, has been a decrease in adipose quality and overall firmness of fat. In many countries, fat is considered unhealthy and will have a significant impact on the consumer's purchasing decision. Japanese consumers primarily consume pork as fresh meat; so, it is imperative to have high fat quality, and the quality of fat is determined by its fatty acid composition (Gatlin et al., 2003; Wood et al., 2004). Large variation exists in the melting point of specific fatty

acids; therefore, fatty acid composition directly affects the firmness and/or softness of adipose (Pitchford et al., 2002).

Fatty acids contribute to the various aspects of meat quality and ultimately, to the nutritional value of the product. Large segments of the medical profession would be more receptive to meat products that contain a greater proportion of unsaturated fat (Pinckney and Pinckney, 1973). Consequently, saturated fatty acids may become the chief health-related issue with regards to meat consumption. The consumption of saturated fatty acids increases plasma LDL-cholesterol in humans (Mattson and Grundy, 1985), and the resulting increase in LDL-cholesterol has been positively correlated with coronary heart disease.

As selection for increased IMF is practiced, it is important to understand the correlated response in fatty acid composition of the various adipose tissues. Attention must be given to the potential corresponding changes that may occur in traits not under direct selection. The objectives of this research are to: 1. Identify the change in fatty acid composition among pigs with varying concentrations of IMF, 2. Determine the effect of gender on fatty acid composition of IMF, 3. Identify the shelf life and product stability of pork loin chops with varying concentrations of IMF, 4. Estimate the genetic parameters of fatty acid composition in pigs selected for IMF for seven generations, and 5. Identify molecular markers for fatty acid composition and IMF in purebred Duroc pigs. This project will help to identify the effect of IMF on meat and eating quality traits and allow for the identification of superior products from a human health and eating quality standpoint.

Dissertation Organization

This dissertation is presented as a general introduction, a literature review, five individual manuscripts, and a general summary. References cited in the general introduction and literature review follow the general summary section. The format of each manuscript and corresponding reference citations are in compliance with the required style and form used by the journal to which the paper is to be submitted (indicated under the title of each manuscript). Each individual paper consists of an abstract or summary and four sections: introduction, materials and methods, results, and discussion. Literature cited within the papers is listed after the results and discussion section of each individual paper.

CHAPTER 2.

LITERATURE REVIEW

Meat and fat quality

Improving overall consumer satisfaction and healthfulness of pork should be one of the single most important goals for pork producers. Intensive selection for increased carcass lean percentage has allowed consumer acceptance issues to arise in the swine industry as a result of decreased meat quality. Quality characteristics that play an integral role in consumer acceptance, such as IMF, have decreased as breeders have intensively selected for increased leanness (Barton-Gade, 1990; Cameron, 1990). Genetic selection for efficient lean meat production over the last few decades can no doubt be responsible for a dramatic decline in eating quality.

To improve eating quality, one must understand the definition of pork quality and, ultimately, what defines eating quality. In my opinion pork quality refers to a product that is "healthy, wholesome, safe, and merits a consumer's repeat purchase". However, what must be understood is that pork quality is very complex and is controlled by many different factors. Yet, pork quality defines the economic value that pork products have from some consumer's point of view.

Consumers generally desire "attractive, economically priced products with desirable color, which are nutritious and healthy, tender, juicy , and flavorful, with no fat or additives" (Jeremiah, 1998). Consumers base purchasing decisions on a combination of factors to ensure a pleasurable eating experience that utilizes their own previous experiences with pork purchases. The factors most likely to influence a consumer's initial purchasing decision include size, shape, and color of pork cuts, along with a desire to minimize fat intake, and

ultimately price (McGill, 1981). Consumers repeat pork purchasing decisions are based on their eating experience, including a variety of sensory attributes, to determine the overall value of the product. With all of this in mind, improving fresh pork quality and various indicator traits is of utmost importance in order to improve consumer demand for U.S. pork. Livestock production today faces the difficult task of effectively meeting emerging consumer concerns while remaining competitive in major target markets domestically and internationally.

Fresh pork quality and overall consumer acceptance continue to be increasingly important as packers and processors attempt to provide wholesome, high quality products to their consumers. Many traits have been investigated as indicators of fresh pork quality and its corresponding consumer acceptance. Much of this research has focused on the *longissimus dorsi* or loin muscle due to its relative value and its use as a determinant of carcass lean composition. Lean composition is traditionally estimated from linear measures taken at approximately the 10th rib of a pork carcass. Because the 10^{th} rib of the loin is already the area of the pork carcass used to estimate carcass cutability, many of the meat quality indicators have been measured there as well (NPPC, 2000).

Meat quality is used to describe any trait or group of traits that impact the consumer acceptability of fresh meat products. Meat color (Faustman and Cassens, 1990), pH (van Laack et al., 2001; Huff-Lonergan et al., 2002), tenderness (Van Oeckel et al., 1999; Huff-Lonergan et al., 2002), postmortem aging and proteolysis (Wood et al., 1996; Lonergan et al., 2001), muscle fiber type (Melody et al., 2004), breed (van Laack et al., 2001), and IMF (DeVol et al., 1988; Fernandez et al., 1999b; Brewer et al., 2001), or some combination of all traits influence meat quality and sensory characteristics of the product. Trained sensory

panels have been used to measure taste, juiciness, tenderness, and flavor as a means to determine how consumers will react to meat samples that differ in one or more of the aforementioned indicators of pork quality (Huff-Lonergan et al., 2002).

Selection for increased quantity of IMF in purebred Duroc pigs is possible (Schwab et al., 2009) and can be accurately measured in the live animal (Newcom et al., 2002; Newcom et al., 2003). Intramuscular fat has a positive effect on flavor and other consumer sensory traits (Van Oeckel et al., 1999). Export markets and up-scale, "White Tablecloth" restaurants have indicated that color and IMF are two of the most important factors determining consumer acceptance of pork products (Faustman and Cassens, 1990; Fernandez et al., 1999a; Fernandez et al., 1999b). Research projects conducted by the National Pork Producers Council and National Pork Board have indicated that IMF is influential in determining taste, juiciness, and flavor of pork, and overall consumer acceptance and willingness to purchase pork instead of chicken (NPPC, 1995). The ideal concentration of IMF has been estimated to be between 2 and 3% (Bejerholm and Barton-Gade, 1986; DeVol et al., 1988; Barton-Gade, 1990). Because IMF is influential in determining juiciness and flavor (Hodgson et al., 1991; Huff-Lonergan et al., 2002), this trait has become important in the genetic improvement of fresh pork quality.

The main impact on pork quality, due to selection for leanness, has been a decrease in adipose quality and overall firmness. In many countries, fat is considered unhealthy and will have a significant impact on the consumer's purchasing decision. However, fat and fatty acids, whether in adipose tissue (subcutaneous fat) or muscle (IMF), contribute to various aspects of meat quality and ultimately, to the nutritional value of the product. The relationship between fatty acid composition of IMF and the composition of pork was

investigated in a European study by Cameron and Enser (1991) who showed that correlations among the concentration of specific fatty acids and eating quality traits were generally weak. However, correlations among polyunsaturated fatty acids (PUFA) and palatability scores were generally negative and those for saturated fatty acids and palatability scores were generally positive, suggesting that the higher the degree of unsaturation of adipose, the greater incidence of abnormal flavors.

Considerable research and interest have arisen in reducing total carcass fat and in altering the profile of fatty acids of pork toward a more unsaturated fatty acid profile. Cereal grains supplemented with protein and fat make up the typical diets being fed to pigs in today's production systems. These diets are often high in PUFA, in order to maximize grow-finish performance and efficiency, however, they can result in soft pork fat. Consistency and composition of pork fat are quality concerns, because thin bellies and soft fat produce more miscuts and a higher percentage yield of lower-quality product. On the other hand, elevated intakes of saturated fatty acids are associated with increased incidence of heart disease and other human health complications (Mattson and Grundy, 1985). Limiting dietary intake of animal products, which are known to be associated with high concentrations of saturated fats, have become the main focus to improve human health.

One of the consequences of the close relationship between the composition of dietary and body fat is that it is relatively easy to manipulate fat composition by altering the fat source fed to the pig (Seerley et al., 1978; Miller et al., 1990; Madsen et al., 2005). Tissue fatty acid composition of non-ruminant animals is a result of the dietary fats consumed. The main fat depots in the pig are subcutaneous adipose tissue (backfat), intermuscular fat, and IMF. Saturated and unsaturated fatty acids from the diet pass through the digestive system

without changing and may be deposited in the different depots. Lipids in these various depots, including adipose tissue and skeletal muscle, strongly reflect the major dietary fatty acids. In a study conducted by Seerly et al. (1978), the primary objectives were to determine the effect of animal fat and poultry fat on performance and carcass characteristics with particular interest in IMF of the longissimus muscle. Pigs fed in groups (n=50) or individuals (n=48) were used to compare the effect of animal and poultry fat sources at concentrations of 0, 2.5, and 5.0% dietary fat on the tissue lipids of grow-finish pigs. Results from this study indicated that fat source and concentration did not influence percentages of total lipids present in the longissimus muscle; however, they did affect individual fatty acid profiles. Pigs fed diets containing poultry fat appeared to have lower oleic acid (C18:1n9) and higher linoleic acid (C18:2n6) contents within the IMF than those of pigs fed diets containing fats from animals. The high fat diets resulted in more linoleic acid (C18:2n6), total unsaturated fatty acids, and less stearic acid (C18:0) when compared with those in the control carcasses. From a performance aspect, the highest energy diets did support improvements for daily gain, feed conversion, and ultimately, feed:gain.

Changing the fatty acid composition of subcutaneous adipose tissue using different dietary oils and grain sources also can change the fatty acid profile of the lipid and ultimately affect the melting point and firmness of the fat. A recent study showed that pigs fed diets containing palm oil produced carcasses with firmer adipose than pigs fed diets containing soybean oil (Teye et al., 2006). The concentration of C12:0 and C14:0 were highest in pigs fed diets containing palm kernel oil. Additionally, proportions of C12:0, C14:0, C18:0, C18:2n6, and C18:2n3 were strongly correlated with the fat quality parameters slip point, bacon cohesion, and total loss. An understanding of the dietary means to control fatty acid

synthesis could be beneficial when exploring the use of alternative feedstuffs in pig production.

Lipid synthesis

A large percentage of lipids are synthesized from dietary glucose, which is the main precursor for fatty acids. Lipogenesis is primarily focused in the liver, which suggests the major role of triglyceride transport by lipoproteins between the site of synthesis (liver) and the site of deposition (adipose tissues). Deposition of lipids chronologically occurs during the growth of the pig. Subcutaneous adipose tissue first, then intermuscular adipose, and finally, IMF (Lee and Kauffman, 1974). This deposition pattern is strongly influenced by age and maturity of the animal.

Discussion of the effect of dietary fat on adipose tissue development can be divided into the effect on cell size (hypertrophy) and on cell number (hyperplasia) (Azain, 2004). A net increase in adipose tissue accumulation can result even during a period of decreased fat synthesis if there also exists an even greater decrease in the turnover and catabolism of fatty acids. Findings suggest (Anderson and Kauffman, 1973) that increased carcass adipose tissue of young pigs up to two months of age was primarily due to increases in cell number (hyperplasia). From two to five months of age, pigs exhibited a combination of increased hyperplasia and hypertrophy. No significant increases in hyperplasia were observed beyond 5 months of age, indicating that increases in adipose mass from that point on were due to an increase in hypertrophy.

Similarly, Damon et al. (2006) observed an increase in cell number as a significant indicator of IMF concentration. Two different lines of pigs representing high and low concentrations of IMF content were used to evaluate various biological mechanisms to

describe variation in IMF content. This study concluded that adipocyte number could describe a significant amount of variation in IMF (R^2=0.47), however, the same result was not found for adipocyte size.

In rodents, lipogenesis occurs in both liver and adipose tissue, whereas in pigs and ruminants it is primarily in adipose tissue. Lipogenic enzyme activity and overall lipogenesis are low in the liver of pigs (Ding et al., 2000; Lee et al., 2000; Gondret et al., 2001). Depression of lipogenesis in porcine adipose tissue also can be attributed to dietary fat concentration. Several studies suggest that saturated fatty acids are more inhibitory of lipogenesis than unsaturated fatty acids (Allee et al., 1972; Smith et al., 1996; Ding et al., 2003). However, de novo fatty acid biosynthesis in porcine adipose tissue was equally depressed when either 10% dietary corn oil or 10% dietary beef tallow was fed to pigs (Allee et al., 1971). Additionally, in species where adipose tissue is the primary site of lipogenesis, saturated fatty acids are at least equivalent if not greater than unsaturated fatty acids (Azain, 2004). Increasing the concentration of dietary fat fed to pigs, whether high in saturated or unsaturated fatty acids, will control de novo fatty acid synthesis from glucose in porcine adipose tissue.

A higher in vitro lipogenic rate has been reported in Duroc pigs that were obese in comparison to those that were lean when measured at a constant age (Scott et al., 1981a). However, rates measured at equal weight yielded no differences, suggesting a differential time course for the development of lipogenic activities. However, it has been demonstrated (Scott et al., 1981b) that there are more saturated fatty acids present in the fat depots of pigs with a genetic predisposition for obesity than in pigs selected for reduced backfat. Pigs with

less IMF content tend to have lower de novo fatty acid synthesis and, consequently have greater concentration of dietary fatty acids incorporated into their tissues (Wood et al., 1989).

Fatty acid synthesis in animals occurs in the cytosol. In the liver and adipose tissue, NADPH is generated in the pentose phosphate pathway and by malic enzyme. The acetyl-CoA produced in the mitochondria from pyruvate oxidation is transported indirectly to the cytosol by the citrate-malate-pyruvate shuttle. A three-carbon intermediate, malonyl-CoA, is synthesized from acetyl-CoA to provide the two-carbon unit that allows for elongation. The main product of the four-step sequence of fatty acid synthesis is palmitic acid (C16:0). Fatty acid elongases present in the mitochondria and smooth endoplasmic reticulum then act upon palmitic acid to de novo synthesize stearic acid or longer chain fatty acids. Single double bonds are introduced to palmitic or stearic acid by stearol-CoA desaturase to convert the fatty acid to their respective monounsaturated forms. Mammals are not capable of producing polyunsaturated fats such as C18:2 or C18:3; however, longer chain PUFA can be produced by elongation and desaturation of these two essential dietary fatty acids.

Muscle lipids are composed primarily of phospholipids located in the cell membranes and neutral lipids consisting of mainly triacylglycerols in the adipocytes (De Smet et al., 2004). The content of phospholipids in the muscle is relatively independent of the total fat content and varies between 0.2 and 1% of muscle weight. However, the content of muscle triacylglycerols is strongly related to the total fat content and varies from 0.2% to more than 5% (Leseigneur-Meynier and Gandemer, 1991; Fernandez et al., 1999a). Phospholipids are high in PUFA, whereas triacylglycerols contain much lower amounts of PUFA. Because phospholipids are membrane components, the PUFA proportion is highly conserved in order to maintain cell membrane integrity. Although PUFA content of the triacylglycerols is

highly influenced by dietary fat compositions, especially in monogastrics, it is diluted by de novo fatty acid synthesis consisting of higher concentrations of saturated fatty acids (SFA) and monounsaturated fatty acids (MUFA), thus reducing overall P:S ratio with increasing fat deposition (Leseigneur-Meynier and Gandemer, 1991; De Smet et al., 2004).

Fatty acids and human health

Meeting consumer demands for a pork product that is healthy and has acceptable eating quality is crucial for the pork industry. The relevance of these issues pertains to production efficiency, economic benefits, and re-establishment of the meat sector image and consumer trust. Meat has historically constituted a large portion of the American diet. The relevance of pork quality issues and a better understanding of consumer-decision making toward meat have also become paramount due to distinct changes at the consumer level.

Large segments of the medical profession would be more receptive to meat products that contain a greater proportion of unsaturated fat (Pinckney and Pinckney, 1973). Consequently, saturated fatty acids may become the chief health-related issue with regards to human consumption of meat. The consumption of saturated fatty acids increases plasma LDL-cholesterol in humans (Mattson and Grundy, 1985), and the resulting increase in LDL-cholesterol has been correlated with coronary heart disease.

Among the SFA, shorter chain fatty acids, such as C6:0 to C10:0, and stearic acid (C18:0) had little effect on plasma cholesterol concentration, whereas lauric (C12:0), myristic (C14:0), and palmitic (C16:0) acids increased plasma cholesterol concentration (McGandy et al., 1970; Keys et al., 1974). Myristic acid was considered to have the highest propensity to cause cardiovascular disease, almost four times the effect of C12:0 and C16:0 (Hegsted et al., 1965; Keys et al., 1974).

Concerns of excess saturated fat and a deficiency of n-3 fatty acids in the human diet have led to recommendations that the ratio of polyunsaturated fatty acids to saturated fatty acids (P:S ratio) be increased to 0.4 or higher and the ratio of n-6 to n-3 fatty acids in the diet be lowered to between 1 and 4 (Department of Health and Social Security, 1994). If the concentration of IMF were higher, a benefit for improved eating quality, the n-6:n-3 ratio in the muscle would be lower overall as a result of the lower ratio in muscle triacylglycerides compared to phospholipids (Enser et al., 2000). Given the high intake of C18:2 from other dietary sources, the effect of meat C18:3 on endogenous synthesis of long-chain PUFA in man may be small relative to the supply of these fatty acids by meats in the diet.

The contributions of individual fatty acids to the atherogenic potential of fat or lipid source has been summarized by Ulbricht and Southgate (1991) in the form of an atherogenic index (AI). The AI described by Ulbricht and Southgate (1991) ranks mixtures of fatty acids according to their propensity to cause atherogenesis, as predicted from concentrations of individual fatty acids in the lipid. The AI is calculated as:

$$AI = \frac{C12:0 + (4 \times C14:0) + C16:0}{\Sigma MUFA + \Sigma PUFA}.$$

The traditional means of evaluating fatty acid composition of pork was concentrated primarily on the adipose tissue, because that is where the bulk of the body's fatty acids are located. Recently, emphasis has now focused on the IMF of pork because of its greater significance in the food retail market place. Additionally, muscle contains high concentrations of long chain n-3 and n-6 fatty acids, which have human health implications (Conquer and Holub, 1998). Several studies have shown an inverse relationship between the proportion of C18:2n6 in subcutaneous fat and the amount of fat. A correlation of 0.3 existed

between the proportion of C18:2n6 in the inner layer of subcutaneous fat and loin fat thickness in Large White pigs from a line selected for lean muscle growth and a control line (Wood et al., 1978).

Synthesis of eicosapentaenoic acid (EPA, C20:5n-3) and docosahexaenoic acid (DHA, C22:6n-3) is highly dependent on its precursor fatty acid, α-Linolenic acid (C18:3n-3). Long chain polyunsaturated fatty acids, such as EPA and DHA play a major role in the control of cardiovascular diseases (Conquer and Holub, 1998) and are now widely recommended in human diets. An effective method to increase the concentration of n-3 PUFA in pork is to simply include more in the diet, thus modifying the human dietary fat intake from pork (Wood and Enser, 1997). Several studies have shown the n-3 PUFA concentration can be increased in pork by feeding sources such as linseed, which contains greater than 50% of C18:3n3 in its lipid (Enser et al., 2000; Nurnberg et al., 2005).

In a study conducted by Nuernberg et al. (2005), 13 female and 12 castrated male Pietrain x German Landrace pigs were fed a basal concentrate diet supplemented with 5% olive oil or 5% linseed oil during the grow-finish period. Results from the study indicated that carcass composition was not affected by the treatment diets. Feeding linseed oil to pigs did significantly increase the relative content of linolenic acid and long chain n-3 fatty acids in IMF, backfat, and the heart at the expense of arachidonic acid. The overall flavor of the combined meat/backfat samples, as evaluated by a trained 6-member panel, was negatively influenced by linseed oil supplementation when compared with flavor of samples from pigs fed the olive oil diet (Nurnberg et al., 2005).

Dietary manipulation of n-3 fatty acid concentration and the effect on lipid fatty acid composition have been examined in pigs (Wiseman and Agunbiade, 1998; Enser et al., 2000;

Nurnberg et al., 2005). A study conducted by Kouba et al. (2003) was conducted to examine the time course of incorporation of n-3 PUFA from linseed into plasma and tissue lipids in comparison with a control diet. Forty-eight Duroc-cross gilts were fed a control or linseed diet containing 60 g of whole crushed linseed/kg. Eight pigs from each treatment were harvested at 20, 60 or 100 d after the start of the experiment to evaluate the carcass and fatty acid composition. Results from this study indicated that feeding the linseed diet increased the content of n-3 PUFA in the plasma, muscle, and adipose tissue, but DHA was not altered by the diet. The proportions of n-3 PUFA were highest in pigs fed the linseed diet for 60 d, regardless of tissue (plasma, muscle, or adipose tissue) or lipid class (neutral or phospholipids)(Kouba et al., 2003). Pigs fed diets containing linseed produced pork with a PUFA:saturated fatty acid ratio ≥ 0.4 in all groups and tissues and had a significant decrease in n-6:n3 ratio. Pigs fed the control diet from 40 kg live weight for 20, 60, or 100 d had an increase in the proportion of C18:0 (10% to 13%), C18:1n9 (38% to 42%), and a decrease in C18:2n6 (19% to 11%). Conclusions from Kouba et al. (2003) suggest that linseed in swine diets is a viable method to modify the nutritional value of pork without affecting pork quality; however, other studies have indicated a negative impact on quality (Nurnberg et al., 2005).

An increase in C18:3 is considered beneficial to consumer health but causes a lower lipid melting point and firmness of backfat, an increase in the iodine value, and increased risk for PUFA peroxidation (Warnants et al., 1996).

Increasing the intake of n-3 fatty acids is associated with human health (Deckelbaum et al., 2006). In general, eicosanoids produced from n-6 fatty acids are more inflammatory, cause vasoconstriction, and promote platelet aggregation, when compared with those

produced from n-3 fatty acids, such as EPA ($20:5^{\Delta 5, 8, 11, 14, 17}$) and DHA ($22:6^{\Delta 7, 10, 13, 16, 19}$). Although n-3 fatty acids have been shown to be less inflammatory than their n-6 counterparts, they have a negative effect on meat quality. Because n-3 fatty acids are liquid at room temperature, products enriched with these fatty acids are often unacceptable to consumers due to their soft and oily texture (Azain, 2004). Products enriched with n-3 fatty acids have greater potential for increased off-flavor and susceptibility to oxidative damage (Wood and Enser, 1997). Consumers often believe that PUFA are desirable because of their role in the prevention of cardiovascular diseases, whereas meat product manufacturers believe that PUFA are associated with soft fat and shorter shelf life of the product (Warnants et al., 1998).

Concentrations of fatty acids C18:0 and C18:2 are most highly correlated with tissue firmness (Wood, 1984). In this study, C18:2 had the highest correlation with tissue firmness, indicating a softer fat, measured both subjectively and objectively. Similarly, shoulder and last rib fat concentrations of C18:2 were also highly related to firmness, suggesting that shoulder fat could be a good indicator of firmness in the loin where backfat is very thin and sometimes difficult to measure. Pigs have much higher proportions of the major polyunsaturated fatty acid 18:2n-6 (linoleic acid) in both tissues than cattle or sheep (Wood et al., 2008). Linoleic acid is derived entirely from the diet. In pigs, it passes through the stomach unchanged and is then absorbed into the blood stream in the small intestine and incorporated from there into tissues. In ruminants, the fatty acid, which is at high concentrations in concentrate feedstuffs, is reduced into monounsaturated and saturated fatty acids in the rumen by microbial biohydrogenation and only a small amount (approx. 10%) is available for incorporation into the tissues. Manipulation of muscle or adipose tissue fatty

acid composition in nonruminants is well documented. Research has shown a linear relationship (r^2=0.70) between dietary linoleic acid intake (C18:2n-6) and percentage of the fatty acid in the carcass (Averette Gatlin et al., 2002).

Backfat thickness and fatty acid composition

Deposition of fat in the various depots, namely adipose tissue and skeletal muscle, is strongly influenced by the balance between energy intake and expenditure, as well as energy intake and mobilization (Nurnberg et al., 1998). Adipose tissue deposition patterns in mammals are different in various species. Within species, age/weight, diet, gender, hormone concentrations, and maintenance requirements can all influence the rate and site of deposition (Wood et al., 2008). Selection for increased lean meat content in pig carcasses has been associated with lower meat and fat quality. Scott et al. (1981a) showed that genetically selected lean and obese lines (Duroc x Yorkshire) gained more slowly and had poorer feed efficiency when compared to the contemporary line (females of reciprocal crosses of Duroc and Large White purebred animals). Adipocyte size and number, at any given age, were larger and higher in the obese line of pigs, respectively. Within a breed, cell numbers were the highest at 3 months of age and tended to decline with increasing animal age, and shifted more toward hypertrophy of adipocytes (Scott et al., 1981a). Additionally, a strong tendency for a higher percentage of saturated fatty acids in pigs of the obese breed than those in the contemporary of lean breed was reported. Obese pigs had proportionally greater C18:0 at younger ages and more C14:0 and C16:0 throughout. There was proportionally less C18:2 in the obese pigs than in pigs in either of the two lines, regardless of age. This increase in proportion of saturated fatty acids was said to be a result of greater *de novo* synthesis of fatty acid in the adipose tissue in the obese line (Scott et al., 1981b). In support of these data,

(Martin et al., 1972) reported positive correlations between total backfat and the percentages of C14:0 and C16:0 as well as a negative correlation between total backfat and C18:2 content.

Wood et al. (1978) showed that pigs selected for efficient growth and low backfat depth had paler 'eye muscles' and greater drip loss. The fatty acid composition of lines was similar; however, the concentration of C18:2 in both the inner and outer layers of backfat was 14% higher in the select line. Negative correlations between the concentration of C18:2 and various backfat measures were found. The melting point of lipid from either of lines was strongly related to the variation in the concentration of C18:0. Conclusions of these studies showed that several selected and crossbred lines indicated differences in the fatty acid composition of backfat between breed lines with similar and differing backfat thickness. The content of SFA and MUFA increases faster with increasing fatness than does the content of polyunsaturated fatty acids, leading to a decrease in the relative proportion of PUFA and consequently, in the P/S ratio (De Smet et al., 2004). Consequently, there can be genetic selection for fatty acid composition of backfat that is independent of the amount or degree of fat.

Gender and fatty acid composition

Fatty acid composition is directly affected by the gonadal status of animals because of its effect on carcass fatness. At equal slaughter weights, castrate male pigs are fatter than gilts and intact males are leanest of the genders (NPPC, 2000). Relative concentration of C18:2 and PUFA in adipose tissue decreases in the order of males > females > castrate males, while the proportion of saturated fatty acids increases (Nurnberg and Ender, 1989).

In a study conducted by Warnants et al. (1996), Pietrain x Hybrid cross (n=110) barrows and gilts were used to compare the incorporation of dietary PUFA in pork tissues. Gender effects were shown in the study for fatty acid fractions as well as total IMF. Barrows had more IMF, mainly apolar lipids triacylglycerides (TAG), when compared to gilts; however the polar fraction (PL) did not change. IMF from gilts had a higher concentration of PUFA than that from barrows. In the case of phospholipids, no difference was observed between genders, suggesting the functional role of the polar lipid fraction in membrane integrity.

Further gender differences in fatty acid composition were investigated by Wood et al. (1989). Intact males and gilts (n=300) were classified into three different fatness categories (8 mm, 12 mm, and 16 mm, P2) and used to determine the chemical composition of subcutaneous adipose (backfat) from the last rib and shoulder regions. Results from this study showed intact males pigs have less C18:1 and more C18:2 and C18:3 when compared to gilts.

Barrows have a greater concentration of saturated fatty acids present in the inner and outer backfat layers when compared to gilts (Elliot and Bowland, 1970). Gender differences were found for C16:0, C18:0, total SFA, and C20:2n6 for both inner and outer subcutaneous backfat layers. This study is in agreement with findings by (Warnants et al., 1999). The more unsaturated fatty acid pattern in the apolar lipid fraction (TAG) for gilts than barrows confirms the results of an earlier study (Warnants et al., 1996).

Shelf life and product stability

Several studies with pigs have shown that high concentrations of vitamin E in the diet that are incorporated into tissues were effective in reducing lipid oxidation in stored and

displayed pork (Buckley et al., 1995). However, extra vitamin E did not increase storage stability in pigs given diets containing 0.5% fish oil (Hertzman et al., 1988) and a concentration of 150 mg/kg of vitamin E in the diet did not prevent the deterioration of flavor of the product when linseed feeding raised the concentration of C18:3n3 to 3% of muscle fatty acids (Kouba et al., 2003). Supranutritional vitamin E has reduced drip loss and improved color stability in pork in some studies, probably by preventing oxidation of muscle pigments by lipid oxidation products but in others, limited effects on drip loss and color stability have been reported (Jensen et al., 1997).

Dietary vitamin E supplementation in meat animals is perhaps the best known method of improving meat quality by reducing lipid oxidation in fresh meat and meat products. Fresh meat is stored for a very short duration and oxidation of the pigment in meat to a brown color limits the display life and costs the meat industry millions of dollars annually. Deterioration in quality and loss of shelf life often are of caused by lipid and myoglobin oxidation occurring in meat and meat products. Factors that often contribute to decreased quality and shelf life include the temperature and duration of storage, packaging, oxygen availability, concentration of antioxidants present, and the composition and amount of lipids in the muscle.

Recent studies have begun focusing on the dietary supplementation of antioxidants (e.g., vitamin E) and their ability to delay lipid oxidation in muscle and further processed meat products (Liu et al., 1995). Improvements in meat quality include a reduction of thiobarbituric acid reactive substance (TBARS, an indicator of rancidity and off-flavors) scores below 0.50 mg malondialdehyde (MDA) equivalents, which is the borderline

concentration for detection of rancidity and off-flavors by trained sensory panelists (Dunshea et al., 2005).

Genetic parameter estimates of fatty acid composition

Studies have shown selection for leaner pigs has had a negative impact on pork quality and ultimately eating quality (Cameron, 1990; Gatlin et al., 2003). Genetic selection for efficient lean meat production over the last few decades can no doubt be responsible for this decline in eating quality. There are few genetic parameter estimates available for meat and eating quality traits (i.e., IMF, flavor, off-flavor, juiciness, tenderness, chewiness). Several studies have estimated the phenotypic correlations between fatty acid composition of subcutaneous fat, particularly concentrations of C18:2, and meat quality traits (Wood et al., 1978; Miller et al., 1990), but there are few estimates of genetic parameters for fatty acid composition traits (Suzuki et al., 2006).

In a recent evaluation representing current industry commercial lines, van Wijk et al. (2005) provided significant genetic correlations among composition and muscle quality traits, suggesting that changes in carcass composition traits may affect meat quality characteristics. Some of the quality parameters that have significant genetic correlations with tenth-rib backfat thickness include: loin marbling score (0.35), firmness (0.25), and ultimate pH (-0.24). Additionally, carcass lean percentage is shown to have similar genetic relationships. These correlations are antagonistic in nature, and some are large enough to significantly increase pork quality problems if ignored while selecting for decreased in tenth-rib backfat thickness.

There is limited information on the phenotypic and genetic relationships among carcass traits and eating quality traits. Positive phenotypic and genetic correlations were

reported between average backfat thickness and taste panel scores for flavor and juiciness, which suggested that selection for reduced carcass fat would also reduce eating quality (Jensen et al., 1965). Intramuscular fat content, pH, and subcutaneous fat moisture were all positively correlated with flavor liking, tenderness, and acceptability, while subcutaneous fat firmness, longissimus light reflectance, and moisture content were all negatively correlated with these same traits (Cameron, 1990).

Potential candidates for gene/marker assisted selection

Marker-assisted selection (MAS) is a process whereby a marker (based on DNA variation) is used for indirect selection of a genetic determinant or determinants of a trait of interest. Considerable developments in biotechnology have led to the development and implementation of MAS in animal breeding programs. The candidate gene approach is the use of marker-assisted selection to select individuals with a particular genotype of interest, where the trait of interest is not directly quantified but rather the genotype for that gene is used as a marker allele. The candidate gene approach has been successful in identifying major genes that affect traits of economic importance. The assumption is that the linked allele associates with the gene and/or quantitative trait loci (QTL) of interest.

The marker type that will be focused on is the use of DNA-based and/or molecular marker. The type of marker is a unique DNA sequence, occurring in proximity to the gene or locus of interest, which can be identified by a molecular technique known as restriction fragment length polymorphism (RFLPs). Analysis of RFLPs has been used in the early determination of genetic fingerprinting. This technique is useful in the identification of samples for characterization in genetic diversity or breeding patterns in animal populations.

Within pig breeding populations, molecular markers that have an influence on meat quality, fatty acid composition, and eating quality will receive added attention. These traits are often lowly heritable, hard to measure, and difficult to make progress in using conventional BLUP selection. Independent of backfat thickness and IMF composition, genetic variation between specific genotypes seems to exist for the synthesis and incorporation of individual fatty acids. This genetic variation may be further explained by possible changes in the mechanisms of fatty acid transport and storage at a molecular level. The following section will review literature that involves candidate genes detected that have been implicated to be associated with adipogenesis, fatty acid composition, meat quality, and IMF.

Stearoyl-Coenzyme A desaturase (SCD) gene

Stearoyl-CoA desaturase (SCD) is a microsomal membrane bound, iron-containing enzyme required for the biosynthesis of unsaturated fatty acids. Located primarily in the endoplasmic reticulum membrane, SCD catalyses the oxidation of fatty acyl-CoA between carbons 9 and 10 with a preference for pamitoyl- and stearoyl-CoA, which are converted to pamitoleoyl-and oleoyl-CoA, respectively.

Numerous studies have been conducted to address the function and location of the SCD gene (Kim and Ntambi, 1999; Ntambi, 1999; Ren et al., 2004). Stearoyl-coenzyme desaturase converts saturated fatty acids (myristic, palmitic, and stearic acid) to their corresponding Δ^9-monounsaturated fatty acids. The desaturation by the SCD enzyme is said to be the rate-limiting step in the desaturation process (Bernert and Sprecher, 1977).

Desaturase gene expression during differentiation previously has been demonstrated in 3T3-L1 preadipocytes. Stearoyl-coenzyme A desaturase mRNA was measured in adipose

tissue from obese (50% Yorkshire x 50% Duroc) and crossbred pigs (Duroc x Hampshire boars mated to Yorkshire x Landrace sows) at several time points before and after weaning. Results of the study showed SCD mRNA was barely detectable at 0 d of age and increased by as much as 20-fold by 49 d of age. When measured, SCD gene expression was the lowest in suckling pigs and highest in the milk-fed pigs. Additionally, obese pigs in the study expressed more SCD mRNA than did crossbred pigs during the suckling the period, however; overall, crossbred pigs exhibited greater SCD gene expression when compared to obese pigs during the post-weaning period. It was suggested that the latter was caused by a strong depression in SCD gene expression in the grain-fed obese pigs. It has been suggested that SCD gene expression is not only linked to, but may also be required for, lipid filling in pig adipose tissue (Smith et al., 1999).

Acetyl-CoA carboxylase (ACC)-1 gene

Acetyl-CoA-carboxylase (ACC) catalyzes the first committed step in the fatty acid biosynthetic process. There is considerable evidence that this enzyme has a key role in the regulation of fatty acid biosynthesis in animal tissues and may catalyze the rate-limiting step in this pathway (Levert et al., 2002). The pattern of ACC activity in swine adipose tissue directly parallels that of in vitro incorporation of glucose into total lipids (Scott et al., 1981a). In a study conducted by Scott et al. (1981a), obese pigs had a marked increase in ACC activity when compared to lean pigs at any given age.

Fatty acid synthase (FASN) gene

In contrast to the attention placed on the effect of SCD on fatty acid composition, the investigation of FASN has focused primarily on the effect of fat accumulation (Moon et al., 2002; Wang et al., 2004). Fatty acid synthase is a multifunctional enzyme complex that

catalyzes the synthesis of long-chain saturated fatty acids. Its main function is to catalyze the synthesis of palmitate from acetyl-CoA and malonyl-CoA in the presence of NADPH. To our knowledge, there have been no previous studies that have focused on the association of polymorphisms of the FASN gene with fatty acid composition in pork.

CHAPTER 3.

FATTY ACID COMPOSITION AND MEAT QUALITY TRAITS IN DUROC PIGS SELECTED FOR INTRAMUSCULAR FAT FOR SEVEN GENERATIONS[1]

A paper to be submitted to the Journal of Animal Science

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ABSTRACT: The objective of this study was to identify the fatty acid composition of pork in Duroc pigs selected for intramuscular fat (IMF). Selection was practiced for seven generations (select line, SL) and based on estimated breeding value for IMF from fitting a 2-trait animal model and the full relationship matrix in MATVEC. A randomly mated, unselected control line (CL) was maintained in the population. The 2 traits emphasized were IMF estimated on the carcass and IMF predicted using real-time ultrasound on the live animal. Longissimus muscle samples (LM) (n=663, 357 in CL, 306 in SL) collected from pigs in generations 3 through 7 and adipose tissue samples from pigs in generations 6 and 7 were used to determine the fatty acid composition of IMF and adipose tissue. Total lipids were extracted from trimmed LM samples and tenth-rib subcutaneous adipose tissue and methylated directly with acetyl chloride and methanol. Triacylglycerols (TAG) were separated from phospholipids (PL) in IMF by thin-layer chromatography. All fatty acid methyl esters were quantified by using gas chromatography. Pigs in the SL had more backfat, less loin muscle area, and consequently, lower carcass lean percentage when compared with pigs in the CL. Control line pigs had more favorable objective color measures. Select line pigs had more flavor and less off-flavor, and were generally more desirable for sensory panel scores when compared with pigs from the CL. Additionally, SL pigs had more total saturated fatty acids in adipose tissue and more monounsaturated fatty acids in the IMF than pigs in the CL. Total polyunsaturated fatty acids were higher in CL pigs, regardless of fat depot. Results suggest that the fatty acid composition of fat depots in pigs is a correlated response to selection for quantity of IMF. When selection for IMF is executed, attention to the correlated response in fatty acid composition must be accounted for when looking at the overall meat and eating quality traits of pork.

Key words: fat quality, intramuscular fat, meat quality, selection, swine

INTRODUCTION

Total lipid content of pork skeletal muscle has been shown to have a role in sensory traits such as tenderness and juiciness of the cooked meat product. The role of intramuscular fat (IMF) is of particular interest in pigs because selection for carcass lean percentage over the last decade has significantly decreased marbling fat to less than 1% of muscle weight in pork (Wood et al., 2004a). In addition, selection for increased lean content in pig carcasses has been associated with lower meat and fat quality (Scott et al., 1981a; Scott et al., 1981b). Intramuscular and subcutaneous adipose tissue fatty acid composition is not only an indicator of carcass fat quality, but also can dramatically influence the eating quality of the meat. Efforts to improve meat quality, namely IMF, have been an objective of producers, processors, retailers, and researchers. The increase in demand for superior quality pork from foreign markets has increased the pressure to produce a higher quality product in the United States. Japanese consumers primarily consume pork as fresh meat; so, it is imperative to have high fat quality, and the quality of fat is determined by its respective fatty acid composition (Gatlin et al., 2002; Wood et al., 2004b). Large variation exists in the melting point of specific fatty acids; therefore, fatty acid composition directly affects the firmness and/or softness of subcutaneous adipose and IMF (Pitchford et al., 2002).

Traditionally, meat fatty acid composition research has concentrated on adipose tissue, the body's major lipid storage depot. However, more emphasis has recently been placed on muscle because of the greater impact on further processing of food products (Wood et al., 2008). In addition, the fatty acids present in the fat depots of pigs with a genetic predisposition for obesity were richer in saturated fatty acids than those from pigs

selected for leaner backfat thickness (Wood et al., 1978; Scott et al., 1981b; Wood, 1984). Fat deposition in various depots, namely subcutaneous adipose tissue and skeletal muscle, are influenced by energy balance between intake and energy expenditure, as well as energy intake and energy mobilization (Nurnberg et al., 1998). Because IMF content is highly heritable (Newcom et al., 2003; Suzuki et al., 2005; Schwab et al., 2009) and the fatty acid composition of muscle lipid is moderately to highly heritable (Cameron and Enser, 1991; Suzuki et al., 2006), attention must be placed on the fatty acid composition of pork (IMF and subcutaneous adipose tissues) as a correlated response to selection for increased IMF.

Previous studies indicate that the fatty acid composition of *longissimus dorsi* muscle was related to the overall eating quality of pork, with polyunsaturated fatty acids having a negative impact on pork flavor where as saturated and monounsaturated acids are correlated positively with eating quality (Cameron and Enser, 1991). Pork flavor, flavor preference, and overall acceptability were correlated positively with the concentration of monounsaturated fatty acids, C16:1 and C18:1 (Cameron et al., 2000). Phospholipids, which are the main structural component of all tissue membranes, are proportionally rich in PUFA, which are susceptible to oxidation and the formation of off-flavors (Warnants et al., 1996; Wood and Enser, 1997). Therefore, the objective of this study was to determine the fatty acid composition and meat eating quality traits of the *longissimus dorsi* muscle and adipose tissue from Duroc pigs selected for increased IMF for seven generations.

MATERIALS AND METHODS

Population

Experimental protocols for the study were approved by the Iowa State University Institutional Animal Care and Use Committee. A purebred Duroc population was initiated in

1998 to evaluate selection for intramuscular fat (IMF) in Duroc swine using real-time ultrasound. After 2 generations of random mating, a line selected for IMF (SL) and a control line (CL) were created and selection began as described by Schwab et al. (2009). Selection was based on breeding values for IMF estimated by fitting a 2-trait (IMF measured on the carcass and IMF predicted via real-time ultrasound) animal model in MATVEC (Wang et al., 2003). Details of this selection, breeding value estimation, mating procedures, and responses after 6 generations are reported by Schwab et al. (2009).

Performance and carcass measurements

Finishing pigs were housed in totally slatted, mechanically ventilated, curtain-sided finishing buildings and were provided a minimum of 0.77 m^2 of floor space with 20 to 25 pigs per pen from 34 kg until they reached an average off test weight of 110 kg. A 19.0% CP, 1.20% lysine corn-soy diet was provided ad libitum from 34 to 68 kg BW, followed by a 18.0% CP, 1.05% lysine corn-soy diet from 68 kg to 91 kg BW, followed by a 15.5% CP, 0.85% lysine corn-soy diet (Table 1) from 91 kg until market weight. Dietary fatty acid analysis for finishing phase 3 is presented in Table 2.

Upon completion of the performance test period, all available barrows and randomly selected gilts were harvested at a commercial abattoir (Hormel Foods, Austin, MN). Carcass measurements were obtained by Iowa State University personnel 24 h post-mortem. Standard carcass collection procedures as outlined in Pork Composition and Quality Assessment Procedures (NPPC, 2000) were followed to obtain measurements of 10^{th} rib backfat (BF10) and loin muscle area (LMA). A section of bone-in *longissimus dorsi* containing the 10^{th} to 12^{th} ribs was excised from the carcass and transported to the Iowa State University Meat Laboratory. A 3.2 mm slice from the 10th rib face was utilized for lipid

content analysis. Carcass pH was measured 48 h post-mortem on the 10th rib face of the longissimus muscle by using a pH star probe (SFK Ltd, Hvidovre, Denmark). Hunter L* score and Minolta reflectance were measured on the 10th rib face of the loin by using a Minolta CR-310 (Minolta Camera Co., Ltd., Osaka, Japan) with a 50-mm-diameter aperture, D65 illuminant, and calibrated to the white calibration tile. The 11th and 12th rib sections were cut into 2.54 cm samples and set cut side up for 10 min to allow the sample to bloom. Subjective measures of color (1 = pale pinkish gray to white; 6 = dark purplish red), marbling (1 = 1% IMF; 10 = 10% IMF), and firmness (1 =soft; 3 = very firm) were evaluated on the 11th rib face according to NPPC (2000) by personnel trained in meat quality evaluation. Water holding capacity was measured on the 11th rib face by using the filter paper method described by Kauffman et al. (1986). Longissimus muscle samples (n=663) collected from generation 3 through 7 pigs (Table 3) in the CL (n=357) and SL (n=306) were used to determine the IMF fatty acid profiles.

Fatty acid analysis

Trimmed loin samples (generations 3 through 7) and all layers of adipose tissue (generations 6 and 7) from the *longissimus dorsi* at the 10-11th rib were utilized for fatty acid determination. Total lipid was extracted from the IMF samples with a chloroform and methanol (2:1, vol:vol) mixture and quantified gravimetrically (Folch et al., 1957). Triacylglycerols (TAG) were separated from phospholipids (PL) by thin-layer chromatography with hexane and ethyl acetate (4:1, vol:vol). Fatty acids in each lipid were derivatized to methyl esters according to Lepage and Roy (1986). Fatty acid methyl ester (FAME) from both subcutaneous adipose tissue and IMF were analyzed by gas chromatography (GC; model 3400, Varian, Palo Alto, CA) equipped with a Supelco SP-2560

column (100 m x 0.25 mm x 0.2 μm film thickness) and a flame ionization detector. The column started at a temperature of 100°C and was increased to 170°C at a rate of 2°C per min, followed by an increase to 180°C at 0.5°C per min and to 250°C at 10°C per minute. Total run time was 77 min and the detector was maintained at 220°C. Based on the fatty acid composition, the atherogenic index (AI) was calculated following Ulbricht and Southgate (1991):

$$AI = \frac{C12:0 + (4 \times C14:0) + C16:0}{\Sigma MUFA + \Sigma PUFA}.$$

Sensory evaluation

Two 2.54-cm chops from the 10th to 12th rib section were vacuum packaged and taken to Iowa State University Food Science Laboratory (McKay Hall, Iowa State University); samples were refrigerated at 0°C for 7 d. Both rib sections were cooked to 71°C in an electric broiler (Amana model ARE 640, Amana, IA), with sample temperature monitored with Chromega/Alomega thermocouples attached to an Omega digital thermometer (DSS-650, Omega Engineering, Inc., Stamford, CT). Weights prior to and immediately after cooking were used to calculate percentage of cooking loss. A 3-member trained sensory panel evaluated cooked loin samples for quality attributes (Huff-Lonergan et al., 2002) on three 1.3 cm^3 cubes from the center of the 11th and 12th rib samples. Eating quality evaluations for juiciness (1 = dry; 10 = juicy), tenderness (1 = tough; 10 = tender), flavor (1 = little pork flavor; 10 = extremely flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor; 10 = abundant non-pork flavor) were recorded by using an end-anchored 10-point scoring system (AMSA, 1995). Individual booths with red overhead lighting were provided for each panelist. Sample evaluations were averaged across panelists for analysis. The 12th

rib section was evaluated for tenderness by using an Instron Universal Testing Machine (Model 1122; Instron Corp., Canton, MA) fitted with a circular, 5-point star probe (9 mm diameter with 6 mm between points) (Oltrogge-Hammernick and Prusa, 1987).

Statistical analysis

Line differences for meat and eating quality traits and fatty acid composition through generation 7 were assessed by using the MIXED procedure of SAS (SAS Inst., Cary, NC). A mixed model with fixed effects of line, gender, generation, and carcass contemporary group, interactions of line×sex and line×generation were utilized to estimate least squares means (±SE) for all dependent variables. Random effect of sire nested within line, and covariate of hot carcass weight were included in all analyses. Least squares means within fixed effects were compared by using pair-wise *t*-tests (*pdiff* option in SAS) and declared to be different at $P < 0.05$.

RESULTS AND DISCUSSION

Correlated responses in carcass composition and meat quality

Direct and correlated responses to 7 generations of selection for carcass composition traits are presented in Table 4. Select line pigs had 5.80 mm ($P < 0.001$), 3.17 mm ($P < 0.001$), and 3.18 mm ($P < 0.001$) more tenth rib, last-rib, and last lumbar backfat, respectively, when compared to control line pigs. Additionally, pigs in the SL had less loin muscle area ($P < 0.001$) and, combined with more overall fat, were less desirable in percentage lean ($P < 0.001$). The direct response in IMF corresponded to 1.66% increase in total lipid in the select line ($P < 0.001$). No significant line differences were observed in the current study for pH measured at 24 h, 48 h, or 7 d post mortem. Additionally, water holding capacity and cook loss were not different between lines ($P > 0.05$).

Selection for quantity of IMF resulted in a correlated response in objective color estimates. Select line pigs had a 1.8, 1.8, 2.2, and 2.2 unit increase in 24 h and 48 h Minolta reflectance and 24 h and 48 h Hunter L values, respectively. Observed color differences may be influenced by the quantity of IMF on the exposed loin muscle surface rather than true differences in lean tissue color. This effect is one pitfall to using objective color reflectance measures on exposed lean tissue with high concentration of IMF. An evaluation of color, independent of IMF, such as myoglobin concentration (Newcom et al., 2004), may be required to determine the true pigmentation of lean tissue and their differences.

Carcass lean percentage is under genetic control and is influenced by numerous traits. When intense selection pressure is placed on lean percentage, unfavorable correlated responses, in the form of decreased meat and fat quality, may result. Long-term selection response for increased carcass leanness has been at the expense of meat quality traits, including IMF percentage (Wood et al., 2004a), objective measures of tenderness (Schwab et al., 2006), and color scores (both objective and subjective measures) (Schwab et al., 2006).

Correlated responses in eating quality

Least squares means for sensory panel score are presented in Table 5. Sensory panel evaluation, such as juiciness, chewiness, and tenderness scores did not differ ($P < 0.05$) between lines. However, loin samples from select line pigs had more flavor ($P < 0.001$) and less off-flavor ($P < 0.05$) than did samples from control line pigs. Carcass lean percentage has an antagonistic effect on meat quality and ultimately, pork eating quality (Lonergan et al., 2001). These results are consistent with other documented relationships with meat and eating quality traits. Flavor has been reported to have a relatively strong relationship with IMF content (Van Oeckel et al., 1999), although there have been reports of little to no

association between eating quality and IMF (Fernandez et al., 1999; van Laack et al., 2001; Channon et al., 2004). Off-flavor scores (flavor perceived as inappropriate) were not influenced by IMF (Fortin et al., 2005). However, in the current study, samples with increased IMF (i.e., SL pigs) had the lowest sensory off-flavor scores. This result is significant because Risvik (1994) reported that the absence of off-flavors is critical for pork consumer acceptance.

Total lipids of longissimus dorsi

Least squares means for total lipid fatty acid composition of the *longissimuss dorsi* muscle are presented in Table 6. The fixed effect of line was a significant source of variation for total MUFA and PUFA, but not a significant source of variation for total saturated fatty acids. Saturated fatty acids, including C12:0 ($P < 0.05$), C15:0 ($P < 0.001$), C17:0 ($P < 0.001$), and C22:0 ($P < 0.001$) were more abundant in loins from pigs in the control line, whereas C18:0 ($P < 0.01$) and C20:0 ($P < 0.01$) were more prevalent in the select line samples. Monounsaturated fatty acids, C18:1*n*-9 ($P < 0.05$), C24:1 ($P < 0.05$), and total MUFA ($P < 0.001$) were more abundant in select line samples when compared to those in the control line. Conversely, C18:2*n*-6 ($P < 0.001$), C20:3*n*-6 ($P < 0.05$), C20:4*n*-6 ($P < 0.001$), and C22:5*n*-3 ($P < 0.001$) and total PUFA ($P < 0.001$) were more abundant in the control line loin samples. Increased concentrations of C18:2*n*6 have a negative correlation with objective color measures of fat (Cameron and Enser, 1991). In the current study, loin samples from CL pigs had more C18:2*n*6 and more desirable objective color measures. Select line loin samples had more α-linolenic (C18:3n3) ($P < 0.001$) and γ-linolenic acid (C18:3n6) ($P < 0.05$) than those from the control line. This increase in essential fatty acids is beneficial from

a human health aspect but poses increased risk for product shelf life due to oxidative stability of fat (Wood and Enser, 1997; Martin et al., 2008).

Fatty acid profiles of IMF in the present study are similar to those presented by Enser et al. (1996), who compared random samples of pork, lamb, and beef from commercially available retail display counters. Because pigs do not synthesize linoleic and linolenic acids, tissue content reflects the amount of those fatty acids present in the diets fed to pigs producing the meat containing these fatty acids (Gatlin et al., 2003). In the present study, pigs in each generation were fed diets formulated to have identical nutrient composition. Raw material ingredients, however, are produced each year; thus, diets for each generation can potentially be slightly different. To account for year-to-year variation in dietary ingredients, potential differences were accounted for by including generation as a fixed effect in the model used to analyze the data. Significant line differences were found for the total lipid content of skeletal muscle and intramuscular adipose lipids. Further research into possible differences in the genetic control of fatty acid transport mechanisms and binding proteins is needed because these variables could influence PUFA content of the IMF and ultimately the healthfulness of pork for consumers' consumption.

In a study conducted by Wood et al. (1996), the negative correlation between unsaturated fatty acid concentration and lipid content was absent for C18:2*n*-3, which suggests different metabolic controls for C18:2*n*-6 and C18:2*n*-3, both of which are entirely dietary-derived and compete for inclusion into lipid depots in pigs. Because of the increase in overall C18:2*n*-6 and C18:2*n*-3 in CL loin samples, one would expect an increased synthesis of the longer chain PUFA, which are the *n*-3 fatty acids involved in potential health benefits (Wood and Enser, 1997). Additionally, subsequent increases in these fatty acids

have elicited a high proportion of negative comments on flavor in bacon derived from pigs fed diets supplemented with ground flaxseed (high in *n*-3 fats) for 25 d (Romans et al., 1995a; Romans et al., 1995b).

Phospholipids of longissimus dorsi

Least squares means by concentration of individual fatty acids in the phospholipid fraction of IMF samples are reported in Table 7. There were no line differences ($P > 0.05$) in total saturated, total MUFA, and total PUFA in the phospholipid fraction; however, loin samples from SL pigs had more C15:0 ($P < 0.01$) present in the PL fraction than those found in the CL. Control line loin samples had a greater percentage of C18:0 ($P < 0.05$), C20:4*n*-6 ($P < 0.05$), and C22:5*n*-3 ($P < 0.05$). Only minor line differences were found for PL concentration due to the conservation of lipids found in membranes and their important role in membrane integrity (Farkas et al., 2000).

Neutral lipids of longissimus dorsi

Least squares means of the concentration of individual fatty acids in the neutral lipid fraction of IMF samples are presented in Table 8. Loin samples form pigs in the CL had more C12:0 ($P < 0.05$), C24:0 ($P < 0.05$), and C18:2*n*-6 ($P < 0.01$) in neutral lipid, whereas loin samples from the SL pigs had more C18:0 ($P < 0.01$), C20:0 ($P < 0.001$), C20:1*n*-9 ($P < 0.001$), C24:1 ($P < 0.01$), and C22:4*n*-6 ($P < 0.001$) present. Overall, there were no differences ($P > 0.05$) in total saturated fatty acids and total MUFA. Intramuscular fat of loin samples from pigs in the CL, however, had more total PUFA ($P <0.05$). Pork flavor has been reported to have a negative correlation with the amount of PUFA, suggesting that a higher concentration of PUFA may result in an increased incidence of off-flavor (Cameron and Enser, 1991; Cameron et al., 2000). A negative correlation between pork flavor and neutral

lipid PUFA (C18:2, C18:3, C20:3, C20:4, C20:5, C22:5, and C22:6) was reported by Cameron et al. (2000), but a positive correlation of pork flavor with MUFA of the neutral lipid (C16:1 and C18:1) was also reported. Although differences in flavor and off-flavor were found in the current study, the only difference in neutral fatty acid composition between lines was increased C18:2 in the CL, which could explain the increased incidence of sensory off-flavor scores observed in this line.

Subcutaneous adipose tissue

Least squares means for individual fatty acid concentration by line present in the tenth-rib adipose tissue (all layers combined) (from pigs in generation 6 and 7 only) are presented in Table 9. Adipose tissue from pigs in the select line had more C14:0 ($P < 0.01$), C16:0 ($P < 0.0001$), and had more total saturated fatty acids ($P < 0.001$) when compared to those in the CL. Control line pigs, however, had more C18:2*n*-6 ($P < 0.001$), C18:3*n*-3 ($P < 0.001$), C20:2*n*-6 ($P < 0.001$), C22:6*n*-3 ($P < 0.05$), and more total PUFA ($P < 0.001$) when compared to the SL. A positive relationship between carcass leanness and the ratio of PUFA:SFA of adipose tissue has been previously reported (Scott et al., 1981b). This relationship can be explained by the smaller contribution of de novo synthesis and larger contribution of the dietary fatty acids to total fat composition in genetically leaner pigs. The dietary intake of C18:2*n*6 was identical in the two lines; however its proportion increases in the CL pigs. These modifications have antagonistic effects on adipose tissue when further processing of pork occurs (decreased melting point and susceptibility to oxidation). However, they have positive implications on human health when incorporated into the diet (essential fatty acid supply) (Sheard et al., 2000).

Decreased PUFA concentration in the SL pigs was a correlated response to 7 generations of selection for increased IMF in that line. Pigs with increased backfat have been shown to have greater saturation present in adipose tissue (Scott et al., 1981b). Greater saturation of subcutaneous backfat and skeletal adipose tissue (IMF) may have resulted from selection for greater de novo synthesis, lower lipolytic rate (thus lower turnover), preferential incorporation of saturated fatty acids during TAG biosynthesis, lower desaturase activity, or some combination of these factors.

Long-term selection for increased lean has come at the expense of meat quality traits, namely IMF percentage, objective loin color, and eating quality traits such as flavor and off-flavor. Results obtained in this study suggest that fatty acid composition of IMF and subcutaneous fat is a correlated response to selection for IMF. Fatty acid composition of fat depots has changed because of selection for a greater quantity of IMF. Therefore, when selection for IMF is practiced, attention must be placed on the correlated response in different fat depots to ensure antagonistic effects on production and eating quality traits do not result.

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Table 1. Dietary components and nutrient composition of finishing diets fed to Duroc pigs in selection project designed to increase intramuscular fat

	Finishing Phase[1]		
Item	**1**	**2**	**3**
Calculated Composition[2]			
Corn, %	68.32	74.75	81.00
Soybean meal, %	26.25	20.00	13.75
Added Fat, %[3]	3.00	3.00	3.00
Base premix, %	2.25	2.25	2.25
Tylan 40, g/ton	0.13	-	-
Cupric sulfate, %	0.05	-	-
Total	100	100	100
Protein, %	19	18	15.5
Lysine, %	1.2	1.05	0.85
Fat, %	6	6	6
Fiber, %	3.2	3.2	3.2
Calcium, %	0.55	0.54	0.54
Phosphorus, %	0.45	0.45	0.45
Salt, %	0.5	0.5	0.5
Zinc, mg/kg	140	140	140
Copper, mg/kg	135	10	10
Phytase-FTU/kg	750	750	750
Selenium, mg/kg	0.3	0.3	0.3

[1]Finishing phase 1 – 34 to 68 kg BW; Finishing phase 2 – 68 to 91 kg BW; Finishing phase 3 – 91 kg to market weight.
[2]Calculated composition based on NRC (1998) values.
[3]Choice white grease

Table 2. Fatty acid composition of the phase 3 finishing diet fed to Duroc pigs in a selection project for intramuscular fat content[1]

Trait	Formula	Finishing Phase 3[2]
Fat, %		6.26
Saturated fatty acids (wt %)		
Lauric acid	C12:0	0.01
Myristic acid	C14:0	0.76
Pentadecanoic acid	C15:0	0.00
Palmitic acid	C16:0	22.18
Margaric acid	C17:0	0.25
Stearic acid	C18:0	8.65
Arachidic acid	C20:0	0.36
Behenic acid	C22:0	0.09
Lignoceric acid	C24:0	0.00
Total saturated		32.30
Monounsaturated fatty acids (wt %)		
Myristoleic acid	C14:1	0.04
Palmitoleic acid	C16:1 *n*-7	1.45
cis-Heptadecenoic acid	C17:1 *n*-10	0.13
Oleic acid	C18:1 *n*-9	17.20
trans-Vaccenic acid	C18:1 *n*-7	1.39
Eicosanoic acid	C20:1 *n*-9	0.74
Nervonic acid	C24:1	0.08
Total MUFA		21.03
Polyunsaturated fatty acids (wt %)		
Linoleic acid	C18:2 *n*-6	44.35
α-Linolenic acid	C18:3 *n*-3	1.56
γ-Linolenic acid	C18:3 *n*-6	0.01
Eicosadienoic acid	C20:2 *n*-6	0.00
Eicosatrienoic acid	C20:3 *n*-6	0.08
Arachidonic acid	C20:4 *n*-6	0.21
Eicosapentaenoic acid	C20:5 *n*-3	0.00
Docosatetraenoic acid	C22:4 *n*-6	0.01
Docosapentaenoic acid	C22:5 *n*-3	0.01
Docosahexaenoic acid	C22:6 *n*-3	0.00
Total PUFA		46.23

[1]Presented as a percentage of total lipid in the feed on an as-fed basis.
[2]Finishing phase 3 fed from 91 kg to market weight.

Table 3. Distribution of records by generation and line from a selection experiment for increased intramuscular fat in Duroc swine

	Generation					
Trait Category	**3**	**4**	**5**	**6**	**7**	**Total**
	No. of observations					
Contol Line[1]						
Gilts	14	5	14	17	6	56
Barrows	67	66	87	60	21	301
Select Line[2]						
Gilts	8	24	24	32	12	100
Barrows	56	53	46	40	11	206
Total						
Gilts	22	29	38	49	18	156
Barrows	123	119	133	100	32	507
Carcass	145	148	171	149	50	663

[1]Control line = unselected, randomly mated population.
[2]Select line = result of 7 generations of selection for increased IMF based on a two-trait animal model that included IMF measured on the carcass and predicted via ultrasound.

Table 4. Least squares means (±SE) for carcass composition and meat quality traits from pigs in generations 3 through 7 of a selection project for increased intramuscular fat in Duroc swine.

	Line[1]			
Item	**CL**	**SL**	**CL - SL**	**P-Value**
Carcass composition				
Length, cm	82.15 ± 0.16	82.49 ± 0.16	-0.34 ± 0.22	0.1279
Tenth rib backfat, mm	19.71 ± 0.50	25.51 ± 0.48	-5.80 ± 0.68	<0.0001
Last rib backfat, mm	23.69 ± 0.40	26.86 ± 0.39	-3.17 ± 0.54	<0.0001
Last lumbar backfat, mm	18.65 ± 0.42	21.83 ± 0.40	-3.18 ± 0.57	<0.0001
Loin muscle area, cm^2	44.19 ± 0.40	38.29 ± 0.39	5.90 ± 0.54	<0.0001
Percentage fat-free lean, (%)	39.63 ± 0.25	36.04 ± 0.24	3.59 ± 0.34	<0.0001
Intramuscular fat, (%, wet basis)	3.02 ± 0.12	4.68 ± 0.12	-1.66 ± 0.16	<0.0001
Meat quality				
24 h pH	5.72 ± 0.01	5.73 ± 0.01	0.01 ± 0.01	0.8527
48 h pH	5.66 ± 0.01	5.68 ± 0.01	0.02 ± 0.01	0.3581
7 d pH	5.70 ± 0.01	5.71 ± 0.01	-0.01 ± 0.01	0.6072
24 h Minolta reflectance	22.77 ± 0.22	24.61 ± 0.22	-1.84 ± 0.30	<0.0001
48 h Minolta reflectance	21.72 ± 0.20	23.54 ± 0.20	-1.82 ± 0.28	<0.0001
24 h Hunter L value	47.40 ± 0.24	49.57 ± 0.24	-2.17 ± 0.33	<0.0001
48 h Hunter L value	46.34 ± 0.25	48.53 ± 0.24	-2.19 ± 0.34	<0.0001
Water holding capacity, mg/wt	57.07 ± 1.77	57.85 ± 1.71	-0.78 ± 2.37	0.7422
Cooking loss, %	17.99 ± 0.22	18.29 ± 0.22	-0.30 ± 0.29	0.3071
Instron tenderness, kg	5.78 ± 0.06	5.49 ± 0.06	0.29 ± 0.08	0.0006

[1]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

Table 5. Least squares means (±SE) for sensory panel traits from pigs in generations 3 through 7 of a selection project for increased intramuscular fat in Duroc swine.

	Line[1]			
Item[2]	**CL**	**SL**	**CL - SL**	**P-Value**
Juiciness score	6.33 ± 0.09	6.43 ± 0.08	-0.10 ± 0.12	0.4368
Chewiness score	3.04 ± 0.09	3.02 ± 0.08	0.02 ± 0.12	0.8225
Tenderness score	6.44 ± 0.11	6.43 ± 0.10	0.01 ± 0.15	0.9337
Flavor score	2.63 ± 0.09	3.17 ± 0.08	-0.54 ± 0.13	<0.0001
Off-flavor score	2.46 ± 0.11	2.17 ± 0.10	0.29 ± 0.15	0.0494

[1]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

[2]Trained sensory panel evaluations of juiciness (1 = dry; 10 = juicy), chewiness (1 = not chewy; 10 = very chewy), tenderness (1= tough; 10 = tender), flavor (1 = little pork flavor, bland; 10 = very flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor, 10 = abundant non-pork flavor).

Table 6. Least squares means (±SE) for total fatty acid composition of intramuscular fat from pigs in generations 3 through 7 of a selection project for intramuscular fat in Duroc swine.[1]

		Line[2]									
Fatty acid	**Formula**	**CL**			**SL**			**CL - SL**			**P-value**
Saturated											
Lauric acid	C12:0	0.08	±	0.00	0.07	±	0.00	0.01	±	0.01	0.0200
Myristic acid	C14:0	1.41	±	0.02	1.48	±	0.02	-0.07	±	0.03	0.0564
Pentadecanoic acid	C15:0	0.51	±	0.03	0.34	±	0.03	0.17	±	0.04	<0.0001
Palmitic acid	C16:0	26.11	±	0.26	26.42	±	0.24	-0.31	±	0.36	0.4042
Margaric acid	C17:0	0.26	±	0.01	0.19	±	0.01	0.07	±	0.02	<0.0001
Stearic acid	C18:0	12.97	±	0.14	13.47	±	0.12	-0.50	±	0.19	0.0082
Arachidic acid	C20:0	0.08	±	0.00	0.10	±	0.00	-0.02	±	0.01	0.0026
Behenic acid	C22:0	0.06	±	0.00	0.05	±	0.00	0.01	±	0.01	0.0299
Lignoceric acid	C24:0	0.02	±	0.00	0.02	±	0.00	0.00	±	0.00	0.3273
Total saturated		41.53	±	0.31	42.14	±	0.28	-0.61	±	0.42	0.1479
Monounsaturated											
Myristoleic acid	C14:1	0.02	±	0.00	0.02	±	0.00	0.00	±	0.00	0.8633
Palmitoleic acid	C16:1 *n*-7	3.31	±	0.05	3.45	±	0.05	-0.14	±	0.07	0.0543
cis-Heptadecenoic acid	C17:1 *n*-10	0.06	±	0.02	0.10	±	0.01	-0.04	±	0.02	0.0996
Oleic acid	C18:1 *n*-9	40.94	±	0.38	42.37	±	0.35	-1.43	±	0.52	0.0064
trans-Vaccenic acid	C18:1 *n*-7	2.44	±	0.28	2.68	±	0.25	-0.24	±	0.33	0.5219
Eicosanoic acid	C20:1 *n*-9	0.15	±	0.01	0.16	±	0.01	-0.01	±	0.02	0.7086
Nervonic acid	C24:1	0.04	±	0.00	0.03	±	0.00	0.01	±	0.00	0.0108
Total MUFA		47.06	±	0.26	48.89	±	0.26	-1.83	±	0.39	<0.0001
Polyunsaturated											
Linoleic acid	C18:2 *n*-6	8.88	±	0.15	6.92	±	0.13	1.96	±	0.20	<0.0001
α-Linolenic acid	C18:3 *n*-3	0.70	±	0.02	0.78	±	0.02	-0.08	±	0.02	0.0005
γ-Linolenic acid	C18:3 *n*-6	0.04	±	0.00	0.06	±	0.00	-0.02	±	0.00	0.0202
Eicosadienoic acid	C20:2 *n*-6	0.27	±	0.01	0.27	±	0.01	0.00	±	0.01	0.9578
Eicosatrienoic acid	C20:3 *n*-6	0.15	±	0.01	0.13	±	0.01	0.02	±	0.01	0.0283
Arachidonic acid	C20:4 *n*-6	0.51	±	0.04	0.34	±	0.03	0.17	±	0.05	0.0005
Eicosapentaenoic acid	C20:5 *n*-3	0.01	±	0.00	0.01	±	0.00	0.00	±	0.00	0.5076
Docosatetraenoic acid	C22:4 *n*-6	0.09	±	0.01	0.07	±	0.01	0.02	±	0.01	0.2045
Docosapentaenoic acid	C22:5 *n*-3	0.07	±	0.01	0.05	±	0.01	0.02	±	0.01	0.0012
Docosahexaenoic acid	C22:6 *n*-3	0.01	±	0.00	0.01	±	0.00	0.00	±	0.00	0.1963
Total PUFA		10.73	±	0.17	8.63	±	0.16	2.10	±	0.24	<0.0001

[1]Presented as g/100g total lipid in the lean tissue (IMF).

[2]SL = select line, selected for 7 generations for intramuscular fat based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

Table 7. Least squares means (±SE) for phospholipid composition of intramuscular fat from pigs in generations 3 through 7 of a selection project for intramuscular fat after seven generations.[1]

		Line[2]									
Fatty acid	**Formula**	**CL**			**SL**			**CL - SL**			**P-value**
Saturated											
Lauric acid	C12:0	1.51	±	0.19	1.50	±	0.19	0.01	±	0.28	0.9586
Myristic acid	C14:0	0.49	±	0.08	0.47	±	0.09	-0.02	±	0.13	0.8808
Pentadecanoic acid	C15:0	6.77	±	0.22	7.64	±	0.19	-0.87	±	0.29	0.0027
Palmitic acid	C16:0	20.05	±	0.45	21.18	±	0.40	-1.13	±	0.53	0.0615
Margaric acid	C17:0	3.45	±	0.14	3.15	±	0.13	0.30	±	0.19	0.1207
Stearic acid	C18:0	9.32	±	0.21	8.72	±	0.19	0.60	±	0.25	0.0400
Arachidic acid	C20:0	0.17	±	0.06	0.22	±	0.05	-0.05	±	0.08	0.5495
Behenic acid	C22:0	0.07	±	0.02	0.09	±	0.01	-0.02	±	0.02	0.4664
Lignoceric acid	C24:0	0.09	±	0.03	0.04	±	0.03	0.05	±	0.03	0.2438
Total saturated		41.93	±	0.51	43.00	±	0.46	-1.07	±	0.12	0.1247
Monounsaturated											
Myristoleic acid	C14:1	0.40	±	0.08	0.32	±	0.08	0.08	±	0.11	0.4918
Palmitoleic acid	C16:1 *n*-7	0.45	±	0.09	0.52	±	0.08	-0.07	±	0.11	0.5752
cis-Heptadecenoic acid	C17:1 *n*-10	1.95	±	0.28	1.56	±	0.25	0.39	±	0.38	0.2993
Oleic acid	C18:1 *n*-9	10.47	±	0.33	10.91	±	0.30	-0.44	±	0.44	0.3227
trans-Vaccenic acid	C18:1 *n*-7	1.75	±	0.11	1.95	±	0.11	-0.20	±	0.17	0.2577
Eicosanoic acid	C20:1 *n*-9	0.14	±	0.13	0.30	±	0.12	-0.16	±	0.18	0.3836
Nervonic acid	C24:1	0.15	±	0.03	0.09	±	0.03	0.06	±	0.04	0.1376
Total MUFA		15.28	±	0.46	15.62	±	0.42	-0.34	±	0.62	0.5866
Polyunsaturated											
Linoleic acid	C18:2 *n*-6	31.89	±	0.59	31.94	±	0.53	-0.05	±	0.79	0.9457
α-Linolenic acid	C18:3 *n*-3	0.16	±	0.04	0.11	±	0.04	0.05	±	0.05	0.4422
γ-Linolenic acid	C18:3 *n*-6	0.24	±	0.06	0.20	±	0.06	0.04	±	0.08	0.6158
Eicosadienoic acid	C20:2 *n*-6	0.24	±	0.20	0.19	±	0.18	0.05	±	0.26	0.8469
Eicosatrienoic acid	C20:3 *n*-6	0.69	±	0.07	0.59	±	0.06	0.10	±	0.09	0.2854
Arachidonic acid	C20:4 *n*-6	5.10	±	0.28	4.18	±	0.26	0.92	±	0.26	0.0166
Eicosapentaenoic acid	C20:5 *n*-3	0.11	±	0.05	0.15	±	0.04	-0.04	±	0.06	0.5327
Docosatetraenoic acid	C22:4 *n*-6	0.38	±	0.04	0.42	±	0.04	-0.04	±	0.06	0.5292
Docosapentaenoic acid	C22:5 *n*-3	0.30	±	0.03	0.19	±	0.03	0.11	±	0.04	0.0105
Docosahexaenoic acid	C22:6 *n*-3	0.11	±	0.06	0.09	±	0.05	0.02	±	0.08	0.8071
Total PUFA		39.40	±	0.65	38.16	±	0.58	1.24	±	0.87	0.1551

[1]Presented as total phospholipid (g/100g lipid) in the lean tissue (IMF).
[2]SL = select line, selected for 7 generations for IMF based on a two-trait animal model that included carcass IMF and predicted via ultrasound; CL = randomly mated, unselected control line.

Table 8. Least squares means (±SE) for fatty acid composition of neutral lipids of intramuscular fat from pigs in generations 3 through 7 of a selection project for intramuscular fat Duroc swine.[1]

		Line[2]		
Fatty acid	**Formula**	**CL**	**SL**	**CL - SL**	**P-value**
Saturated					
Lauric acid	C12:0	0.26 ± 0.05	0.13 ± 0.04	0.13 ± 0.06	0.0367
Myristic acid	C14:0	1.87 ± 0.06	1.76 ± 0.06	0.11 ± 0.09	0.1942
Pentadecanoic acid	C15:0	0.11 ± 0.04	0.03 ± 0.03	0.08 ± 0.05	0.1135
Palmitic acid	C16:0	28.27 ± 0.36	27.96 ± 0.32	0.31 ± 0.48	0.5153
Margaric acid	C17:0	0.09 ± 0.02	0.11 ± 0.02	-0.02 ± 0.02	0.4234
Stearic acid	C18:0	12.55 ± 0.19	13.32 ± 0.17	-0.77 ± 0.25	0.0029
Arachidic acid	C20:0	0.11 ± 0.01	0.16 ± 0.01	-0.05 ± 0.01	0.0004
Behenic acid	C22:0	0.004 ± 0.006	0.008 ± 0.005	-0.004 ± 0.008	0.5733
Lignoceric acid	C24:0	0.05 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.0246
Total saturated		43.32 ± 0.41	43.50 ± 0.37	-0.18 ± 0.56	0.7509
Monounsaturated					
Myristoleic acid	C14:1	0.08 ± 0.03	0.02 ± 0.03	0.06 ± 0.04	0.1339
Palmitoleic acid	C16:1 *n*-7	3.83 ± 0.07	3.84 ± 0.06	-0.01 ± 0.09	0.9324
cis-Heptadecenoic acid	C17:1 *n*-10	0.07 ± 0.01	0.09 ± 0.01	-0.02 ± 0.01	0.1689
Oleic acid	C18:1 *n*-9	42.95 ± 0.57	42.22 ± 0.51	0.73 ± 0.76	0.3382
trans-Vaccenic acid	C18:1 *n*-7	3.41 ± 0.33	4.22 ± 0.30	-0.81 ± 0.44	0.0699
Eicosanoic acid	C20:1 *n*-9	0.54 ± 0.02	0.66 ± 0.02	-0.12 ± 0.03	0.0003
Nervonic acid	C24:1	0.001 ± 0.003	0.013 ± 0.003	-0.012 ± 0.004	0.0029
Total MUFA		50.88 ± 0.43	51.07 ± 0.39	-0.19 ± 0.58	0.7490
Polyunsaturated					
Linoleic acid	C18:2 *n*-6	5.02 ± 0.10	4.63 ± 0.09	0.39 ± 0.13	0.0038
α-Linolenic acid	C18:3 *n*-3	0.23 ± 0.04	0.24 ± 0.03	-0.01 ± 0.05	0.8738
γ-Linolenic acid	C18:3 *n*-6	0.07 ± 0.02	0.02 ± 0.02	0.05 ± 0.02	0.0843
Eicosadienoic acid	C20:2 *n*-6	0.19 ± 0.01	0.18 ± 0.01	0.01 ± 0.02	0.8255
Eicosatrienoic acid	C20:3 *n*-6	0.05 ± 0.03	0.06 ± 0.02	-0.01 ± 0.03	0.6866
Arachidonic acid	C20:4 *n*-6	0.05 ± 0.01	0.07 ± 0.01	-0.02 ± 0.01	0.3356
Eicosapentaenoic acid	C20:5 *n*-3	0.12 ± 0.02	0.12 ± 0.02	0.00 ± 0.03	0.8273
Docosatetraenoic acid	C22:4 *n*-6	0.004 ± 0.002	0.013 ± 0.002	-0.009 ± 0.003	0.0009
Docosapentaenoic acid	C22:5 *n*-3	0.002 ± 0.001	0.004 ± 0.001	-0.002 ± 0.002	0.2504
Docosahexaenoic acid	C22:6 *n*-3	0.02 ± 0.02	0.02 ± 0.02	0.00 ± 0.02	0.9211
Total PUFA		5.77 ± 0.13	5.40 ± 0.12	0.37 ± 0.17	0.0335

[1]Presented as total neutral lipid (g/100g lipid) in the lean tissue (IMF).
[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

Table 9. Least squares means (±SE) for fatty acid composition of tenth-rib subcutaneous adipose tissue (all layers combined) from pigs in generations 6 and 7 of a selection project for intramuscular fat in Duroc swine.[1]

		Line[2]			
Fatty acid	**Formula**	**CL**	**SL**	**CL - SL**	**P-value**
Saturated					
Lauric acid	C12:0	0.053 ± 0.005	0.055 ± 0.005	-0.002 ± 0.007	0.7784
Myristic acid	C14:0	1.34 ± 0.03	1.44 ± 0.03	-0.10 ± 0.04	0.0084
Pentadecanoic acid	C15:0	0.033 ± 0.004	0.030 ± 0.004	0.003 ± 0.005	0.5873
Palmitic acid	C16:0	23.78 ± 0.27	25.58 ± 0.24	-1.80 ± 0.37	<0.0001
Margaric acid	C17:0	0.45 ± 0.02	0.43 ± 0.02	0.02 ± 0.03	0.4968
Stearic acid	C18:0	12.51 ± 0.20	12.88 ± 0.18	-0.37 ± 0.27	0.1786
Arachidic acid	C20:0	0.17 ± 0.01	0.18 ± 0.01	-0.01 ± 0.01	0.3501
Behenic acid	C22:0	0.015 ± 0.003	0.015 ± 0.002	0.000 ± 0.003	0.9727
Lignoceric acid	C24:0	0.04 ± 0.02	0.02 ± 0.02	0.02 ± 0.03	0.3568
Total saturated		38.41 ± 0.42	40.65 ± 0.38	-2.24 ± 0.57	0.0003
Monounsaturated					
Myristoleic acid	C14:1	0.02 ± 0.01	0.02 ± 0.01	0.00 ± 0.01	0.7897
Palmitoleic acid	C16:1 *n*-7	1.99 ± 0.04	2.20 ± 0.04	-0.21 ± 0.05	0.0005
cis-Heptadecenoic acid	C17:1 *n*-10	0.25 ± 0.01	0.25 ± 0.01	0.00 ± 0.02	0.7781
Oleic acid	C18:1 *n*-9	38.93 ± 0.51	39.20 ± 0.48	-0.27 ± 0.70	0.6901
trans-Vaccenic acid	C18:1 *n*-7	2.33 ± 0.37	1.63 ± 0.36	0.70 ± 0.52	0.1785
Eicosanoic acid	C20:1 *n*-9	0.61 ± 0.02	0.59 ± 0.02	0.02 ± 0.03	0.4392
Nervonic acid	C24:1	0.048 ± 0.003	0.043 ± 0.003	0.005 ± 0.004	0.2481
Total MUFA		44.13 ± 0.36	43.93 ± 0.33	0.20 ± 0.49	0.6778
Polyunsaturated					
Linoleic acid	C18:2 *n*-6	15.32 ± 0.36	13.58 ± 0.33	1.74 ± 0.49	0.0009
α-Linolenic acid	C18:3 *n*-3	0.93 ± 0.02	0.82 ± 0.02	0.11 ± 0.03	0.0008
γ-Linolenic acid	C18:3 *n*-6	0.015 ± 0.005	0.013 ± 0.005	0.002 ± 0.007	0.7781
Eicosadienoic acid	C20:2 *n*-6	0.75 ± 0.02	0.65 ± 0.02	0.10 ± 0.02	<0.0001
Eicosatrienoic acid	C20:3 *n*-6	0.10 ± 0.03	0.07 ± 0.03	0.03 ± 0.04	0.4316
Arachidonic acid	C20:4 *n*-6	0.15 ± 0.01	0.14 ± 0.01	0.01 ± 0.01	0.2786
Eicosapentaenoic acid	C20:5 *n*-3	0.005 ± 0.001	0.005 ± 0.001	0.000 ± 0.002	0.9479
Docosatetraenoic acid	C22:4 *n*-6	0.05 ± 0.01	0.05 ± 0.01	0.00 ± 0.01	0.8001
Docosapentaenoic acid	C22:5 *n*-3	0.030 ± 0.005	0.025 ± 0.005	0.005 ± 0.007	0.4621
Docosahexaenoic acid	C22:6 *n*-3	0.001 ± 0.001	0.00 ± 0.00	0.001 ± 0.001	0.0417
Total PUFA		17.35 ± 0.40	15.35 ± 0.36	2.00 ± 0.54	0.0005

[1]Presented as g/100g of total lipid from tenth-rib adipose tissue from generations 6 and 7 only.
[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

CHAPTER 4.

THE EFFECT OF GENDER ON FATTY ACID COMPOSITION, MEAT QUALITY AND SENSORY CHARACTERISTICS IN DUROC PIGS SELECTED FOR INTRAMUSCULAR FAT FOR SEVEN GENERATIONS[1]

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ABSTRACT: The objective of this study was to evaluate the effect of gender on fatty acid composition, meat quality, and sensory characteristics of Duroc pigs selected for increased IMF for 7 generations. Selection was based on estimated breeding value for IMF from fitting a 2-trait animal model and the full relationship matrix in MATVEC. The 2 traits emphasized were IMF estimated on the carcass and IMF predicted using real-time ultrasound on the live animal. Longissimus muscle samples (LM) (n=663, 357 in CL, 306 in SL) collected from generations 3 through 7 and adipose tissue samples from generations 6 and 7 were used to determine fatty acid composition. Total lipids were extracted and methylated directly with acetyl chloride and methanol. Triacylglycerols (TAG) were separated from phospholipids (PL) in IMF by thin-layer chromatography. All fatty acid methyl esters were quantified by using gas chromatography. Results from this study indicated that gilts were compositionally leaner and had greater LMA when compared to barrows, although loin samples from barrows had more IMF. Barrows had more favorable sensory panel scores for juiciness, chewiness, tenderness, and overall flavor, indicating that IMF may have an influence on sensory panel characteristics of pork. All measures of color for loin samples from gilts indicated darker color when compared to barrows. Additionally, there were no gender differences for pH, percent cook loss, and water holding capacity. Fatty acid profiles for total lipid and TAG from IMF and subcutaneous fat samples from barrows had greater concentrations of SFA and less PUFA. There were no differences in fatty acid composition for the PL fraction. Gilts had lower atherogenic index values indicating a healthier product; however, the increase in PUFA content may lead to decreased shelf life and oxidative stability. Gender is a significant source of variation for fatty acid composition, meat quality, and sensory characteristics of pork from purebred Duroc pigs selected for increased IMF.

Key words: fat quality, gender, intramuscular fat, meat quality, swine

INTRODUCTION

Gender differences for fatty acid composition have been evaluated by several authors (Cameron and Enser, 1991; Warnants et al., 1996; Warnants et al., 1999). Fatty acid composition of muscle phospholipid does not differ between gilts and barrows; however, gilts have repeatedly been found to have greater PUFA concentrations in triacylglycerols (TAG) and total lipid, even after correction for gender (De Smet et al., 2004). As suggested by De Smet et al. (2004), a residual gender effect independent of fat content may exist for fatty acid composition.

It is well documented that physiological differences exist among castrates, intact males, and females (NRC, 1998). Intact males are compositionally leaner and grow at a faster rate than females (Wagner et al., 1999). Average daily gain was greater in boars with high testosterone concentration (Robison et al., 1994). These growth performance and compositional differences among gender groups are largely due to differences in endogenous hormone concentration (i.e. testosterone) (Lubritz et al., 1991). Understanding the effect of endogenous hormone concentration on compositional changes in meat quality, fat quality, and sensory traits would be beneficial in identifying superior product for both eating quality and healthfulness for consumers.

Because differences in backfat thickness and lean muscle are inherent between gender groups, it is imperative to further investigate fatty acid composition of adipose depots to see if variation may exist. Fatty acid composition of adipose tissue can be useful in predicting overall fat quality. Variation in fatty acid composition has been shown to significantly affect the firmness or softness of fat due to differences in the melting point of the individual fatty

acids. Adipose tissue with the lowest thickness (<15mm) lacks consistency because it has the highest proportion of polyunsaturated fatty acids (PUFA) and the lowest proportion of saturated fatty acids (SFA) (Villegas et al., 1973; Wood, 1973). The objective of this study was to determine gender differences for fatty acid composition, meat quality, and sensory characteristics of loins from purebred Duroc pigs selected for increased intramuscular fat (IMF).

MATERIALS AND METHODS

Population

Experimental protocols for the study were approved by the Iowa State University Institutional Animal Care and Use Committee. A purebred Duroc population was initiated in 1998 to evaluate selection IMF in Duroc swine using real-time ultrasound. After 2 generations of random mating, a select line (SL) and a control line (CL) were created and selection began as described by Schwab et al. (2009). Selection was based on breeding values for IMF estimated by fitting a 2-trait (IMF measured on the carcass and IMF predicted via real-time ultrasound) animal model in MATVEC (Wang et al., 2003). Details of this selection, breeding value estimation, mating procedures, and responses after 6 generations are reported by Schwab et al. (2009).

Performance and carcass measurements

Finishing pigs were housed in totally slatted, mechanically ventilated, curtain-sided finishing buildings and were provided a minimum of 0.77 m^2 of floor space with 20 to 25 pigs per pen from 34 kg until they reached an average off test weight of 110 kg. A 19.0% CP, 1.20% lysine corn-soy diet was provided ad libitum from 34 to 68 kg BW, followed by a 18.0% CP, 1.05% lysine corn-soy diet from 68 kg to 91 kg BW, followed by a 15.5% CP,

0.85% lysine corn-soy diet (Table 1) from 91 kg until market weight. Dietary fatty acid analysis for finishing phase 3 is presented in Table 2.

Upon completion of the performance test period, all available barrows and randomly selected gilts were harvested at a commercial abattoir (Hormel Foods, Austin, MN). Carcass measurements were obtained by Iowa State University personnel 24 h post-mortem. Standard carcass collection procedures as outlined in Pork Composition and Quality Assessment Procedures (NPPC, 2000) were followed to obtain measurements of 10^{th} rib backfat (BF10) and loin muscle area (LMA). A section of bone-in *longissimus dorsi* containing the 10^{th} to 12^{th} ribs was excised from the carcass and transported to the Iowa State University Meat Laboratory. A 3.2 mm slice from the 10th rib face was utilized for lipid content analysis. Carcass pH was measured 48 h post-mortem on the 10^{th} rib face of the longissimus muscle by using a pH star probe (SFK Ltd, Hvidovre, Denmark). Hunter L^* score and Minolta reflectance were measured on the 10^{th} rib face of the loin by using a Minolta CR-310 (Minolta Camera Co., Ltd., Osaka, Japan) with a 50-mm-diameter aperture, D65 illuminant, and calibrated to the white calibration tile. The 11^{th} and 12^{th} rib sections were cut into 2.54 cm samples and set cut side up for 10 min to allow color development. Subjective measures of color (1 = pale pinkish gray to white; 6 = dark purplish red), marbling (1 = 1% IMF; 10 = 10% IMF), and firmness (1 =soft; 3 = very firm) were evaluated on the 11^{th} rib face according to NPPC (2000) by personnel trained in meat quality evaluation. Water holding capacity was measured on the 11^{th} rib face using the filter paper method described by Kauffman et al. (1986). Longissimus muscle samples (n=663) collected from generation 3 through 7 pigs (Table 3) in the CL (n=357) and SL (n=306) were used to determine fatty acid profiles of IMF.

Fatty acid analysis

Trimmed loin samples (Generations 3 through 7) and all layers of adipose tissue (Generation 6 and 7 pigs only) from the *longissimus dorsi* at the 10-11th rib were utilized for fatty acid determination. Total lipid was extracted from IMF samples with a chloroform and methanol (2:1, vol:vol) mixture and quantified gravimetrically (Folch et al., 1957). Triacylglycerols (TAG) were separated from phospholipids (PL) by thin-layer chromatography with hexane and ethyl acetate (4:1, vol:vol). Fatty acids in each lipid were derivatized to methyl esters according to Lepage and Roy (1986). Fatty acid methyl ester (FAME) from both subcutaneous adipose tissue and IMF were analyzed by gas chromatography (GC; model 3400, Varian, Palo Alto, CA) equipped with a Supelco SP-2560 column (100 m x 0.25 mm x 0.2 μm film thickness) and a flame ionization detector. The column started at a temperature of 100°C and was increased to 170°C at a rate of 2°C per min, followed by an increase to 180°C at 0.5°C per min and to 250°C at 10°C per minute. The detector was maintained at 220°C and total run time was 77 min. Based on the fatty acid composition, atherogenic index (AI) was calculated following Ulbricht and Southgate (1991):

$$AI = \frac{C12:0 + (4 \times C14:0) + C16:0}{\Sigma MUFA + \Sigma PUFA}.$$

Sensory evaluation

Two 2.54-cm thick chops from the 10th to 12th rib section were vacuum packaged and taken to the Iowa State University Food Science Laboratory (McKay Hall, Iowa State University). Samples were refrigerated at 0°C for 7 d. Chops were cooked to 71°C in an electric broiler (Amana model ARE 640, Amana, IA), with sample temperature monitored by

Chromega/Alomega thermocouples attached to an Omega digital thermometer (DSS-650, Omega Engineering, Inc., Stamford, CT). Weights prior to and immediately after cooking were used to calculate percent cooking loss. A 3-member trained sensory panel evaluated cooked loin samples for quality attributes (Huff-Lonergan et al., 2002) on three 1.3 cm^3 cubes from the center of the 11^{th} and 12^{th} rib samples. Eating quality evaluations for juiciness (1 = dry; 10 = juicy), tenderness (1 = tough; 10 = tender), flavor (1 = little pork flavor; 10 = extremely flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor; 10 = abundant non-pork flavor) were recorded by using an end-anchored 10-point scoring system (AMSA, 1995). Individual booths with red overhead lighting were provided for each panelist. Sample evaluations were averaged across panelists for analysis. The 12^{th} rib section was evaluated for tenderness by using an Instron Universal Testing Machine (Model 1122; Instron Corp., Canton, MA) fitted with a circular, 5-point star probe (9 mm diameter with 6 mm between points) (Oltrogge-Hammernick and Prusa, 1987).

Statistical analysis

Gender differences for meat and eating quality traits and fatty acid composition through generation 7 were assessed by using the MIXED procedure of SAS (SAS Inst., Cary, NC). A mixed model with fixed effects of line, gender, and carcass contemporary group, the interaction of gender by line, random effects of sire nested within line and dam nested within line, and a covariate of hot carcass weight was used to estimate least squares means for all dependent variables. Least squares means within fixed effects were compared by using pair-wise *t*-tests (*pdiff* option in SAS) and declared to be different at $P < 0.05$.

RESULTS AND DISCUSSION

Carcass composition and meat quality

Least squares means by gender for carcass composition, meat quality, and sensory panel traits are presented in Table 4. Gilts were leaner at the tenth-rib, last-rib, and last-lumbar vertebrae, and had greater LMA ($P < 0.001$). Barrows had more IMF (0.78%) when compared to gilts ($P < 0.001$). This result was in agreement with previous studies (Leszczynski et al., 1992; Warnants et al., 1996; Zhang et al., 2007). In the current study, there were no differences between sexes ($P > 0.05$) for pH, water-holding capacity, and percent cook loss.

Gilts had lower Minolta reflectance and Hunter L^* values, indicating darker colored loins. These observed color differences may be influenced by the quantity of IMF on the exposed loin muscle surface, rather than by true differences in lean tissue color.

Fat quality and fatty acid composition

Least squares means for fat quality traits and fatty acid composition of intramuscular fat are presented in Table 5. Loin samples from barrows had more C14:0, C16:0, and C18:0 ($P < 0.001$) present in the total lipid fraction of intramuscular fat when compared to gilts, similar to results found by Barton-Gade (1987). Additionally, total lipid of IMF had a greater concentration of SFA and lower PUFA concentration ($P < 0.001$), so consequently had a lower IV ($P < 0.001$) for IMF. There were no differences between sexes ($P > 0.05$) in the phospholipid fraction of IMF, although gilts had a greater concentration of C20:4*n*6 ($P < 0.001$). Gilts had a greater concentration of C18:2*n*6 ($P < 0.001$) present in the neutral lipid fraction of IMF, but had less SFA ($P < 0.05$). The more unsaturated fatty acid composition in the TAG fraction for gilts than barrows in the current study is consistent with Warnants et

al. (1996). The PL fraction, in contrast to the TAG fraction, was very similar for barrows and gilts (Warnants et al., 1996). This would be expected due to the role that phospholipids have in membrane integrity of all tissues (Warnants et al., 1996; Farkas et al., 2000). Gender effects in the current study were consistent with those of Nurnberg et al. (2005), who reported that barrows had greater SFA and lower PUFA than gilts in total lipid of LM. A previous study conducted by Leszczynski et al. (1992) showed a significant effect of gender on SFA, MUFA and PUFA content of total lipid of LM.

Fat quality in pigs has been shown to be dependent upon gonadal status (Barton-Gade, 1987). In that study, boars had the highest iodine values and castrate males the lowest, with gilt values being intermediate. Twenty percent of the boars had iodine values ≥ 70, which is often used as an indicator of soft fat with poor shelf life. In the current study, gilts had greater predicted iodine values ($P < 0.001$) than barrows in both intramuscular fat (59.06 compared to 56.34) and subcutaneous (67.17 compared to 63.47) fat samples.

Subcutaneous adipose tissue samples from barrows had greater concentrations of SFA, C16:0, and C18:0, and less PUFA ($P < 0.001$) when compared to gilts (Table 6). Similar findings were reported by Elliot and Bowland (1970). This increase in saturated fatty acids can be described by the difference in backfat thickness between sexes, with gilts being leaner than castrates (Wood, 1984). Warnants et al. (1999) reported that barrows had greater concentration of C16:0, C18:0, and total SFA in backfat and greater content of C16:0 in the total lipid of IMF than gilts. In the current study, there were no differences between sexes for the concentration of MUFA found in subcutaneous fat. Additionally, gilts had more PUFA concentration in subcutaneous adipose when compared to barrows. This increase in

PUFA may lead to a decrease in shelf life due to the susceptibility of unsaturated fatty acids to oxidation.

A thinner back fat layer corresponds to lower percentage of extractable fat, greater protein and water content, greater iodine value, and more unsaturated fatty acids (Barton-Gade, 1984). Further research has shown higher concentrations of C18 polyunsaturated fatty acids and lower concentrations of C18:1 in entire male pigs when compared to gilts (Wood et al., 1989). Pigs with the genetic potential to become obese have been shown to have subcutaneous fat with a greater concentration of saturated fatty acids when compared to lean pigs in a similar contemporary group (Scott et al., 1981).

Stearoyl-CoA desaturase (SCD), or Δ^9-desaturase, catalyzes the conversion of C16:0 and C18:0 to C16:1 and C18:1, the 2 major MUFA found in pork lipids (Warnants et al., 1996). A decrease in SCD activity has been shown to decrease total MUFA in pigs fed crushed linseed for 60 d (Kouba et al., 2003). Additional studies have reported elevated concentration of C16:1 in breeds of beef cattle may be attributed to increased SCD activity (Sturdivant et al., 1992; Laborde et al., 2001).

Activity of SCD was estimated using 3 different ratios for IMF (Table 5) and subcutaneous fat (Table 6). Greater index values mean greater desaturase activity. The Δ^9-desaturase (C16) index, which is an indicator of the SCD influence on the conversion of C16:0 to C16:1, was not different ($P > 0.05$) between sexes in the current study. However, the Δ^9-desaturase (C18) index, which is an indicator of the influence of SCD conversion of C18:0 to C18:1, was greater in gilts ($P < 0.05$). Because the concentration of C18:1 present in IMF was much greater than that of C16:1, the differences in Δ^9-desaturase (C16+C18) index (indicator of the conversion of C16:0 and C18:0 to their respective MUFAs), are

similar to those of Δ^9-desaturase (C18). In the current study, there were differences in Δ^9-desaturase activity between the 2 gender groups, indicating similar enzyme activities in barrows and gilts. In a multi-breed study conducted by Zhang et al. (2007), there were no significant differences ($P > 0.05$) found between barrows and gilts for Δ^9-desaturase activity. Gillis et al. (1973) reported a significantly higher level of linoleic acid and lower level of oleic acid in subcutaneous and intramuscular fat of bulls compared to steers. In the current study, there was no difference in oleic acid concentration between sexes, however, gilts had a greater concentration of linoleic acid ($P < 0.001$) when compared to barrows. Possible effects of endogenous sex hormones on the enzyme systems such as Δ^9-desaturase may interfere with the interconversion of fatty acids from saturated to monounsaturated forms.

Concentration of linoleic acid (C18:2*n*6) in both IMF and subcutaneous adipose tissue was greater in gilts when compared to barrows ($P < 0.001$) (Tables 5 and 6). Linoleic acid cannot be synthesized in vivo in pigs, and therefore carcass content of this fatty acid directly reflects the dietary intake. Concentration of C18:2*n*6 has been shown to be negatively correlated with IMF content (-0.68) (Zhang et al., 2007). Pigs with less IMF content tend to have lower de novo fatty acid synthesis and consequently, dietary fatty acids make up a greater concentration of the fatty acids in adipose tissue (Wood et al., 1989). These results indicate that the differences in C18:2*n*6 content observed in the current study may be the result of differences in IMF content between sexes, which may be described by greater de novo fatty acid synthesis in barrows that also had greater IMF (4.24% compared to 3.46%).

Overall healthfulness of pork and meat products can be described by lipid quality, which can be an indicator of the propensity to cause atherogenicity. Ulbricht and Southgate

(1991) developed the AI in order to measure atherogenicity of dietary lipids. This method is often considered a better measurement than the traditional PUFA to SFA ratio (P:S) because it includes total MUFA and places more weight on C14:0, which is considered to be the most atherogenic (Hegsted et al., 1965; Keys et al., 1974). Additionally, these authors stated that C14:0 is almost 4 times more harmful for human cardiovascular effects than C16:0. In the current study, gilts had the greatest P:S ratio in both IMF and subcutaneous fat when compared to barrows. Additionally, barrows had a greater AI ($P < 0.01$) in both IMF and subcutaneous fat.

Eating quality traits

Gender was a significant source of variation for sensory panel scores for eating quality traits. Least squares means by gender for these traits are presented in Table 4. Sensory panel subjective scoring of pork loin samples from barrows were more favorable for juiciness ($P < 0.01$), chewiness ($P < 0.001$), tenderness ($P < 0.01$), and flavor ($P < 0.001$) when compared to gilts. There were no differences ($P > 0.05$) for off-flavor scores when chops were evaluated from the 2 gender groups. These results are supported by the findings reported by Fortin et al. (2005) which showed no eating quality differences between sexes with varying levels of intramuscular fat. In that same study, level of intramuscular fat, independent of gender, was a significant source of variation and was correlated with tenderness (-0.31), average shear force (-0.41), chewiness (-0.27) and flavor (0.24) (Fortin et al., 2005). In the current study, barrows had greater IMF and overall sensory panel scores for tenderness, chewiness, and flavor, agreeing with the correlations between IMF and sensory traits reported by Fortin et al. (2005).

Addressing consumer health concerns over fat intake, especially saturated fatty acids, is currently the most important objective for meat animal producers to achieve. Significant gender differences in carcass composition, fatty acid composition, and sensory characteristics were observed in the current study. These differences may be sufficiently large enough that they may be exploited in selecting pork products from different sexes to achieve a more ideal product selection when processors sell pork to niche markets focusing on healthfulness of pork with superior sensory characteristics.

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Table 1. Dietary components and nutrient composition of finishing diets fed to Durocpigs in selection project designed to increase intramuscular fat

	Finishing Phase[1]		
Item	**1**	**2**	**3**
Calculated Composition[2]			
Corn, %	68.32	74.75	81.00
Soybean meal, %	26.25	20.00	13.75
Added Fat, %[3]	3.00	3.00	3.00
Base premix, %	2.25	2.25	2.25
Tylan 40, g/ton	0.13	-	-
Cupric sulfate, %	0.05	-	-
Total	100	100	100
Protein, %	19	18	15.5
Lysine, %	1.2	1.05	0.85
Fat, %	6	6	6
Fiber, %	3.2	3.2	3.2
Calcium, %	0.55	0.54	0.54
Phosphorus, %	0.45	0.45	0.45
Salt, %	0.5	0.5	0.5
Zinc, mg/kg	140	140	140
Copper, mg/kg	135	10	10
Phytase-FTU/kg	750	750	750
Selenium, mg/kg	0.3	0.3	0.3

[1]Finishing phase 1 – 34 to 68 kg BW; Finishing phase 2 – 68 to 91 kg BW; Finishing phase 3 – 91 kg to market weight.
[2]Calculated composition based on NRC (1998) values.
[3]Choice white grease

Table 2. Fatty acid composition of the phase 3 finishing diet fed to Duroc pigs in a selection project for intramuscular fat content[1]

Trait	Formula	Finishing Phase 3[2]
Fat, %		6.26
Saturated fatty acids (wt %)		
Lauric acid	C12:0	0.01
Myristic acid	C14:0	0.76
Pentadecanoic acid	C15:0	0.00
Palmitic acid	C16:0	22.18
Margaric acid	C17:0	0.25
Stearic acid	C18:0	8.65
Arachidic acid	C20:0	0.36
Behenic acid	C22:0	0.09
Lignoceric acid	C24:0	0.00
Total saturated		32.30
Monounsaturated fatty acids (wt %)		
Myristoleic acid	C14:1	0.04
Palmitoleic acid	C16:1 *n*-7	1.45
cis-Heptadecenoic acid	C17:1 *n*-10	0.13
Oleic acid	C18:1 *n*-9	17.20
trans-Vaccenic acid	C18:1 *n*-7	1.39
Eicosanoic acid	C20:1 *n*-9	0.74
Nervonic acid	C24:1	0.08
Total MUFA		21.03
Polyunsaturated fatty acids (wt %)		
Linoleic acid	C18:2 *n*-6	44.35
α-Linolenic acid	C18:3 *n*-3	1.56
γ-Linolenic acid	C18:3 *n*-6	0.01
Eicosadienoic acid	C20:2 *n*-6	0.00
Eicosatrienoic acid	C20:3 *n*-6	0.08
Arachidonic acid	C20:4 *n*-6	0.21
Eicosapentaenoic acid	C20:5 *n*-3	0.00
Docosatetraenoic acid	C22:4 *n*-6	0.01
Docosapentaenoic acid	C22:5 *n*-3	0.01
Docosahexaenoic acid	C22:6 *n*-3	0.00
Total PUFA		46.23

[1]Presented as a percentage of total lipid in the feed on an as-fed basis.
[2]Finishing phase 3 fed from 91 kg to market weight.

Table 3. Distribution of records by generation and line from a selection experiment for increased intramuscular fat in Duroc swine

	Generation					
Trait Category	**3**	**4**	**5**	**6**	**7**	**Total**
	No. of observations					
Contol Line[1]						
Gilts	14	5	14	17	6	56
Barrows	67	66	87	60	21	301
Select Line[2]						
Gilts	8	24	24	32	12	100
Barrows	56	53	46	40	11	206
Total						
Gilts	22	29	38	49	18	156
Barrows	123	119	133	100	32	507
Carcass	145	148	171	149	50	663

[1]Control line = unselected, randomly mated population.
[2]Select line = result of 7 generations of selection for increased IMF based on a two-trait animal model that included IMF measured on the carcass and predicted via ultrasound.

Table 4. Least squares means (±SE) for carcass composition, meat quality, and sensory traits by gender from pigs in generations 3 through 7 of a selection project for intramuscular fat in Duroc swine.

Item	Gender		Significance[1]
	Gilts	Barrows	
Carcass composition			
Length, cm	82.86 ± 0.18	81.82 ± 0.12	***
Tenth rib backfat, mm	19.80 ± 0.51	25.53 ± 0.36	***
Last rib backfat, mm	23.30 ± 0.45	27.17 ± 0.39	***
Last lumbar backfat, mm	18.62 ± 0.45	21.91 ± 0.31	***
Loin muscle area, cm^2	43.44 ± 0.42	39.04 ± 0.29	***
Intramuscular fat, %	3.46 ± 0.13	4.24 ± 0.09	***
Meat Quality			
24 h pH	5.72 ± 0.01	5.73 ± 0.01	NS
48 h pH	5.66 ± 0.01	5.69 ± 0.01	NS
7 d pH	5.70 ± 0.01	5.71 ± 0.01	NS
24 h Minolta reflectance	22.97 ± 0.23	24.35 ± 0.16	***
48 h Minolta reflectance	22.05 ± 0.23	23.24 ± 0.16	***
24 h Hunter L^* value	47.77 ± 0.27	49.14 ± 0.18	***
48 h Hunter L^* value	46.94 ± 0.31	48.02 ± 0.19	**
Water holding capacity, mg/wt	55.58 ± 2.14	58.11 ± 1.34	NS
Cooking loss, %	17.87 ± 0.30	18.33 ± 0.17	NS
Instron tenderness, kg	5.79 ± 0.08	5.49 ± 0.05	***
Sensory Evaluation[2]			
Juiciness score	6.09 ± 0.10	6.39 ± 0.06	**
Chewiness score	3.23 ± 0.09	2.87 ± 0.05	***
Tenderness score	6.12 ± 0.12	6.54 ± 0.07	**
Flavor score	2.59 ± 0.10	3.02 ± 0.06	***
Off-flavor score	2.51 ± 0.11	2.27 ± 0.07	NS

[1] NS = no significant difference ($P > 0.05$); **$P < 0.01$; ***$P < 0.001$.

[2]Trained sensory panel evaluations of juiciness (1 = dry; 10 = juicy), chewiness (1 = not chewy; 10 = very chewy), tenderness (1= tough; 10 = tender), flavor (1 = little pork flavor, bland; 10 = very flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor, 10 = abundant non-pork flavor).

Table 5. Least squares means (±SE) for fatty acid composition of total lipid, phospholipid, and neutral lipid of LM intramuscular fat from pigs in generations 3 through 7 of a selection project for intramuscular fat in Duroc swine.

		Gender		
Trait	**Formula**	**Gilts**	**Barrows**	**Significance[1]**
Total Lipid[2]				
Myristic acid	C14:0	1.40 ± 0.03	1.50 ± 0.02	***
Palmitic acid	C16:0	25.64 ± 0.27	26.70 ± 0.17	***
Palmitoleic acid	C16:1 *n*-7	3.33 ± 0.06	3.44 ± 0.04	NS
Stearic acid	C18:0	12.81 ± 0.14	13.53 ± 0.09	***
Oleic acid	C18:1 *n*-9	41.94 ± 0.44	41.85 ± 0.26	NS
Linoleic acid	C18:2 *n*-6	8.83 ± 0.16	7.12 ± 0.10	***
α-Linolenic acid	C18:3 *n*-3	0.68 ± 0.02	0.72 ± 0.01	*
Arachidonic acid	C20:4 *n*-6	0.43 ± 0.04	0.36 ± 0.02	NS
SFA		40.83 ± 0.29	42.57 ± 0.20	***
MUFA		47.72 ± 0.31	48.16 ± 0.18	NS
PUFA		10.63 ± 0.19	8.81 ± 0.12	***
AI[3]		0.54 ± 0.02	0.58 ± 0.01	**
IV[4]		59.06 ± 0.34	56.34 ± 0.22	***
P:S ratio[5]		0.27 ± 0.01	0.21 ± 0.01	***
Phospholipid[6]				
Myristic acid	C14:0	0.53 ± 0.17	0.48 ± 0.06	NS
Palmitic acid	C16:0	20.51 ± 0.51	21.13 ± 0.30	NS
Palmitoleic acid	C16:1 *n*-7	0.52 ± 0.10	0.49 ± 0.06	NS
Stearic acid	C18:0	8.90 ± 0.24	9.20 ± 0.14	NS
Oleic acid	C18:1 *n*-9	10.47 ± 0.36	10.99 ± 0.21	NS
Linoleic acid	C18:2 *n*-6	31.31 ± 0.67	32.03 ± 0.38	NS
α-Linolenic acid	C18:3 *n*-3	0.18 ± 0.05	0.11 ± 0.03	NS
Arachidonic acid	C20:4 *n*-6	5.40 ± 0.27	4.29 ± 0.18	***
SFA		42.44 ± 0.58	42.91 ± 0.35	NS
MUFA		15.23 ± 0.52	15.78 ± 0.30	NS
PUFA		39.13 ± 0.73	38.39 ± 0.43	NS
Neutral Lipid[7]				
Myristic acid	C14:0	1.79 ± 0.07	1.86 ± 0.04	NS
Palmitic acid	C16:0	27.81 ± 0.65	28.59 ± 0.24	NS
Palmitoleic acid	C16:1 *n*-7	3.81 ± 0.07	3.89 ± 0.04	NS
Stearic acid	C18:0	12.57 ± 0.21	13.16 ± 0.13	*
Oleic acid	C18:1 *n*-9	42.91 ± 0.66	42.00 ± 0.37	NS
Linoleic acid	C18:2 *n*-6	5.26 ± 0.11	4.49 ± 0.07	***
α-Linolenic acid	C18:3 *n*-3	0.21 ± 0.04	0.25 ± 0.02	NS
Arachidonic acid	C20:4 *n*-6	0.06 ± 0.01	0.05 ± 0.01	NS
SFA		42.77 ± 0.48	44.15 ± 0.27	*
MUFA		51.12 ± 0.50	50.62 ± 0.29	NS
PUFA		6.06 ± 0.15	5.20 ± 0.09	***
Fatty Acid Indices				
Δ^9-desaturase (C16) index[8]		11.99 ± 0.35	11.63 ± 0.29	NS
Δ^9-desaturase (C18) index[9]		76.86 ± 0.68	74.93 ± 0.39	*
Δ^9-desaturase (C16+C18) index[20]		54.11 ± 0.48	52.74 ± 0.28	*
Thioesterase index[11]		19.33 ± 2.00	20.38 ± 1.24	NS
Elongase index[12]		14.97 ± 14.57	14.95 ± 14.57	NS

[1]NS = no significant difference ($P > 0.05$); *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
[2]Presented as g/100g of lipid fraction in the lean tissue (IMF).
[3]Atherogenic index, calculated as (C12:0 + 4 × C14:0 + C16:0)/(∑ MUFA + ∑ PUFA).
[4]Iodine Value =(C16:1*n*7*0.95) + ((C18:1*n*9+18:1*n*7)*0.86) + (C18:2*n*6*1.732) + ((C18:3*n*3+C18:3*n*6)*2.616) + (C20:1*0.785) + (C22:1*0.723).
[5]The ratio of total PUFA to total SFA.
[6]Presented as least squares means of the percentage of phospholipid in the lean tissue (IMF).
[7]Presented as least squares means of the percentage of neutral lipid in the lean tissue (IMF).
[8]Calculated as 100 × [C16:1n7/(C16:1n7 + C16:0)].
[9]Calculated as 100 × [C18:1n9/(C18:1n9 + C18:0)].
[10]Calculated as 100 × [(C16:1n7 + C18:1n9)/(C16:1n7 + C16:0 + C18:1n9 + C18:0)].
[11]Calculated as C16:0/C14:0.
[12]Calculated as C18:0/C16:0.

Table 6. Least squares means (±SE) for fatty acid composition of subcutaneous adipose tissue and fatty acid indices from pigs in generations 3 through 7 of selection project for intramuscular fat in Duroc swine[1]

Trait	Formula	Gender		Significance[2]
		Gilts	Barrows	
Total Lipid				
Myristic acid	C14:0	1.36 ± 0.03	1.39 ± 0.02	NS
Palmitic acid	C16:0	23.84 ± 0.23	25.24 ± 0.18	***
Palmitoleic acid	C16:1 *n*-7	2.06 ± 0.04	2.12 ± 0.03	NS
Stearic acid	C18:0	12.42 ± 0.19	13.17 ± 0.14	***
Oleic acid	C18:1 *n*-9	39.82 ± 0.47	39.21 ± 0.39	NS
Linoleic acid	C18:2 *n*-6	15.50 ± 0.32	13.54 ± 0.25	***
α-Linolenic acid	C18:3 *n*-3	0.98 ± 0.02	0.87 ± 0.01	***
Arachidonic acid	C20:4 *n*-6	0.14 ± 0.01	0.10 ± 0.01	***
SFA		38.42 ± 0.37	40.62 ± 0.29	***
MUFA		43.91 ± 0.32	43.94 ± 0.25	NS
PUFA		17.56 ± 0.34	15.35 ± 0.27	***
AI[3]		0.48 ± 0.01	0.52 ± 0.01	***
IV[4]		67.17 ± 0.53	63.47 ± 0.41	***
P:S ratio[5]		0.46 ± 0.01	0.38 ± 0.01	***
Fatty Acid Indices				
Δ^9-desaturase (C16) index[6]		7.98 ± 0.15	7.73 ± 0.10	NS
Δ^9-desaturase (C18) index[7]		75.86 ± 0.80	73.90 ± 0.72	**
Δ^9-desaturase (C16+C18) index[8]		53.51 ± 0.59	51.49 ± 0.50	***
Thioesterase index[9]		14.78 ± 4.79	21.98 ± 3.33	NS
Elongase index[10]		0.52 ± 0.01	0.52 ± 0.01	NS

[1]Presented as g/100g of total lipid in tenth-rib subcutaneous adipose tissue from generations 6 and 7 only (all layers combined).
[2]NS = no significant difference ($P > 0.05$); **$P < 0.01$; ***$P < 0.001$.
[3]Atherogenic index, calculated as (C12:0 + 4 × C14:0 + C16:0)/(∑ MUFA + ∑ PUFA)
[4]Iodine Value =(C16:1*n*7*0.95) + ((C18:1*n*9+18:1*n*7)*0.86) + (C18:2*n*6*1.732) + ((C18:3*n*3+C18:3*n*6)*2.616) + (C20:1*0.785) + (C22:1*0.723).
[5]The ratio of total PUFA to total SFA.
[6]Calculated as 100 × [C16:1n7/(C16:1n7 + C16:0)].
[7]Calculated as 100 × [C18:1n9/(C18:1n9 + C18:0)].
[8]Calculated as 100 × [(C16:1n7 + C18:1n9)/(C16:1n7 + C16:0 + C18:1n9 + C18:0)].
[9]Calculated as C16:0/C14:0.
[10]Calculated as C18:0/C16:0.

CHAPTER 5.

EVALUATION OF SHELF LIFE AND PRODUCT STABILITY FROM PIGS WITH DIFFERING LEVELS OF INTRAMUSCULAR FAT[1]

A paper to be submitted to the Journal of Animal Science

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ABSTRACT: The objective of this study was to identify shelf life, objective color stability and oxidative status of fresh pork chops with differing levels of intramuscular fat after 7 generations of selection (select line, SL) for intramuscular fat in Duroc swine. A randomly mated, unselected control line (CL) was maintained in the population. The 2 traits emphasized were IMF estimated on the carcass and IMF predicted using real-time ultrasound on the live animal. *Longissimus dorsi* muscle samples collected from generation 7 pigs (n=50) were used to estimate meat quality characteristics, fatty acid composition, volatile compound formation, and sensory scores of pork. Total lipids were extracted from trimmed LM samples and adipose tissue, then methylated directly with acetyl chloride and methanol. Triacylglycerols (TAG) were separated from phospholipids (PL) in IMF by thin-layer chromatography. All fatty acid methyl esters were quantified by using gas chromatography. Pigs in the SL had more subcutaneous fat, less loin muscle, and consequently less carcass percent lean when compared to carcass from pigs in the CL. Loin muscle samples from pigs in the CL had more desirable objective color scores. No differences were found for most sensory characteristics, however, samples from pigs in the SL tended to have more flavor. No differences in volatile compound formation or thiobarbituric acid values (TBA) were found. Oxidative stability of the fresh pork loins declined over the 28 d aging period. Fat quality is important not only in fresh product, but in further processing, due to the oxidation of unsaturated fats.

Key words: fat quality, intramuscular fat, meat quality, pork, shelf life

INTRODUCTION

Consumer acceptance of fresh meat products depends largely on quality characteristics, such as intramuscular fat, pH, color, and tenderness, all of which have

decreased as breeders have extensively selected for increased lean growth (Barton-Gade, 1990; Cameron, 1990). Efforts to improve meat quality, particularly intramuscular fat, have been the focus of producers, processors, and ultimately, consumers due to the increased demand for highly marbled pork for the export market, branded retail sales, and food service establishments. Intramuscular fat in pork has been reported to positively influence juiciness, tenderness, and flavor (DeVol et al., 1988; Fernandez et al., 1999b; Brewer et al., 2001) . Bejerholm (1986) and Barton-Gade (1990) suggested that the intramuscular fat content of pork needs to be greater than 2% before any noticeable improvements in sensory attributes of pork can be detected. DeVol et al. (1988) concluded that a threshold level of 2.5 to 3.0% intramuscular fat was necessary to attain acceptable tenderness in roasted chops.

With increased emphasis on producing pork with higher levels of intramuscular fat, it is important that product stability and shelf life be maintained. Lipid oxidation is one of the main causes quality deterioration of meat products during storage and processing due to the compounds generated that may produce rancid or off-flavor in pork (Larick et al., 1992). A more unsaturated fatty acid profile may limit shelf-life and product stability because polyunsaturated fatty acids (PUFA) are more susceptible to oxidation (Shackelford et al., 1990; Romans et al., 1995). The objective of this study was to investigate the effect of differing levels of intramuscular fat content on color stability, shelf life, and lipid oxidation of chops from the *longissimus dorsi* during refrigerated storage.

MATERIALS AND METHODS

Population

Experimental protocols for the study were approved by the Iowa State University Institutional Animal Care and Use Committee. A purebred Duroc population was initiated in

1998 to evaluate selection for intramuscular fat (IMF) using real-time ultrasound. After 2 generations of random mating, a line selected for IMF (SL) and a control line (CL) were created and selection began as described by Schwab et al. (2009). Selection was based on breeding values for IMF estimated by fitting a 2-trait (IMF measured on the carcass and IMF predicted via real-time ultrasound) animal model in MATVEC (Wang et al., 2003). Details of this selection, breeding value estimation, mating procedures, and responses after 6 generations are reported by Schwab et al. (2009).

Performance and carcass measurements

Finishing pigs were housed in totally slatted, mechanically ventilated, curtain-sided finishing buildings and were provided a minimum of 0.77 m^2 of floor space with 20 to 25 pigs per pen from 34 kg until they reached an average off test weight of 110 kg. A 19.0% CP, 1.20% lysine corn-soy diet was provided ad libitum from 34 to 68 kg BW, followed by a 18.0% CP, 1.05% lysine corn-soy diet from 68 kg to 91 kg BW, followed by a 15.5% CP, 0.85% lysine corn-soy diet (Table 1) from 91 kg until market weight. Dietary fatty acid analysis of the diet fed in the final finishing phase to all pigs in generation 7 presented in Table 2.

Upon completion of the performance test period, all barrows and randomly selected gilts were harvested at a commercial abattoir (Hormel Foods, Austin, MN). Carcass measurements were obtained by Iowa State University personnel 24 h post-mortem. Standard carcass collection procedures as outlined in Pork Composition and Quality Assessment Procedures (NPPC, 2000) were followed to obtain measurements of 10^{th} rib backfat (BF10) and loin muscle area (LMA). A section of bone-in loin containing the 8^{th} to the last ribs was excised from the left side of the carcass and transported to the Iowa State

University Meat Laboratory. Rib sections were deboned, cut into 2.54 cm samples and allowed to bloom for 20 min to allow color development. A 3.2 mm slice from the 10th rib face was utilized for percent lipid content analysis. Carcass pH was measured 48 h post-mortem on the 10^{th} rib face of the longissimus muscle using a pH star probe (SFK Ltd, Hvidovre, Denmark). Objective color measurements of Hunter L, a^*, and b^* scores and Minolta reflectance were measured on the 10^{th} rib face of the loin using a Minolta CR-310 (Minolta Camera Co., Ltd., Osaka, Japan) with a 50-mm-diameter aperture, D65 illuminant, and calibrated to the white calibration plate. Subjective measures of color (1 = pale pinkish gray to white; 6 = dark purplish red), marbling (1 = 1% IMF; 10 = 10% IMF), and firmness (1 =soft; 3 = very firm) were evaluated on the 11^{th} rib face according to NPPC (2000) by personnel trained in meat quality evaluation. Water holding capacity was measured on the 11^{th} rib face using the filter paper method described by (Kauffman et al., 1986). *Longissimus muscle* samples (n=50) collected from generation 7 pigs in the CL (n=27) and SL (n=23) were used to determine fatty acid composition, volatile composition, and sensory characteristics of samples with differing levels of IMF. To simulate a retail display, 3 chops from each loin were overwrapped and stored on shelves under 7.0 lux of white florescent lighting (constant lighting 24 h/day) at 2 to 4°C. Lights were suspended 61 cm above the overwrapped packages during the 28 d storage period. Color of the lean (L^*, a^*, b^* values) was measured every 7 d. Muscle lipid oxidation, assessed as thiobarbituric acid reacting substances (TBARS) (Tarladgis and Watts, 1960), was measured on one chop at day 0, 7, 14, and 28.

Sensory analysis

Two 2.54 cm thick chops were vacuum packaged and taken to Iowa State University Food Science Laboratory where they were refrigerated at 0°C for 7 d. Both rib sections were cooked to 71°C in an electric broiler (Amana model ARE 640, Amana, IA), with sample temperature monitored by Chromega/Alomega thermocouples attached to an Omega digital thermometer (DSS-650, Omega Engineering, Inc., Stamford, CT). Weights prior to and immediately after cooking were used to calculate percent cooking loss. A trained sensory panel with 3 members evaluated cooked loin quality attributes (Huff-Lonergan et al., 2002) on three 1.3 cm^3 cubes from the center of the 11^{th} and 12^{th} rib samples. Trained sensory panel evaluations for juiciness (1 = dry; 10 = juicy), tenderness (1 = tough; 10 = tender), flavor (1 = little pork flavor; 10 = extremely flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor; 10 = abundant non-pork flavor) were recorded using an end-anchored 10-point scoring system (AMSA, 1995). Individual booths with red overhead lighting were provided for each panelist. Sample evaluations were averaged across panelists for analysis. The 12^{th} rib section was evaluated for tenderness using an Instron Universal Testing Machine (Model 1122; Instron Corp., Canton, MA) fitted with a circular, 5-point star probe (9mm diameter with 6 mm between points) (Oltrogge-Hammernick and Prusa, 1987).

Fatty acid composition analysis

A trimmed loin sample and adipose tissue (all layers combined) were each utilized to determine their fatty acid composition. Total lipid was extracted from adipose and intramuscular fat samples with a chloroform and methanol (2:1, vol:vol) mixture and quantified (Folch et al., 1957). Triacylglycerols (TAG) were separated from phospholipids (PL) by thin-layer chromatography run in hexane and ethyl acetate (4:1, vol:vol). The

individual lipid spots were derivatized to methyl esters according to Lepage and Roy (1986). Fatty acid methyl ester (FAME) from both adipose tissue and intramuscular fat were analyzed by gas chromatography (GC; model 3400, Varian, Palo Alto, CA) equipped with a Supelco SP-2560 column (100m x 0.25mm x 0.2µm film thickness) and a flame ionization detector. The column started at a temperature of 100°C and was increased to 170°C at a rate of 2°C per min, followed by an increase to 180°C at 0.5°C per min and to 250°C at 10°C per minute. The detector was maintained at 220°C and total run time was 77 min. Based on the fatty acid composition, the atherogenic index (AI) was calculated as proposed by Ulbricht and Southgate (1991):

$$AI = \frac{C12:0 + (4 \times C14:0) + C16:0}{\Sigma MUFA + \Sigma PUFA}.$$

Volatile compound analysis

Approximately 20 g of lean was excised from each chop sample after 14 d of storage to estimate the volatile compound formation. Volatile compounds were analyzed using a dynamic headspace GC/mass spectrometry method (Ahn et al., 2001). A 2-gram sample of minced pork loin was placed in a 40 ml sample vial and flushed with helium gas (99.999%) for 5 s at 40 psi, capped airtight with a Teflon*fluorocarbon resin/silicone septum (I-Chem Co., Rockwood, TN), and placed in a refrigerated (4°C) sample-tray. Maximum holding time was restricted to 2 h to minimize oxidative changes during the sample retention. Samples were purged with helium gas (40 ml/min) for 15 min. Volatile compounds were trapped at 20°C using a Tenax/Silica gel/Charcoal column (Tekmar-Dorham) and desorbed for 2 min at 220°C. The desorbed volatile compounds were concentrated at -80°C using a cyrofocusing unit, and then thermally desorbed and injected (60 s) into a capillary GC

column. Four columns were utilized to determine volatile compounds: an HP-Wax column (60 m, 0.25 mm i.d., 0.25 μm nominal), an HP-624 column (7.5 m, 0.25 mm i.d., 1.4 μm nominal), an HP-1 column (60 m, 0.25 mm i.d., 0.25 μm nominal), and an HP-Wax column (7.5 m, 0.25 mm i.d., 0.25 μm nominal) were connected using zero-dead volume column connectors (J and W Scientific, Folsom, CA). Ramped oven temperature was used to improve volatile separation. The initial oven temperature (0°C) was held for 1.5 min. Then the oven temperature was then increased to 15°C at 2.5°C/min, increased to 45°C at 5°C/min, increased to 110°C at 20°C/min, and increased to 210°C at 10°C/min and held for 2.25 min. Constant column pressure at 20 psi was maintained. Ionization potential of the mass selective detector was 70 eV and the scan range was 19.1 to 350 *m/z*. Identification of volatile compounds was achieved by comparing mass spectral data of samples with those of the Wiley library (Hewlett-Packard Co.). Standards, when available, were used to confirm the identification of volatile compounds by the mass selective detector. The area of each peak was integrated using ChemStation software (Hewlett-Packard Co.), and total ion counts$\times 10^4$ was reported as an indicator of volatile compounds generated from the meat samples.

Statistical analysis

Treatment differences for meat and eating quality traits, thiobarbituric acid values (TBA), volatile compound analysis, and fatty acid composition were assessed using the GLM procedure of SAS (SAS Inst., Cary, NC). A linear model with fixed effects of line, sex, and carcass contemporary group, the interaction of line x sex, and a covariate of hot carcass weight was utilized to estimate least squares means and standard errors for meat and eating quality traits, fatty acid composition and volatile compounds. Mean values were compared

using the pairwise t-tests (*pdiff* option in SAS). For the analysis of color over time, a repeated measures model that included the effects of line, sex, and day, all two-way interactions, and a covariate of carcass contemporary group was used.

RESULTS AND DISCUSSION

Carcass composition traits

Least squares means for carcass composition and meat quality traits are presented in Table 3. Carcasses from pigs in the CL had less tenth-rib ($P < 0.001$), last-rib ($P = 0.002$), and last lumbar ($P = 0.051$) backfat when compared to pigs in the SL. Additionally, carcasses from pigs in the CL had greater loin muscle ($P < 0.001$), and combined with reduced backfat measures, had greater percent lean on a live and/or carcass basis ($P < 0.001$). Carcasses from pigs in the SL had 2.89% more IMF ($P < 0.001$) compared to carcasses from CL pigs. No differences between lines were found for pH, water holding capacity, instron tenderness, and cooking loss.

Sensory results

Several studies have reported no association of IMF with sensory panel flavor scores (Fernandez et al., 1999a; van Laack et al., 2001; Channon et al., 2004). However, Van Oeckel et al. (1999) reported IMF was strongly related to flavor. In the current study, no differences were found between lines for the sensory traits of juiciness, chewiness, tenderness, and off-flavor score (Table 4). However, there was a trend for pigs with more intramuscular fat (SL) to have a higher flavor score ($P = 0.104$). Clearly, lipid content (IMF) is not the only factor that influences flavor and consumer acceptance of fresh pork products. Other factors such as pH (van Laack et al., 2001; Huff-Lonergan et al., 2002), tenderness (Van Oeckel et al., 1999; Huff-Lonergan et al., 2002), postmortem aging and proteolysis

(Wood et al., 1996; Lonergan et al., 2001), muscle fiber type (Melody et al., 2004), and breed (van Laack et al., 2001), or a combination of these traits influence sensory characteristics of the product.

Lipid oxidation and volatile compound analysis

Pigs with higher levels of intramuscular fat in the SL had greater TBA values at d 0 (P =0.015) when compared to pigs within the CL, suggesting more initial oxidation had taken place (Table 5). Although no differences between lines were found after 14 d or 28 d of aging for TBA values, there was a trend for oxidative stability of the chops to decline over time. No differences between lines were found in volatile compound concentrations; further classification of sensory panel scores for flavor intensity (pork flavor) and reason for off-flavor may have limited the identification volatile compounds responsible for the development of flavor or off-flavor by the sensory panelists (Table 6). Flavor development or formation of off-flavors may be dependent on volatile formation and oxidation of fatty acids or some combination of these factors. In a study by Shackelford et al. (1990) a high proportion of the sensory panelists (65%) detected off-flavors in bacon from pigs fed high levels of oleic acid (C18:1*n*9). This was a result of increased concentrations of linoleic acid (C18:2*n*6) derivatives formed during processing. Although, in the current study, there were no line differences ($P > 0.05$) for C18:1*n*9 concentrations in IMF total lipid, there was a greater concentration of C18:2*n*6 present in IMF in CL pigs when compared to samples from the SL pigs.

Total lipids of intramuscular fat

Least squares means for fatty acid composition are presented in Table 7. Samples from pigs in the SL had more saturated fatty acids (C14:0, C17:0, and C18:0), although total

saturated fatty acids were not different between lines. Samples from pigs in the CL had more C18:2*n*6, C20:4*n*6, and total PUFA when compared to those in the SL. This increase in PUFA present in the total lipid fraction could play a role in shelf life and oxidative stability of the product. Several studies have shown that the susceptibility of PUFA to oxidation, and thus the formation of rancid or off-flavors (Cameron and Enser, 1991; Cameron et al., 2000), is greater. Changes in fatty acid composition may be relevant to meat flavor and variability in consumer acceptance (Melton, 1990). In previous work, generally negative correlations have been reported between pork flavor and flavor intensity and concentrations of unsaturated fatty acids (Cameron and Enser, 1991), although fewer PUFA were evaluated when compared to the present study. Results in the current study show a significant increase in some individual fatty acids and overall PUFA concentration, however, this did not translate into sensory panel score differences for off-flavor.

Phospholipids of intramuscular fat

Table 8 shows that pigs in the SL had more total saturated fatty acids in the polar lipid fraction with a 1.5% increase in lauric acid (C12:0). No differences in monounsaturated fatty acids were found between lines, however, there was a trend (P =0.071) for CL pigs to have a greater percentage of PUFA present in the polar fraction. It is not known whether differences in phospholipid concentration in intramuscular fat found in this study were large enough to result in differences in sensitivity to oxidation, consequently affecting membrane stability. Differences in phospholipid content reported in the current study are similar to those found in other studies (Monahan et al., 1992; van Laack and Spencer, 1999). Variation of 3 to 5 % in fatty acid composition of phospholipids may affect membrane stability and oxidation, leading to an increase in off-flavor (Monahan et al., 1992). Fatty acid composition

of phospholipids should be taken into account when studying oxidation-related quality aspects of pork. Flavor and water-holding capacity could be dramatically changed based on a 3 to 5% change in phospholipid fatty acid composition.

Triacylglycerides of intramuscular fat

Overall, few differences between lines were found in the percentage of monounsaturated and polyunsaturated fatty acids present in the neutral lipid fraction, however, there was a trend ($P = 0.029$) for the chops from SL pigs to have a more saturated fatty acid profile (Table 9). The greater saturated fat content found in SL pigs may be of concern for consumer health. Increased intake of saturated fatty acids has been directly related to the development of cardiovascular disease (CVD). Excess SFA intake causes elevated plasma cholesterol, which is the main contributor to CVD (Hegsted et al., 1959; Keys et al., 1974). Furthermore, myristic acid (C14:0) was reported to have the most harmful cardiovascular effect on humans, having 4 times the effect of C12:0 and C16:0 (Hegsted et al., 1965; Keys et al., 1974), while the other saturated fatty acids appear to have a neutral effect on increasing plasma cholesterol levels. No differences between lines were observed in C14:0 ($P = 0.73$) and C16:0 ($P = 0.77$) in the current study, however, loin chops from CL pigs had more lauric acid ($P < 0.05$).

Subcutaneous adipose tissue

Loin chops from pigs in SL had a greater percentage of saturated fatty acids ($P < 0.001$) present in adipose tissue when compared pigs in the CL (Table 10). Fatty acid composition of adipose tissue is directly affected by dietary fat inclusion. Since pigs in both lines were fed the same diet, the 1% difference in PUFA may be due to differences in

transport mechanisms, suggesting that further investigation into transport mechanisms of fatty acids is warranted.

De novo fat synthesis consists almost exclusively of SFA and MUFA, while C18:2*n*6 and C18:3*n*3 are essential and readily incorporated into adipose tissue. This suggests that pigs in the SL had greater de novo synthesis of fatty acids when compared with CL pigs. There was a trend for pigs in the CL to have increased concentration of PUFA (P =0.095) when compared to SL pigs.

Color stability

Changes in muscle color were observed in the current study. Loin chop samples from CL pigs had lower Minolta reflectance and Hunter L (lightness) color values ($P < 0.001$) at both 24 h and 48 h when compared to pigs in the SL (Figure 1). Chops from both lines had reduced subjective color scores over the 28 d aging period in the simulated retail display (Figure 2). Differences in a^* color scores were seen on d 0, however, did not differ between lines over time. Magnitude of difference between lines over time were similar for all measures of color, however, b^* values increased over the 28 d aging period.

In general, pigs in SL with higher levels of IMF had a more saturated fatty acid profile in both adipose tissue and intramuscular fat. Although no differences were found in sensory characteristics for juiciness, chewiness, tenderness, and off-flavor scores, there was a tendency for chops from pigs selected for intramuscular fat to receive higher flavor scores from sensory panelists. It is apparent that overall meat quality is a very complex factor that is controlled by numerous quality characteristics including pH, tenderness, overall fat composition, volatile formation, post-mortem proteolysis, and breed as well as a variety of environmental factors. Evaluation of lines with greater differences in IMF, then were

available in the current study, may result in more off-flavors due to lipid oxidation of unsaturated fatty acids. Understanding the fatty acid composition of pork with higher levels of intramuscular fat is important in order to maintain consumer acceptance of fresh pork and further processed pork products.

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Table 1. Dietary components and nutrient composition of finishing diets fed to Duroc pigs in selection project designed to increase intramuscular fat

	Finishing Phase[1]		
Item	**1**	**2**	**3**
Calculated Composition[2]			
Corn, %	68.32	74.75	81.00
Soybean meal, %	26.25	20.00	13.75
Added Fat, %[3]	3.00	3.00	3.00
Base premix, %	2.25	2.25	2.25
Tylan 40, g/ton	0.13	-	-
Cupric sulfate, %	0.05	-	-
Total	100	100	100
Protein, %	19	18	15.5
Lysine, %	1.2	1.05	0.85
Fat, %	6	6	6
Fiber, %	3.2	3.2	3.2
Calcium, %	0.55	0.54	0.54
Phosphorus, %	0.45	0.45	0.45
Salt, %	0.5	0.5	0.5
Zinc, mg/kg	140	140	140
Copper, mg/kg	135	10	10
Phytase-FTU/kg	750	750	750
Selenium, mg/kg	0.3	0.3	0.3

[1]Finishing phase 1 – 34 to 68 kg BW; Finishing phase 2 – 68 to 91 kg BW; Finishing phase 3 – 91 kg to market weight.
[2]Calculated composition based on NRC (1998) values.
[3]Choice white grease

Table 2. Fatty acid composition of the phase 3 finishing diet fed to Duroc pigs in a selection project for intramuscular fat content[1]

Trait	Formula	Finishing Phase 3[2]
Fat, %		6.26
Saturated fatty acids (wt %)		
Lauric acid	C12:0	0.01
Myristic acid	C14:0	0.76
Pentadecanoic acid	C15:0	0.00
Palmitic acid	C16:0	22.18
Margaric acid	C17:0	0.25
Stearic acid	C18:0	8.65
Arachidic acid	C20:0	0.36
Behenic acid	C22:0	0.09
Lignoceric acid	C24:0	0.00
Total saturated		32.30
Monounsaturated fatty acids (wt %)		
Myristoleic acid	C14:1	0.04
Palmitoleic acid	C16:1 *n*-7	1.45
cis-Heptadecenoic acid	C17:1 *n*-10	0.13
Oleic acid	C18:1 *n*-9	17.20
trans-Vaccenic acid	C18:1 *n*-7	1.39
Eicosanoic acid	C20:1 *n*-9	0.74
Nervonic acid	C24:1	0.08
Total MUFA		21.03
Polyunsaturated fatty acids (wt %)		
Linoleic acid	C18:2 *n*-6	44.35
α-Linolenic acid	C18:3 *n*-3	1.56
γ-Linolenic acid	C18:3 *n*-6	0.01
Eicosadienoic acid	C20:2 *n*-6	0.00
Eicosatrienoic acid	C20:3 *n*-6	0.08
Arachidonic acid	C20:4 *n*-6	0.21
Eicosapentaenoic acid	C20:5 *n*-3	0.00
Docosatetraenoic acid	C22:4 *n*-6	0.01
Docosapentaenoic acid	C22:5 *n*-3	0.01
Docosahexaenoic acid	C22:6 *n*-3	0.00
Total PUFA		46.23

[1]Presented as a percentage of total lipid in the feed on an as-fed basis.
[2]Finishing phase 3 fed from 91 kg to market weight.

Table 3. Least squares means (±SE) for carcass composition and meat quality traits from pigs with different levels of intramuscular fat.

Item	Line[1] CL	Line[1] SL	CL - SL	P-Value
Carcass composition				
Length, cm	80.11 ± 0.41	80.62 ± 0.38	-0.51 ± 0.56	0.3678
Tenth rib backfat, mm	24.11 ± 1.26	33.00 ± 1.17	-8.89 ± 1.74	<0.0001
Last rib backfat, mm	24.71 ± 0.88	28.67 ± 0.81	-3.96 ± 1.21	0.0021
Last lumbar backfat, mm	21.70 ± 0.88	24.13 ± 0.81	-2.43 ± 1.21	0.0512
Loin muscle area, cm^2	43.14 ± 1.38	33.68 ± 1.27	9.46 ± 1.89	<0.0001
Percent lean, %	38.11 ± 0.65	32.49 ± 0.60	5.62 ± 0.89	<0.0001
Intramuscular fat, %	3.41 ± 0.35	6.30 ± 0.32	-2.89 ± 0.47	<0.0001
Meat quality				
24 h pH	5.65 ± 0.02	5.68 ± 0.02	-0.03 ± 0.03	0.1943
48 h pH	5.63 ± 0.02	5.63 ± 0.02	0.00 ± 0.03	0.8604
7 d pH	5.67 ± 0.02	5.65 ± 0.02	0.02 ± 0.03	0.6275
24 h Minolta reflectance	24.38 ± 0.48	28.19 ± 0.47	-3.81 ± 0.47	<0.0001
48 h Minolta reflectance	21.17 ± 0.41	24.02 ± 0.37	-2.85 ± 0.56	<0.0001
24 h Hunter L value	49.34 ± 0.49	52.85 ± 0.48	-3.51 ± 0.69	<0.0001
48 h Hunter L value	45.97 ± 0.42	48.98 ± 0.38	-3.01 ± 0.57	<0.0001
Water holding capacity, mg	58.63 ± 7.86	69.23 ± 7.43	-10.6 ± 10.94	0.3382
Cooking loss, %	18.26 ± 0.56	18.64 ± 0.52	-0.38 ± 0.78	0.6311
Instron tenderness, kg	5.09 ± 0.23	4.75 ± 0.21	0.34 ± 0.31	0.2881

[1]SL= select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

Table 4. Least squares means (±SE) for sensory panel traits from pigs with varying levels of intramuscular fat.

Item[2]	Line[1]						P-Value
	CL		SL		CL - SL		
Juiciness score	7.67	± 0.20	7.81	± 0.19	-0.14	± 0.28	0.6210
Chewiness score	2.48	± 0.11	2.26	± 0.10	0.22	± 0.15	0.1480
Tenderness score	7.27	± 0.22	7.61	± 0.21	-0.34	± 0.31	0.2772
Flavor score	3.27	± 0.31	3.97	± 0.29	-0.70	± 0.42	0.1042
Off-flavor score	1.44	± 0.21	1.56	± 0.19	-0.12	± 0.29	0.7007

[1]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

[2]Trained sensory panel evaluations of juiciness (1 = dry; 10 = juicy), chewiness (1 = not chewy; 10 = very chewy), tenderness (1= tough; 10 = tender), flavor (1 = little pork flavor, bland; 10 = very flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor, 10 = abundant non-pork flavor)

Table 5. Least squares means (±SE) for thiobarbituric acid (TBA) values from pigs with different levels of intramuscular fat.

	Line[1]			
Item[2]	**CL**	**SL**	**CL - SL**	**P-Value**
TBA, d 0	0.11 ± 0.01	0.16 ± 0.01	-0.05 ± 0.02	0.0148
TBA, d 14	0.36 ± 0.07	0.46 ± 0.06	-0.10 ± 0.09	0.2981
TBA, d 28	0.79 ± 0.20	1.08 ± 0.19	-0.29 ± 0.28	0.3032
TBA, d 14-0	0.26 ± 0.07	0.30 ± 0.06	-0.04 ± 0.09	0.6063
TBA, d 28-14	0.43 ± 0.15	0.62 ± 0.14	-0.19 ± 0.21	0.3578
TBA, d 28-0	0.57 ± 0.21	0.92 ± 0.18	-0.35 ± 0.28	0.2179

[1]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

Table 6. Least squares means (±SE) for volatile compounds from longissimus dorsi samples of pigs with different levels of intramuscular fat[1]

		Line[2]			
Volatile Family	**Volatile**	**CL**	**SL**	**CL - SL**	**P-value**
Alcohols	1-Butanol	143 ± 20	169 ± 16	-26 ± 26	0.3056
	Ethanol	91042 ± 21353	65624 ± 19532	25418 ± 28938	0.3845
	1-Propanol	1388 ± 294	881 ± 269	507 ± 398	0.2091
	2-Propanol	2428 ± 227	2098 ± 208	330 ± 308	0.2909
	2-Methyl-1-propanol	7208 ± 1526	4340 ± 1396	2868 ± 2069	0.1725
	3-Methyl-1-butanol	10181 ± 2379	5655 ± 2177	4526 ± 3225	0.1675
Ketone	2-Butanone	1096 ± 51	996 ± 47	100 ± 70	0.1577
	2-Propanone	10215 ± 2355	8312 ± 2154	1903 ± 3191	0.5539
	2-Pentanone	462 ± 47	497 ± 43	-35 ± 64	0.5845
Aldehydes	Acetaldehyde	2091 ± 1761	830 ± 1605	1261 ± 2336	0.5924
	Hexanal	193 ± 44	201 ± 31	-8 ± 53	0.8799
	2-Methyl propanal	1201 ± 531	467 ± 446	734 ± 701	0.3032
	2-Methyl butanal	447 ± 146	235 ± 131	212 ± 196	0.2876
	3-Methyl butanal	697 ± 180	556 ± 187	141 ± 261	0.5928
Hydrocarbons	Hexane	207 ± 19	184 ± 18	23 ± 27	0.3964
	Pentane	1033 ± 329	1084 ± 308	-51 ± 447	0.9087
	Octane	668 ± 81	664 ± 85	4 ± 4	0.9771
Nitriles	Acetonitrile	------ ± ------	1233 ± ------	------ ± ------	------
Pyrrolines	2-Methyl-1-pyrroline	1185 ± 157	1399 ± 143	-214 ± 212	0.3207

[1]Least squares means of total ion counts for each volatile compound.

[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL = randomly mated, unselected control line.

Table 7. Least squares means (±SE) for total fatty acid composition from pigs with different levels of intramuscular fat[1]

		Line[2]									
Fatty acid	**Formula**	**CL**			**SL**			**CL - SL**			**P-value**
Saturated											
Lauric acid	C12:0	0.18	±	0.02	0.06	±	0.02	0.12	±	0.03	0.0012
Myristic acid	C14:0	1.27	±	0.07	1.47	±	0.06	-0.20	±	0.09	0.0414
Pentadecanoic acid	C15:0	0.88	±	0.05	0.50	±	0.04	0.38	±	0.06	<0.0001
Palmitic acid	C16:0	27.57	±	0.55	27.28	±	0.51	0.29	±	0.75	0.7017
Margaric acid	C17:0	0.09	±	0.02	0.16	±	0.02	-0.07	±	0.02	0.0049
Stearic acid	C18:0	12.76	±	0.39	14.51	±	0.36	-1.75	±	0.53	0.0021
Arachidic acid	C20:0	0.01	±	0.01	0.00	±	0.00	0.01	±	0.01	0.0735
Behinic acid	C22:0	0.02	±	0.01	0.01	±	0.01	0.01	±	0.01	0.6754
Lignoceric acid	C24:0	0.06	±	0.02	0.02	±	0.02	0.04	±	0.03	0.2435
Total saturated		42.83	±	0.83	44.02	±	0.77	-1.19	±	1.13	0.3040
Monousaturated											
Myristoleic acid	C14:1	0.02	±	0.01	0.00	±	0.01	0.02	±	0.01	0.0732
Palmitoleic acid	C16:1 *n*-7	2.95	±	0.18	3.21	±	0.17	-0.26	±	0.24	0.2875
cis-Heptadecenoic acid	C17:1 *n*-10	0.06	±	0.01	0.10	±	0.01	-0.04	±	0.02	0.0431
Oleic acid	C18:1 *n*-9	39.92	±	1.01	40.81	±	0.94	-0.89	±	1.38	0.5253
trans-Vaccenic acid	C18:1 *n*-7	3.99	±	0.09	3.77	±	0.08	0.22	±	0.12	0.0707
Eicosanoic acid	C20:1 *n*-9	0.02	±	0.01	0.00	±	0.01	0.02	±	0.01	0.1321
Nervonic acid	C24:1	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.4840
Total MUFA		47.60	±	0.91	48.68	±	0.85	-1.08	±	0.85	0.3924
Polyunsaturated											
Linoleic acid	C18:2 *n*-6	8.30	±	0.29	6.09	±	0.27	2.21	±	0.40	<0.0001
α-Linolenic acid	C18:3 *n*-3	0.71	±	0.05	0.88	±	0.05	-0.17	±	0.07	0.0149
γ-Linolenic acid	C18:3 *n*-6	0.05	±	0.02	0.14	±	0.02	-0.09	±	0.03	0.0023
Eicosadienoic acid	C20:2 *n*-6	0.14	±	0.02	0.23	±	0.02	-0.09	±	0.03	0.0053
Eicosatrienoic acid	C20:3 *n*-6	0.06	±	0.01	0.08	±	0.01	-0.02	±	0.02	0.3182
Arachidonic acid	C20:4 *n*-6	0.85	±	0.06	0.60	±	0.05	0.25	±	0.08	0.0026
Eicosapentaenoic acid	C20:5 *n*-3	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.5901
Docosatetraenoic acid	C22:4 *n*-6	0.05	±	0.02	0.04	±	0.02	0.01	±	0.02	0.6814
Docosapentaenoic acid	C22:5 *n*-3	0.03	±	0.01	0.01	±	0.01	0.02	±	0.02	0.1575
Docosahexaenoic acid	C22:6 *n*-3	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.4502
Total PUFA		10.20	±	0.33	8.08	±	0.30	2.12	±	0.45	<0.0001

[1]Least squares means of the percentage of total lipid in the lean tissue.
[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL= randomly mated, unselected control line.

Table 8. Least squares means (±SE) for phospholipid fatty acid composition from pigs with different levels of intramuscular fat[1]

		Line[2]									
Fatty acid	**Formula**	**CL**			**SL**			**CL - SL**			**P-value**
Saturated											
Lauric acid	C12:0	1.49	±	0.27	2.98	±	0.25	-1.49	±	0.37	0.0003
Myristic acid	C14:0	0.07	±	0.07	0.21	±	0.07	-0.14	±	0.10	0.1706
Pentadecanoic acid	C15:0	7.79	±	0.32	8.47	±	0.30	-0.68	±	0.45	0.1327
Palmitic acid	C16:0	17.58	±	0.80	18.36	±	0.75	-0.78	±	1.11	0.4848
Margaric acid	C17:0	4.10	±	0.39	3.70	±	0.36	0.40	±	0.53	0.4645
Stearic acid	C18:0	7.55	±	0.62	7.43	±	0.58	0.12	±	0.86	0.8816
Arachidic acid	C20:0	0.04	±	0.03	0.04	±	0.03	0.00	±	0.04	0.8996
Behinic acid	C22:0	0.17	±	0.04	0.09	±	0.04	0.08	±	0.06	0.1999
Lignoceric acid	C24:0	0.03	±	0.04	0.04	±	0.04	-0.01	±	0.06	0.7701
Total saturated		38.81	±	0.81	41.32	±	0.76	-2.51	±	1.11	0.0293
Monounsaturated											
Myristoleic acid	C14:1	0.13	±	0.15	0.31	±	0.14	-0.18	±	0.21	0.4049
Palmitoleic acid	C16:1 *n*-7	0.35	±	0.17	0.37	±	0.16	-0.02	±	0.24	0.9443
cis-Heptadecenoic acid	C17:1 *n*-10	2.59	±	0.25	1.85	±	0.23	0.74	±	0.34	0.0376
Oleic acid	C18:1 *n*-9	9.13	±	0.43	10.46	±	0.41	-1.33	±	0.60	0.0325
trans-Vaccenic acid	C18:1 *n*-7	2.30	±	0.19	2.54	±	0.18	-0.24	±	0.27	0.3703
Eicosanoic acid	C20:1 *n*-9	0.14	±	0.03	0.02	±	0.03	0.12	±	0.04	0.0101
Nervonic acid	C24:1	0.04	±	0.04	0.01	±	0.03	0.03	±	0.05	0.5899
Total MUFA		14.68	±	0.61	15.56	±	0.57	-0.88	±	0.84	0.3036
Polyunsaturated											
Linoleic acid	C18:2 *n*-6	33.94	±	0.97	33.37	±	0.91	0.57	±	1.34	0.6715
α-Linolenic acid	C18:3 *n*-3	0.02	±	0.02	0.04	±	0.02	-0.02	±	0.03	0.5886
γ-Linolenic acid	C18:3 *n*-6	0.16	±	0.10	0.22	±	0.10	-0.06	±	0.14	0.6704
Eicosadienoic acid	C20:2 *n*-6	0.19	±	0.05	0.07	±	0.04	0.12	±	0.06	0.0650
Eicosatrienoic acid	C20:3 *n*-6	0.85	±	0.12	0.54	±	0.11	0.31	±	0.17	0.0759
Arachidonic acid	C20:4 *n*-6	0.02	±	0.02	0.05	±	0.02	-0.03	±	0.03	0.3054
Eicosapentaenoic acid	C20:5 *n*-3	0.18	±	0.06	0.07	±	0.06	0.11	±	0.08	0.1589
Docosatetraenoic acid	C22:4 *n*-6	1.09	±	0.13	0.61	±	0.12	0.48	±	0.18	0.0134
Docosapentaenoic acid	C22:5 *n*-3	0.91	±	0.11	0.20	±	0.11	0.71	±	0.16	<0.0001
Docosahexaenoic acid	C22:6 *n*-3	0.07	±	0.02	0.04	±	0.02	0.03	±	0.03	0.3868
Total PUFA		37.47	±	0.86	35.26	±	0.81	2.21	±	1.19	0.0709

[1]Least squares means of the percentage of total phospholipid in the lean tissue.
[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL= randomly mated, unselected control line.

Table 9. Least squares means (±SE) for neutral fatty acid composition from pigs with different levels of intramuscular fat[1]

		Line[2]									
Fatty acid	**Formula**	**CL**			**SL**			**CL - SL**			**P-value**
Saturated											
Lauric acid	C12:0	0.22	±	0.03	0.15	±	0.02	0.07	±	0.04	0.0441
Myristic acid	C14:0	1.50	±	0.08	1.54	±	0.08	-0.04	±	0.12	0.7346
Pentadecanoic acid	C15:0	0.007	±	0.003	0.010	±	0.003	-0.003	±	0.004	0.4762
Palmitic acid	C16:0	25.97	±	0.97	26.36	±	0.91	-0.39	±	1.34	0.7693
Margaric acid	C17:0	0.12	±	0.02	0.13	±	0.02	-0.01	±	0.03	0.8089
Stearic acid	C18:0	13.04	±	0.31	14.60	±	0.29	-1.56	±	0.43	0.0008
Arachidic acid	C20:0	0.15	±	0.01	0.19	±	0.01	-0.04	±	0.02	0.1364
Behinic acid	C22:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.2355
Lignoceric acid	C24:0	0.02	±	0.01	0.00	±	0.01	0.02	±	0.01	0.0900
Total saturated		41.03	±	0.83	42.98	±	0.78	-1.95	±	1.15	0.0979
Monounsaturated											
Myristoleic acid	C14:1	0.02	±	0.01	0.02	±	0.01	0.00	±	0.02	0.8887
Palmitoleic acid	C16:1 *n*-7	3.62	±	0.11	3.52	±	0.11	0.10	±	0.16	0.5083
cis-Heptadecenoic acid	C17:1 *n*-10	0.13	±	0.01	0.10	±	0.01	0.03	±	0.02	0.0856
Oleic acid	C18:1 *n*-9	44.28	±	0.68	43.03	±	0.64	1.25	±	0.94	0.1918
trans-Vaccenic acid	C18:1 *n*-7	4.37	±	0.11	3.96	±	0.11	0.41	±	0.15	0.0132
Eicosanoic acid	C20:1 *n*-9	0.72	±	0.03	0.73	±	0.02	-0.01	±	0.03	0.7968
Nervonic acid	C24:1	0.00	±	0.03	0.04	±	0.02	-0.04	±	0.03	0.2450
Total MUFA		53.13	±	0.82	51.40	±	0.77	1.73	±	1.14	0.1348
Polyunsaturated											
Linoleic acid	C18:2 *n*-6	4.94	±	0.19	4.66	±	0.18	0.28	±	0.26	0.3008
α-Linolenic acid	C18:3 *n*-3	0.26	±	0.02	0.25	±	0.01	0.01	±	0.02	0.6015
γ-Linolenic acid	C18:3 *n*-6	0.02	±	0.01	0.01	±	0.01	0.01	±	0.01	0.4742
Eicosadienoic acid	C20:2 *n*-6	0.17	±	0.04	0.21	±	0.04	-0.04	±	0.06	0.4876
Eicosatrienoic acid	C20:3 *n*-6	0.06	±	0.01	0.05	±	0.01	0.01	±	0.02	0.8134
Arachidonic acid	C20:4 *n*-6	0.12	±	0.01	0.10	±	0.01	0.02	±	0.02	0.2086
Eicosapentaenoic acid	C20:5 *n*-3	0.13	±	0.08	0.26	±	0.08	-0.13	±	0.11	0.2111
Docosatetraenoic acid	C22:4 *n*-6	0.01	±	0.01	0.01	±	0.01	0.00	±	0.01	0.7073
Docosapentaenoic acid	C22:5 *n*-3	0.004	±	0.002	0.002	±	0.002	0.002	±	0.003	0.4150
Docosahexaenoic acid	C22:6 *n*-3	0.08	±	0.03	0.01	±	0.03	0.07	±	0.04	0.0798
Total PUFA		5.80	±	0.22	5.59	±	0.20	0.21	±	0.30	0.4950

[1]Least squares means of the percentage of total neutral lipid in the lean tissue.
[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL= randomly mated, unselected control line.

Table 10. Least squares means (±SE) for fatty acid composition of adipose tissue from pigs with different levels of intramuscular fat.[1]

		Line[2]									
Fatty acid	**Formula**	**CL**			**SL**			**CL - SL**			**P-value**
Saturated											
Lauric acid	C12:0	0.04	±	0.01	0.04	±	0.01	0.00	±	0.01	0.8412
Myristic acid	C14:0	1.42	±	0.04	1.50	±	0.04	-0.08	±	0.06	0.1489
Pentadecanoic acid	C15:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00	0.1288
Palmitic acid	C16:0	24.31	±	0.41	26.03	±	0.39	-1.72	±	0.58	0.0055
Margaric acid	C17:0	0.34	±	0.02	0.36	±	0.02	-0.02	±	0.02	0.4155
Stearic acid	C18:0	11.91	±	0.26	12.65	±	0.25	-0.74	±	0.36	0.0495
Arachidic acid	C20:0	0.17	±	0.01	0.18	±	0.01	-0.01	±	0.01	0.4430
Behinic acid	C22:0	0.013	±	0.003	0.010	±	0.003	0.003	±	0.004	0.4142
Total saturated		38.21	±	0.48	40.77	±	0.46	-2.56	±	0.68	0.0006
Monounsaturated											
Myristoleic acid	C14:1	0.039	±	0.004	0.043	±	0.004	-0.004	±	0.006	0.4981
Palmitoleic acid	C16:1 *n*-7	2.10	±	0.07	2.23	±	0.07	-0.13	±	0.10	0.2107
cis-Heptadecenoic acid	C17:1 *n*-10	0.22	±	0.01	0.22	±	0.01	0.00	±	0.02	0.7549
Oleic acid	C18:1 *n*-9	36.94	±	1.52	36.95	±	1.46	-0.01	±	2.16	0.9956
trans-Vaccenic acid	C18:1 *n*-7	4.84	±	1.46	3.18	±	1.41	1.66	±	2.07	0.4285
Eicosanoic acid	C20:1 *n*-9	0.72	±	0.05	0.65	±	0.05	0.07	±	0.07	0.2758
Nervonic acid	C24:1	0.09	±	0.01	0.09	±	0.01	0.00	±	0.01	0.7539
Total MUFA		44.95	±	0.47	43.35	±	0.45	1.60	±	0.66	0.0205
Polyunsaturated											
Linoleic acid	C18:2 *n*-6	14.96	±	0.35	14.19	±	0.34	0.77	±	0.50	0.1291
α-Linolenic acid	C18:3 *n*-3	0.77	±	0.02	0.73	±	0.02	0.04	±	0.03	0.1311
γ-Linolenic acid	C18:3 *n*-6	0.011	±	0.003	0.012	±	0.003	-0.001	±	0.005	0.8394
Eicosadienoic acid	C20:2 *n*-6	0.72	±	0.02	0.63	±	0.02	0.09	±	0.03	0.0034
Eicosatrienoic acid	C20:3 *n*-6	0.10	±	0.01	0.08	±	0.01	0.02	±	0.01	0.0742
Arachidonic acid	C20:4 *n*-6	0.22	±	0.01	0.21	±	0.01	0.01	±	0.02	0.4017
Eicosapentaenoic acid	C20:5 *n*-3	0.01	±	0.01	0.01	±	0.01	0.00	±	0.01	0.8357
Docosapentaenoic acid	C22:5 *n*-3	0.04	±	0.01	0.04	±	0.01	0.00	±	0.01	0.5481
Docosahexaenoic acid	C22:6 *n*-3	0.002	±	0.001	0.000	±	0.001	0.002	±	0.001	0.1288
Total PUFA		16.84	±	0.39	15.88	±	0.38	0.96	±	0.56	0.0955

[1]Least squares means of the percentage of total lipid from tenth-rib adipose tissue.
[2]SL = select line, selected for 7 generations for IMF based on a 2-trait animal model that included IMF measured on the carcass and IMF predicted via ultrasound; CL= randomly mated, unselected control line.

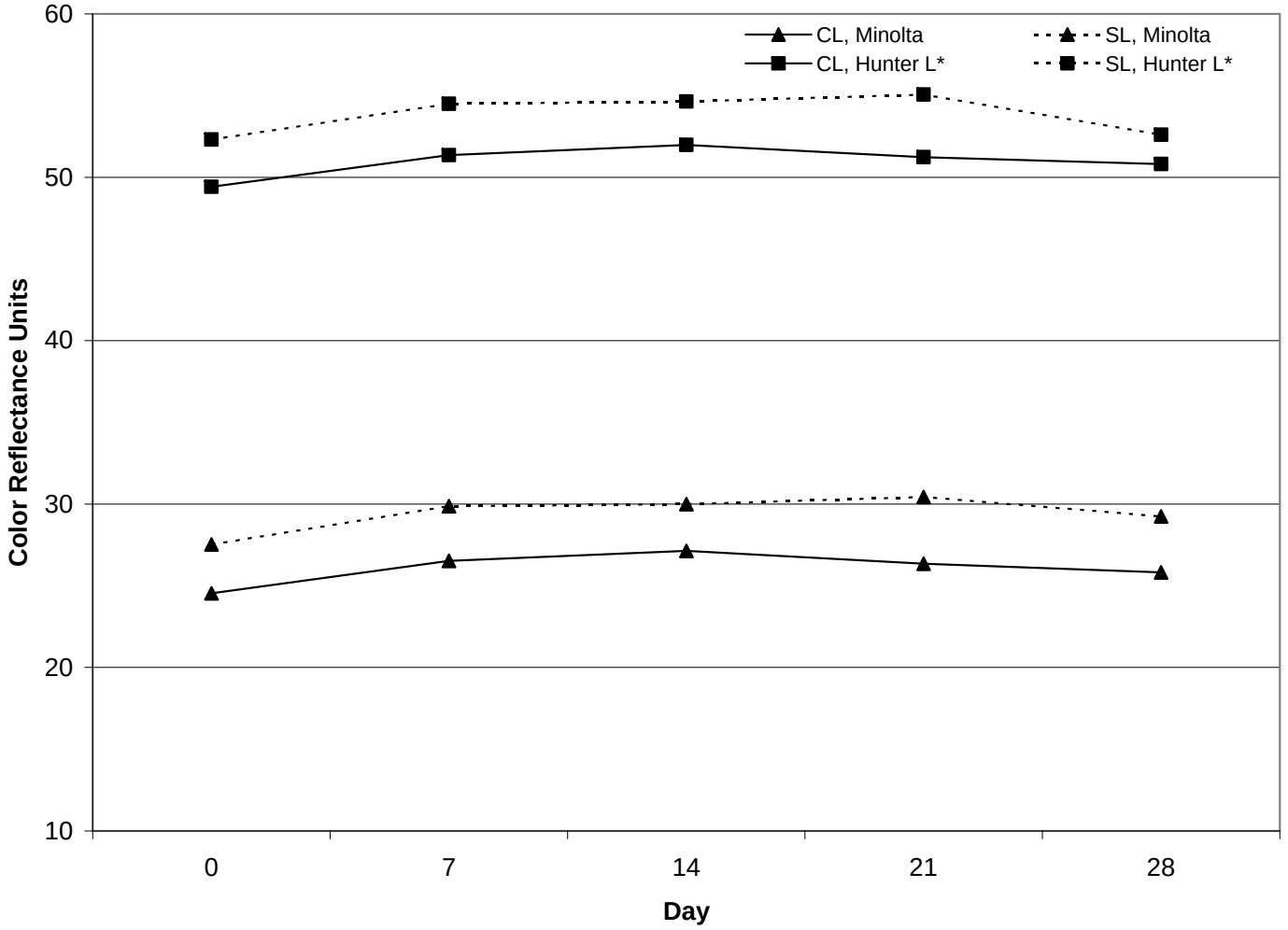

Figure 1. Effect of day on Minolta reflectance and Hunter L* value of the *longissimus dorsi* from pigs with different levels of intramuscular fat. Within day and trait, color values were not different by line ($P > 0.05$).

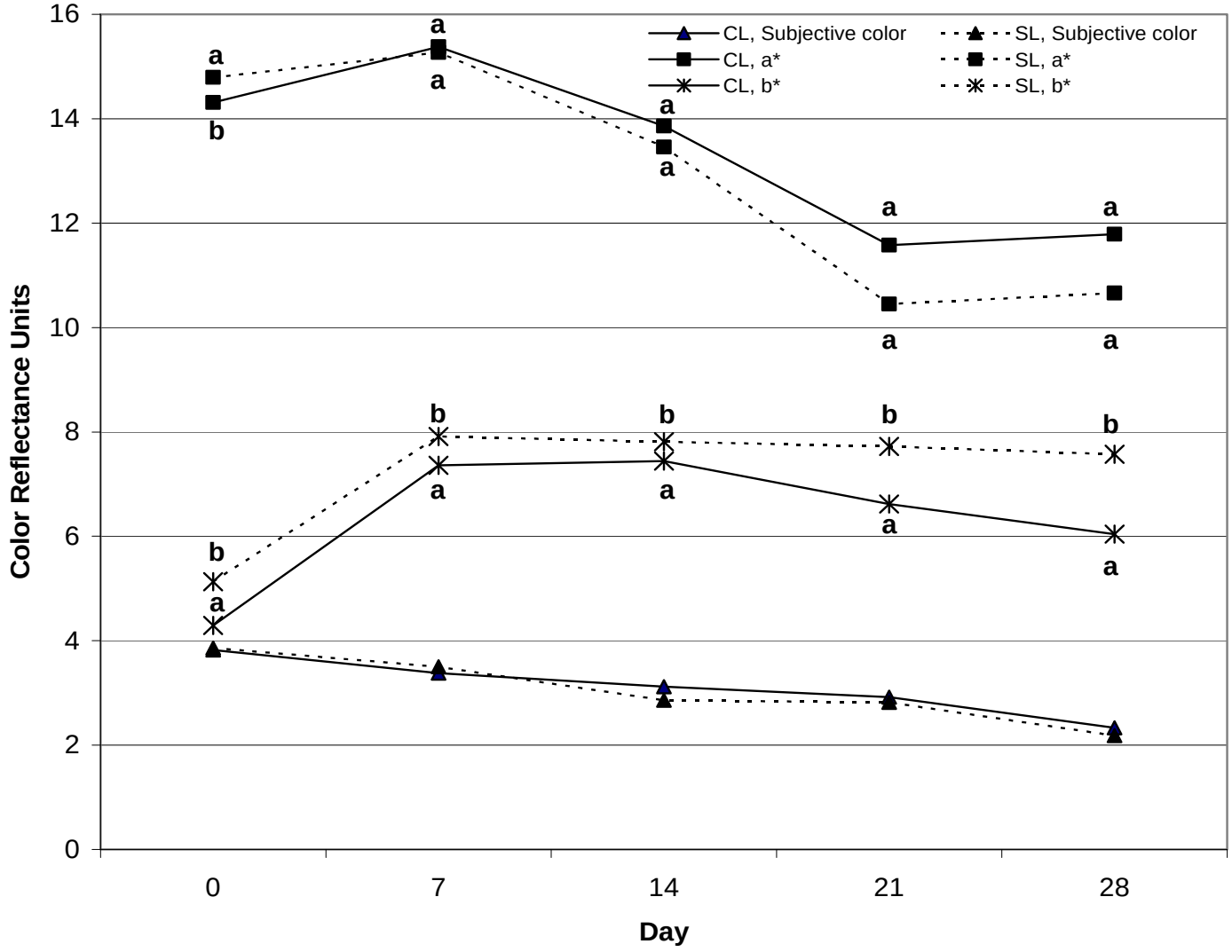

Figure 2. Effect of day on a*, b*, and subjective color values of the *longissimus dorsi* from pigs with different levels of intramuscular fat. [ab]Within day and trait, color values without a common superscript differ ($P < 0.05$).

CHAPTER 6.

GENETIC PARAMETER ESTIMATES OF FATTY ACID COMPOSITION IN DUROC PIGS SELECTED FOR INTRAMUSCULAR FAT FOR SEVEN GENERATIONS[1]

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ABSTRACT: The objective of this study was to identify genetic parameter estimates for fatty acid composition of pigs selected for intramuscular fat. Selection was practiced for 7 generations and was based on estimated breeding value for IMF from fitting a 2-trait animal model and the full relationship matrix in MATVEC. Traits emphasized were IMF estimated on the carcass and IMF predicted via real-time ultrasound on the live animal. Longissimus muscle samples (LM) (n=663) collected from pigs in generations 3 through 7 were used to determine the fatty acid composition of IMF. Total lipids were extracted from trimmed LM samples and methylated directly with acetyl chloride and methanol. Triacylglycerides (TAG) were separated from phospholipids (PL) in IMF by thin layer chromatography. All fatty acid methyl esters were quantified by using gas chromatography. Genetic parameters were calculated with the DMUAI software and all pedigree relationships were included in the model. A bivariate model which included IMF was used to estimate heritabilities. Fatty acids, meat and eating quality, and production traits were included in a multivariate analysis. The greatest heritability estimates were for lauric acid (0.73), palmitoleic acid (0.40), and stearic acid (0.36). Fatty acid heritability estimates for TAG and PL were low (0.00 to 0.25). There was a strong genetic correlation between IMF and linoleic acid (-0.80). Linoleic acid was positively correlated with LMA (0.75) and negatively correlated with backfat (-0.62). No significant genetic correlations were found among fatty acids and eating quality traits. Results obtained in this study suggest that the fatty acid composition of longissimus dorsi muscle is lowly heritable and linoleic acid is highly correlated with LMA and backfat in Duroc pigs.

Key words: fatty acids, genetic parameters, heritability, intramuscular fat, swine

INTRODUCTION

Fatty acid composition of various fat depots can be utilized as an overall indicator of fat quality. Variation in fatty acid composition has an important effect on firmness or softness of meat adipose tissue, both subcutaneous and intermuscular fat, and also affects intramuscular fat (Wood et al., 2004). Traditionally, fat analysis has been conducted on subcutaneous fat; however, recently more emphasis has been placed on the intramuscular fat composition because of its implications in further product processing. Fat quality (i.e. fatty acid composition) is especially important in international markets (namely, Japan) because of overall consumption of fresh pork products. Several studies have shown correlations of fatty acids with flavor, flavor preference, and overall acceptability (Cameron et al., 2000).

Numerous studies have reported fatty acid composition of lipids in different muscles and adipose depots (Cameron and Enser, 1991; Enser et al., 1996; Fernandez et al., 1999). To this point, very little research has been focused on estimating genetic parameters of fatty acid composition, and particularly of separated triacylglycerides and phospholipids. Genetic parameter estimates of fatty acid composition of these various lipid stores could lend valuable information regarding their correlation with production, meat quality, and eating quality traits. Previously, fatty acid composition has been shown to be a correlated response to selection for intramuscular fat (Burkett, 2009). In addition, intramuscular fat increased and some meat quality traits changed with selection (Suzuki et al., 2005). The objective of the current study was to estimate genetic parameters for fatty acid composition of intramuscular fat and meat and eating quality traits.

MATERIALS AND METHODS

Population

Experimental protocols for this study were approved by the Iowa State University Institutional Animal Care and Use Committee. A purebred Duroc population was initiated in 1998 to evaluate selection for intramuscular fat (IMF) in Duroc swine using real-time ultrasound. After 2 generations of random mating, a line selected for IMF (SL) and a control line (CL) were created and selection began as described by Schwab et al. (2009b). Selection was based on breeding values for IMF estimated by fitting a 2-trait animal model (IMF measured on the carcass and IMF predicted via real-time ultrasound) in MATVEC (Wang et al., 2003). Details of this selection, breeding value estimation, mating procedures, and responses after 6 generations are reported by Schwab et al. (2009b).

Performance and carcass measurements

Finishing pigs were housed in totally slatted, mechanically ventilated, curtain-sided finishing buildings and were provided a minimum of 0.77 m^2 of floor space with 20 to 25 pigs per pen from 34 kg until they reached an average off test weight of 110 kg. A 19.0% CP, 1.20% lysine corn-soy diet was provided ad libitum from 34 to 68 kg BW, followed by a 18.0% CP, 1.05% lysine corn-soy diet from 68 kg to 91 kg BW, followed by a 15.5% CP, 0.85% lysine corn-soy diet (Table 1) from 91 kg until market weight. Dietary fatty acid analysis for finishing phase 3 is presented in Table 2.

Upon completion of the performance test period, all available barrows and randomly selected gilts were harvested at a commercial abattoir (Hormel Foods, Austin, MN). Carcass measurements were obtained by Iowa State University personnel 24 h post-mortem. Standard carcass collection procedures as outlined in Pork Composition and Quality

Assessment Procedures (NPPC, 2000) were followed to obtain measurements of 10th rib backfat (BF10) and loin muscle area (LMA). A section of bone-in *longissimus dorsi* containing the 10th to 12th ribs was excised from the carcass and transported to the Iowa State University Meat Laboratory. A 3.2 mm slice from the 10th rib face was utilized for lipid content analysis. Carcass pH was measured 48 h post-mortem on the 10th rib face of the *longissimus dorsi* muscle by using a pH star probe (SFK Ltd, Hvidovre, Denmark). Hunter L^* score and Minolta reflectance were measured on the 10th rib face of the loin by using a Minolta CR-310 (Minolta Camera Co., Ltd., Osaka, Japan) with a 50-mm-diameter aperture, D65 illuminant, and calibrated to the white calibration tile. The 11th and 12th rib sections were cut into 2.54 cm samples and set cut side up for 10 min to allow the sample to bloom. Subjective measures of color (1 = pale pinkish gray to white; 6 = dark purplish red), marbling (1 = 1% IMF; 10 = 10% IMF), and firmness (1 =soft; 3 = very firm) were evaluated on the 11th rib face according to NPPC (2000) by personnel trained in meat quality evaluation. Water holding capacity was measured on the 11th rib face by using the filter paper method described by Kauffman et al. (1986). Longissimus muscle samples (n=663) collected from generation 3 through 7 pigs (Table 3) in the CL (n=357) and SL (n=306) were used to determine the fatty acid profiles of IMF.

Fatty acid analysis

Trimmed loin samples (Generations 3 through 7) from the *longissimus dorsi* at 10-11th rib were utilized for fatty acid determination. Total lipid was extracted from the IMF samples with a chloroform and methanol (2:1, vol:vol) mixture and quantified gravimetrically (Folch et al., 1957). Triacylglycerols (TAG) were separated from phospholipids (PL) by thin-layer chromatography with hexane and ethyl acetate (4:1,

vol:vol). Fatty acids in each lipid were derivatized to methyl esters according to Lepage and Roy (1986). Fatty acid methyl ester (FAME) from IMF were analyzed by gas chromatography (GC; model 3400, Varian, Palo Alto, CA) equipped with a Supelco SP-2560 column (100 m x 0.25 mm x 0.2 μm film thickness) and a flame ionization detector. The column started at a temperature of 100°C and was increased to 170°C at a rate of 2°C per min, followed by an increase to 180°C at 0.5°C per min and to 250°C at 10°C per minute. The total run time was 77 min and the detector was maintained at 220°C. Based on the fatty acid composition, the atherogenic index (AI) was calculated following Ulbricht and Southgate (1991):

$$AI = \frac{C12:0 + (4 \times C14:0) + C16:0}{\Sigma MUFA + \Sigma PUFA}.$$

Sensory evaluation

Two 2.54-cm thick chops from the 10th to 12th rib section were vacuum packaged and taken to the Iowa State University Food Science Laboratory (McKay Hall, Iowa State University). Samples were refrigerated at 0°C for 7 d. Both rib sections were cooked to 71°C in an electric broiler (Amana model ARE 640, Amana, IA), with sample temperature monitored by Chromega/Alomega thermocouples attached to an Omega digital thermometer (DSS-650, Omega Engineering, Inc., Stamford, CT). Weights prior to and immediately after cooking were used to calculate percent cooking loss. A 3-member trained sensory panel evaluated cooked loin samples for quality attributes (Huff-Lonergan et al., 2002) on three 1.3 cm^3 cubes from the center of the 11th and 12th rib samples. Eating quality evaluations for juiciness (1 = dry; 10 = juicy), tenderness (1 = tough; 10 = tender), flavor (1 = little pork flavor; 10 = extremely flavorful, abundant pork flavor), and off-flavor (1 = no off-flavor; 10

= abundant non-pork flavor) were recorded by using an end-anchored 10-point scoring system (AMSA, 1995). Individual booths with red overhead lighting were provided for each panelist. Sample evaluations were averaged across panelists for analysis. The 12^{th} rib section was evaluated for tenderness by using an Instron Universal Testing Machine (Model 1122; Instron Corp., Canton, MA) fitted with a circular, 5-point star probe (9 mm diameter with 6 mm between points) (Oltrogge-Hammernick and Prusa, 1987).

Statistical analysis

A mixed linear model was used to investigate fixed effects on the traits of interest (SAS Inst., Cary, NC). For each trait, fixed effects of sex and contemporary group were included and hot carcass weight was included as a covariate in all analyses. The DMU statistical software package (Madsen and Jensen, 2000) with the average information restricted maximum likelihood procedure (DMUAI) was used to estimate genetic parameters from an animal model. All pedigree relationships back to the animals used to initiate the population were included. The number of animals in the pedigree with a non-zero inbreeding coefficient was 5,101.

Bivariate analysis

Each fatty acid trait was analyzed with a 2-trait model that included IMF to obtain initial estimates for components of variance due to animal additive genetic, common environment of birth litter, and residual effects. The convergence criterion of the norm update vector was 1.0×10^{-7} for all bivariate analyses. To account for selection, IMF was included in each bivariate analysis (Meyer, 1989). Heritability estimates were calculated as the ratio of animal genetic variance to the sum of additive genetic, common environmental, and residual variances.

Multivariate analysis

A multivariate analysis was performed to evaluate fatty acid composition, meat and eating quality, and production traits. An 8-trait analysis was performed that included carcass composition, production, and eating quality traits as well as each of the major fatty acids. Since selection was based on EBV for IMF, this trait was included in the model to account for selection (Meyer, 1989). A multi-trait convergence criterion of 10^{-5} was designated to determine (co)variance estimates. After initial convergence was attained, 3 cold starts were performed to ensure global convergence, as determined when (co)variance estimates did not change to the second decimal.

RESULTS AND DISCUSSION

Heritability estimates for individual fatty acids

Traditionally, fatty acid composition has concentrated on adipose tissue, the body's major lipid storage depot. However, more emphasis has recently been placed on fatty acid composition of IMF because of its impact on further processing of food products (Wood et al., 2008). Total lipid heritability estimates for fatty acid composition of IMF are presented in Table 4.

The greatest heritability estimates were found for lauric acid (C12:0), palmitoleic acid (C16:1*n*7), stearic acid (C18:0), linoleic acid (C18:2*n*6), and α-Linolenic acid (C18:3*n*3) (0.73, 0.40, 0.36, 0.33, and 0.26, respectively). Similar results were reported by Sellier (1998) who found mean heritability estimates of 0.51 (0.42 to 0.57) for C18:0 and 0.58 (0.47 to 0.70) for C18:2 of subcutaneous fat, a different fat depot than evaluated in the present study. Fatty acid heritability estimates from subcutaneous fat analyzed using near-infrared spectroscopy were reported by (Fernández et al., 2003). The greatest heritability estimate

(0.41) was found for stearic acid (C18:0) with C18:2, C18:1 and C16:0 having heritability estimates of 0.29, 0.31, and 0.31, respectively.

A study conducted by Suzuki et al. (2006), showed that the percentage of C18:2 present in intramuscular fat was half that of the inner and outer layers of subcutaneous fat, suggesting that fatty acid accumulation may be under different physiological and genetic control for subcutaneous and intramuscular fats. Fatty acid composition of intramuscular fat is influenced by dietary fat source and content, and to a lesser extent, by genetics (Cameron et al., 2000). However, heritability estimates in the current study are moderate to high for the major fatty acids found in the intramuscular fat of the *longissimus dorsi* muscle, demonstrating genetic control for accumulation and storage of these fatty acids.

Few studies have reported genetic parameters for fatty acids from various adipose depots in swine, especially for PL and TAG lipid fractions of IMF. Heritability estimates for PL and TAG from intramuscular fat samples are reported in Tables 5 and 6, respectively. Heritability estimates for TAG for IMF were nearly zero for all estimates except C16:1*n*7, C18:0, and C18:2*n*6, which were low with estimates of 0.17, 0.25, and 0.19, respectively. Total SFA (0.12), total MUFA (0.10), and total PUFA (0.11) concentrations were also lowly heritable in the TAG lipid fraction of IMF. Heritability estimates of PL in IMF were nearly zero (0.00 to 0.14), with the greatest heritability estimate for C16:0 (0.14). These low heritability estimates could be explained by the small variation that exists in this population in TAG and PL concentrations.

Genetic and phenotypic correlations between fatty acids and meat quality traits

Genetic and phenotypic correlations between meat quality traits and saturated fatty acids are presented in Table 7 and between unsaturated fatty acids are presented in Table 8.

Fernandez et al. (2003) estimated that the genetic correlations between IMF content and C16:0, C18:0, C18:1, and C18:2 were nearly zero (-0.06 to 0.09). In the present study, genetic correlations between IMF content and C16:0, C18:0, and C18:1 did not differ from zero. However, negative genetic correlations between IMF and C17:0, and between IMF and C18:2 were found (-0.61 and -0.80, respectively). Loin muscle area was positively correlated with C18:2 concentration (0.75), and tenth-rib backfat was negatively correlated with C18:2 (-0.62). Monounsaturated fat concentrations from IMF were negatively correlated with LMA (-0.70), but positively correlated with BF10 (0.77). Intramuscular fat PUFA concentrations were negatively correlated with IMF and BF10, and positively correlated with LMA. This could be explained by the higher content of C18:2 found in the genetically leaner pigs of the CL, of which the contribution of dietary fatty acids to total fat deposition is larger than that of de novo fatty acid synthesis (Wood et al., 2008).

Phenotypic correlations for BF and saturated fatty acids and BF and C18:1 have been reported to be positive, however, the phenotypic correlation of BF with polyunsaturated fatty acids is negative (Cameron, 1990). Similarly, correlations with C18:1 and last rib and C18:1 with average backfat were reported as 0.09 and 0.22, respectively (Piedrafita et al., 2001). In the same study, a positive correlation of LMA and C18:2 and negative phenotypic correlation between LMA and C18:1 was reported.

Understanding changes in fatty acid composition as a correlated response to selection for IMF is more important than direct selection for fatty acid composition. As suggested by Suzuki et al. (2006), fatty acid composition is very complex and it is unclear on how many fatty acids should be included in a breeding program. Also, the expense to measure and calculate breeding values for fatty acid composition on numerous animals for breeding

purposes is not practical (De Smet et al., 2004). However, selection strategies that make use of stearoyl-CoA desaturase (SCD), the single gene responsible for the synthesis of all MUFA, may be effective. Because fatty acid content impacts pork quality and may influence consumer acceptance, it is imperative to understand fatty acid composition as a correlated response to selection for increased quantity of IMF. Sellier (1998) reported a greater carcass lean:fat ratio is genetically associated with lower total lipid or low C18:0 (stearic acid) content and softer fat.

No significant genetic correlations were found in the current study between eating quality traits (flavor score and off-flavor score) and individual fatty acids. Eating quality traits have been shown to have unfavorable genetic correlations with carcass lean:fat ratio (Sellier, 1998). The positive genetic correlation between carcass leanness and ratio of PUFA:SFA of adipose tissue mainly originates from the relatively small contribution of *de novo* fatty acid synthesis and the relatively large contribution of dietary fatty acids to total fat deposition in genetically leaner pigs (Scott et al., 1981).

The variation that exists in backfat thickness among breeds often directly reflects the variation in fat quality (Sellier, 1998). In studies where similar or higher backfat thickness for Duroc pigs compared to Large White pigs, the Duroc had softer and more unsaturated fat (Barton-Gade, 1987; Cameron, 1990). This could represent a breed effect on fat quality, in the case of Duroc, independent of overall carcass fat composition (Sellier, 1998).

Genetic trends for meat and eating quality traits and fatty acid composition

Results from regressions of estimated breeding values for individual fatty acids by line are given in Table 9. Plots of average EBV by generation for each line are presented for BF10, LMA, IMF, individual fatty acids, total fatty acids, and eating quality traits (flavor and

off-flavor scores) in Figures 1 through 6, respectively. Genetic trends generally agree with estimated genetic correlations. In some cases, significant genetic changes were detected in the unselected CL, generally opposite in direction of those in the SL. This result may be attributed to random genetic drift.

The direct genetic response in IMF measures observed in the SL corresponded to a significant decrease in EBV for LMA compared to the CL (-4.59 cm^2 in SL to 4.08 cm^2 in the CL). The direct genetic response in IMF measures observed in the SL corresponded to a significant decrease in EBV for carcass loin muscle area and increase in EBV for tenth-rib backfat (Schwab et al., 2009a). In the current study, a significant genetic response was observed for C16:0 and C18:2*n*6 when compared to EBV of pigs in the control line. As illustrated in Figure 3 and detailed in Table 9, selection for IMF has led to a change in fatty acid composition for C16:0 and C18:2*n*6. The EBV for SFA, MUFA, and PUFA directly reflected the increase in EBV for IMF. Pigs with less IMF had greater concentration of PUFA, and less SFA and MUFA in IMF when compared to pigs in the SL. This is verified by the high correlation of C18:2*n*6 with IMF (-0.80) with tenth-rib backfat (-0.62), and with loin-muscle area (0.75). The strong genetic correlation between MUFA and tenth-rib backfat (0.77), and between MUFA and loin-muscle area (-0.70), as well as the correlations between PUFA and IMF (-0.84), tenth-rib backfat (-0.73), and loin muscle area (0.78) confirm this genetic trend.

Results obtained in the current study suggest that the fatty acid composition of IMF of the *longissimus dorsi* muscle is correlated genetically with production and meat quality traits. Changes in fatty acid composition of IMF are a correlated response to selection for increased quantity of IMF. Therefore, when selection for IMF is executed, we must understand the

possible changes that may occur (either positive or negative) on fatty acid composition of the adipose type. Further studies investigating the genetic and dietary control of fatty acid composition in the various fat depots is warranted.

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Table 1. Dietary components and nutrient composition of finishing diets fed to Durocpigs in selection project designed to increase intramuscular fat

	Finishing Phase[1]		
Item	**1**	**2**	**3**
Calculated Composition[2]			
Corn, %	68.32	74.75	81.00
Soybean meal, %	26.25	20.00	13.75
Added Fat, %	3.00	3.00	3.00
Base premix, %	2.25	2.25	2.25
Tylan 40, g/ton	0.13	-	-
Cupric sulfate, %	0.05	-	-
Total	100	100	100
Protein, %	19	18	15.5
Lysine, %	1.2	1.05	0.85
Fat, %	6	6	6
Fiber, %	3.2	3.2	3.2
Calcium, %	0.55	0.54	0.54
Phosphorus, %	0.45	0.45	0.45
Salt, %	0.5	0.5	0.5
Zinc, mg/kg	140	140	140
Copper, mg/kg	135	10	10
Phytase-FTU/kg	750	750	750
Selenium, mg/kg	0.3	0.3	0.3

[1]Finishing phase 1 – 34 to 68 kg BW; Finishing phase 2 – 68 to 91 kg BW; Finishing phase 3 – 91 kg to market weight.
[2]Calculated compostion based on NRC (1998) values.

Table 2. Fatty acid composition of the phase 3 finishing diet fed to pigs in a selection project for intramuscular fat content[1]

Trait	Formula	Finishing Phase 3[2]
Fat, %		6.26
Saturated fatty acids (wt %)		
Lauric acid	C12:0	0.01
Myristic acid	C14:0	0.76
Pentadecanoic acid	C15:0	0.00
Palmitic acid	C16:0	22.18
Margaric acid	C17:0	0.25
Stearic acid	C18:0	8.65
Arachidic acid	C20:0	0.36
Behenic acid	C22:0	0.09
Lignoceric acid	C24:0	0.00
Total saturated		32.30
Monounsaturated fatty acids (wt %)		
Myristoleic acid	C14:1	0.04
Palmitoleic acid	C16:1 *n*-7	1.45
cis-Heptadecenoic acid	C17:1 *n*-10	0.13
Oleic acid	C18:1 *n*-9	17.20
trans-Vaccenic acid	C18:1 *n*-7	1.39
Eicosanoic acid	C20:1 *n*-9	0.74
Nervonic acid	C24:1	0.08
Total MUFA		21.03
Polyunsaturated fatty acids (wt %)		
Linoleic acid	C18:2 *n*-6	44.35
α-Linolenic acid	C18:3 *n*-3	1.56
γ-Linolenic acid	C18:3 *n*-6	0.01
Eicosadienoic acid	C20:2 *n*-6	0.00
Eicosatrienoic acid	C20:3 *n*-6	0.08
Arachidonic acid	C20:4 *n*-6	0.21
Eicosapentaenoic acid	C20:5 *n*-3	0.00
Docosatetraenoic acid	C22:4 *n*-6	0.01
Docosapentaenoic acid	C22:5 *n*-3	0.01
Docosahexaenoic acid	C22:6 *n*-3	0.00
Total PUFA		46.23

[1]Presented as a percentage of total lipid in the feed on an as-fed basis.
[2]Finishing phase 3 fed from 91 kg to market weight.

Table 3. Distribution of records by generation and line from a selection experiment for increased intramuscular fat in Duroc swine

	Generation					
Trait Category	**3**	**4**	**5**	**6**	**7**	**Total**
	No. of observations					
Contol Line[1]						
Gilts	14	5	14	17	6	56
Barrows	67	66	87	60	21	301
Select Line[2]						
Gilts	8	24	24	32	12	100
Barrows	56	53	46	40	11	206
Total						
Gilts	22	29	38	49	18	156
Barrows	123	119	133	100	32	507
Carcass	145	148	171	149	50	663

[1]Control line = unselected, randomly mated population.

[2]Select line = result of 7 generations of selection for increased IMF based on a two-trait animal model that included IMF measured on the carcass and predicted via ultrasound.

Table 4. Phenotypic variance (σ_p), animal genetic variance (σ_a), common environmental variance of litter (σ_l), and heritability (h^2, ±SE) estimates for IMF fatty acid composition from a bivariate animal model evaluation of purebred Duroc swine (n=628)[1]

Trait	Formula	σ_p	σ_a	σ_l	h^2
Lauric acid	C12:0	0.0023	0.0017	0.0006	0.73 ± 0.21
Myristic acid	C14:0	0.0815	0.0185	0.0002	0.23 ± 0.10
Pentadecanoic acid	C15:0	0.1233	0.0051	0.0004	0.04 ± 0.06
Palmitic acid	C16:0	8.3580	0.2972	0.9449	0.04 ± 0.08
Palmitoleic acid	C16:1*n*-7	0.3534	0.1425	0.0034	0.40 ± 0.12
Margaric acid	C17:0	0.0240	0.0057	0.0007	0.24 ± 0.10
Stearic acid	C18:0	2.4780	0.8883	0.1709	0.36 ± 0.12
Oleic acid	C18:1*n*-9	21.7476	0.4547	3.1301	0.02 ± 0.06
Linoleic acid	C18:2*n*-6	2.8828	0.9649	0.0203	0.33 ± 0.09
α-Linolenic acid	C18:3*n*-3	0.0355	0.0091	0.0019	0.26 ± 0.13
SFA[2]		12.0339	3.2143	0.2313	0.27 ± 0.11
MUFA[3]		11.8274	1.8441	1.0636	0.16 ± 0.08
PUFA[4]		3.8837	1.1115	0.0011	0.29 ± 0.08
AI[5]		0.0329	0.0004	0.0028	0.01 ± 0.06
Iodine value[6]		12.8441	4.3329	0.0008	0.34 ± 0.11

[1]All estimates obtained from a 2-trait model which included IMF and each trait
[2]SFA = Total saturated fatty acids.
[3]MUFA = Total monounsaturated fatty acids.
[4]PUFA = Total polyunsaturated fatty acids.
[5]AI = Atherogenic index calculated as (C12:0+4×C14:0+C16:0)/(∑MUFA+∑PUFA).
[6]Iodine Value = (C16:1*n*7*0.95) + ((C18:1*n*9+18:1*n*7)*0.86) + (C18:2*n*6*1.732) + ((C18:3*n*3+C18:3*n*6)*2.616) + (C20:1*0.785) + (C22:1*0.723).

Table 5. Phenotypic variance (σ_p), animal genetic variance (σ_a), common environmental variance of litter (σ_l), and heritability (h^2, ±SE) estimates for phospholipid fatty acid concentration from a bivariate animal model evaluation of purebred Duroc swine (n=628)[1]

Trait	Formula	σ_p	σ_a	σ_l	h^2
Lauric acid	C12:0	8.7581	0.0037	0.12651	0.00 ± 0.13
Myristic acid	C14:0	2.9840	0.0105	0.00165	0.00 ± 0.23
Pentadecanoic acid	C15:0	6.7824	0.0408	0.64421	0.01 ± 0.06
Palmitic acid	C16:0	32.0081	4.6262	1.91546	0.14 ± 0.10
Palmitoleic acid	C16:1*n*-7	2.2037	0.2805	0.55273	0.13 ± 0.22
Margaric acid	C17:0	2.1036	0.1628	0.03310	0.08 ± 0.08
Stearic acid	C18:0	6.9336	0.2866	0.54197	0.04 ± 0.07
Oleic acid	C18:1*n*-9	16.5384	0.0868	0.80316	0.01 ± 0.08
Linoleic acid	C18:2*n*-6	54.4674	0.5874	3.74379	0.01 ± 0.07
α-Linolenic acid	C18:3*n*-3	1.7053	0.0001	1.56231	0.00 ± 0.76
SFA[2]		42.7388	0.2986	6.14259	0.01 ± 0.08
MUFA[3]		35.3204	0.1475	2.78431	0.00 ± 0.07
PUFA[4]		62.5635	2.3097	5.46557	0.04 ± 0.08
AI[5]		0.0686	0.0002	0.01245	0.00 ± 0.08

[1]All estimates obtained from a 2-trait model which included IMF and each trait .
[2]SFA = Total saturated fatty acids.
[3]MUFA = Total monounsaturated fatty acids.
[4]PUFA = Total polyunsaturated fatty acids.
[5]AI = Atherogenic index calculated as (C12:0+4×C14:0+C16:0)/(∑MUFA+∑PUFA).

Table 6. Phenotypic variance (σ_p), animal genetic variance (σ_a), common environmental variance of litter (σ_l), and heritability (h^2, ±SE) estimates for neutral lipid fatty acid concentration from a bivariate animal model evaluation of purebred Duroc swine (n=628)[1]

Trait	Formula	σ_p	σ_a	σ_l	h^2
Lauric acid	C12:0	0.4765	0.01215	0.0086	0.03 ± 0.14
Myristic acid	C14:0	0.6937	0.00302	0.0926	0.00 ± 0.06
Pentadecanoic acid	C15:0	0.8756	0.02854	0.8279	0.03 ± 0.31
Palmitic acid	C16:0	22.3323	1.23694	1.6418	0.06 ± 0.08
Palmitoleic acid	C16:1*n*-7	0.6674	0.11640	0.0973	0.17 ± 0.09
Margaric acid	C17:0	0.0945	0.00065	0.0004	0.01 ± 0.18
Stearic acid	C18:0	5.4548	1.35576	0.0526	0.25 ± 0.10
Oleic acid	C18:1*n*-9	18.3236	0.01239	1.8854	0.00 ± 0.07
Linoleic acid	C18:2*n*-6	1.4219	0.27682	0.1158	0.19 ± 0.10
α-Linolenic acid	C18:3*n*-3	0.2605	0.00207	0.0002	0.01 ± 0.09
SFA[2]		29.3207	3.45453	1.6620	0.12 ± 0.09
MUFA[3]		31.9815	3.30256	2.5886	0.10 ± 0.09
PUFA[4]		2.7022	0.31070	0.1586	0.11 ± 0.09
AI[5]		0.1460	0.00012	0.0025	0.00 ± 0.09

[1]All estimates obtained from a 2-trait model which included IMF and each trait.
[2]SFA = Total saturated fatty acids.
[3]MUFA = Total monounsaturated fatty acids.
[4]PUFA = Total polyunsaturated fatty acids.
[5]AI = Atherogenic index calculated as (C12:0+4×C14:0+C16:0)/(∑MUFA+∑PUFA).

Table 7. Genetic (r_G) and phenotypic (r_P) correlations among saturated fatty acids of IMF, and meat quality and sensory traits from a selection project after 7 generations of selection for intramuscular fat in Duroc swine.[1]

	C12:0		C14:0		C15:0		C16:0		C17:0		C18:0		SFA	
Trait	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P
Intramuscular fat, (%)	-0.17	-0.07	**0.50**	0.10	-0.57	-0.27	0.65	0.05	**-0.61**	-0.21	0.22	0.21	0.40	0.08
Tenth-rib backfat, (mm)	-0.02	-0.01	0.20	0.09	-0.23	-0.09	0.15	0.14	-0.18	-0.09	-0.25	0.81	0.01	0.16
Loin muscle area, (cm^2)	0.16	0.01	-0.10	-0.07	0.44	0.10	-0.24	-0.09	**0.47**	0.14	0.03	0.24	-0.12	-0.13
48 h pH	0.29	0.05	0.43	0.04	-0.21	-0.07	0.19	-0.01	-0.06	-0.10	0.19	0.08	0.09	0.00
Cook loss, (%)	-0.18	0.06	-0.17	0.09	0.00	-0.05	-0.05	0.01	-0.21	-0.03	0.02	0.01	-0.10	-0.01
Flavor score[2]	0.07	-0.01	0.53	0.06	-0.07	-0.14	0.34	-0.01	-0.41	-0.11	0.20	0.15	0.26	0.04
Off-flavor score[2]	-0.20	-0.06	-0.69	-0.11	0.08	0.09	-0.36	-0.09	0.25	0.06	0.01	0.06	-0.15	-0.07

[1]Genetic correlation estimates that differ more than 1.96 × SE from zero ($P < 0.05$) are presented in bold.

[2]Trained sensory panel evaluations of flavor (1= little pork flavor, bland; 10 = extremely flavorful, abundant pork flavor), off-flavor (1 = no off-flavor; 10 = abundant non-pork flavor).

Table 8. Genetic (r_G) and phenotypic (r_P) correlations among unsaturated fatty acids IMF, and meat quality and sensory traits from a selection project after 7 generations of selection for intramuscular fat in Duroc swine.[1]

	C16:1		C18:1		C18:2		C18:3n3		MUFA		PUFA	
Trait	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P
Intramuscular fat	0.32	0.10	-0.18	0.14	**-0.80**	-0.51	0.01	0.11	0.27	0.27	**-0.84**	-0.49
Tenth-rib backfat, (mm)	0.35	0.12	0.51	0.07	**-0.62**	-0.42	-0.09	-0.05	**0.77**	0.79	**-0.73**	-0.41
Loin muscle area, (cm^2)	-0.02	-0.05	-0.66	-0.05	**0.75**	0.33	0.00	0.01	**-0.70**	0.30	**0.78**	0.31
48 h pH	-0.35	-0.03	-0.66	0.06	-0.04	-0.11	-0.14	0.00	-0.26	0.04	-0.07	-0.08
Cook loss, (%)	0.37	0.12	0.76	0.03	-0.18	-0.07	0.24	0.01	0.39	0.93	-0.18	-0.08
Flavor score[2]	0.04	0.07	-0.65	0.04	-0.40	-0.22	-0.41	0.04	0.00	0.29	-0.41	-0.20
Off-flavor score[2]	-0.39	-0.14	0.81	-0.01	0.09	0.21	0.33	0.01	0.19	0.30	0.18	0.20

[1]Genetic correlation estimates that differ more than 1.96 × SE from zero ($P < 0.05$) are presented in bold.

[2]Trained sensory panel evaluations of flavor (1= little pork flavor, bland; 10 = extremely flavorful, abundant pork flavor), off-flavor (1 = no off-flavor; 10 = abundant non-pork flavor)

Table 9. Coefficients (b) and standard errors (SE) for regressions of estimated breeding values on generation by trait and line from Duroc swine selected for increased IMF for 7 generations

		CL[1]			SL[2]		
Trait[3]	Formula	b	SE	*P*[d]	b	SE	*P*[4]
Lauric acid	C12:0	0.0041	0.0008	**	-0.0005	0.0009	NS
Myristic acid	C14:0	-0.0070	0.0014	**	0.0193	0.0028	***
Pentadecanoic acid	C15:0	0.0123	0.0008	***	-0.0215	0.0012	***
Palmitic acid	C16:0	-0.0493	0.0104	**	0.1533	0.0152	***
Palmitoelic acid	C16:1 *n*-7	-0.0075	0.0077	NS	0.0548	0.0058	***
Margaric acid	C17:0	0.0083	0.0022	**	-0.0124	0.0021	**
Arachidic acid	C18:0	-0.0209	0.0131	NS	0.0378	0.0153	NS
Oleic acid	C18:1 *n*-9	-0.1114	0.0134	***	0.0346	0.0120	NS
Linoleic acid	C18:2 *n*-6	0.1471	0.0135	***	-0.2841	0.0117	***
α-Linolenic acid	C18:3 *n*-3	-0.0015	0.0008	NS	0.0057	0.0006	***
BF10		-0.4686	0.0227	***	0.9101	0.0372	***
LMA		0.5808	0.0199	***	-0.7762	0.0345	***
IMF		-0.1074	0.0132	***	0.3052	0.0165	***
FS		-0.0252	0.0061	**	0.0988	0.0079	***
OFS		0.0023	0.0052	NS	-0.0647	0.0071	***
SFA		-0.0439	0.0206	NS	0.2101	0.0389	**
MUFA		-0.1468	0.0062	***	0.1931	0.0171	***
PUFA		0.1721	0.0133	***	-0.3367	0.0135	***
AI		-0.0017	0.0003	**	0.0026	0.0005	**

[1]CL = control line

[2]SL = select line

[3]BF10 = carcass 10th rib backfat; LMA = carcass 10th rib loin muscle area; IMF = intramuscular fat of the longissimus dorsi muscle; FS = trained sensory panel score for flavor (1 = little pork flavor, bland; 10 = very flavorful, abundant pork flavor); OFS = trained sensory panel score for off-flavor (1 = no off-flavor, 10 = abundant non-pork flavor); SFA = total saturated fat of IMF; MUFA = total monounsaturated fat of IMF; PUFA = total polyunsaturated fat of IMF; AI = Atherogenic index calculated as (C12:0+4×C14:0+C16:0)/(∑MUFA+∑PUFA).

[4]NS = no significant difference ($P > 0.05$); **$P < 0.01$; ***$P < 0.001$.

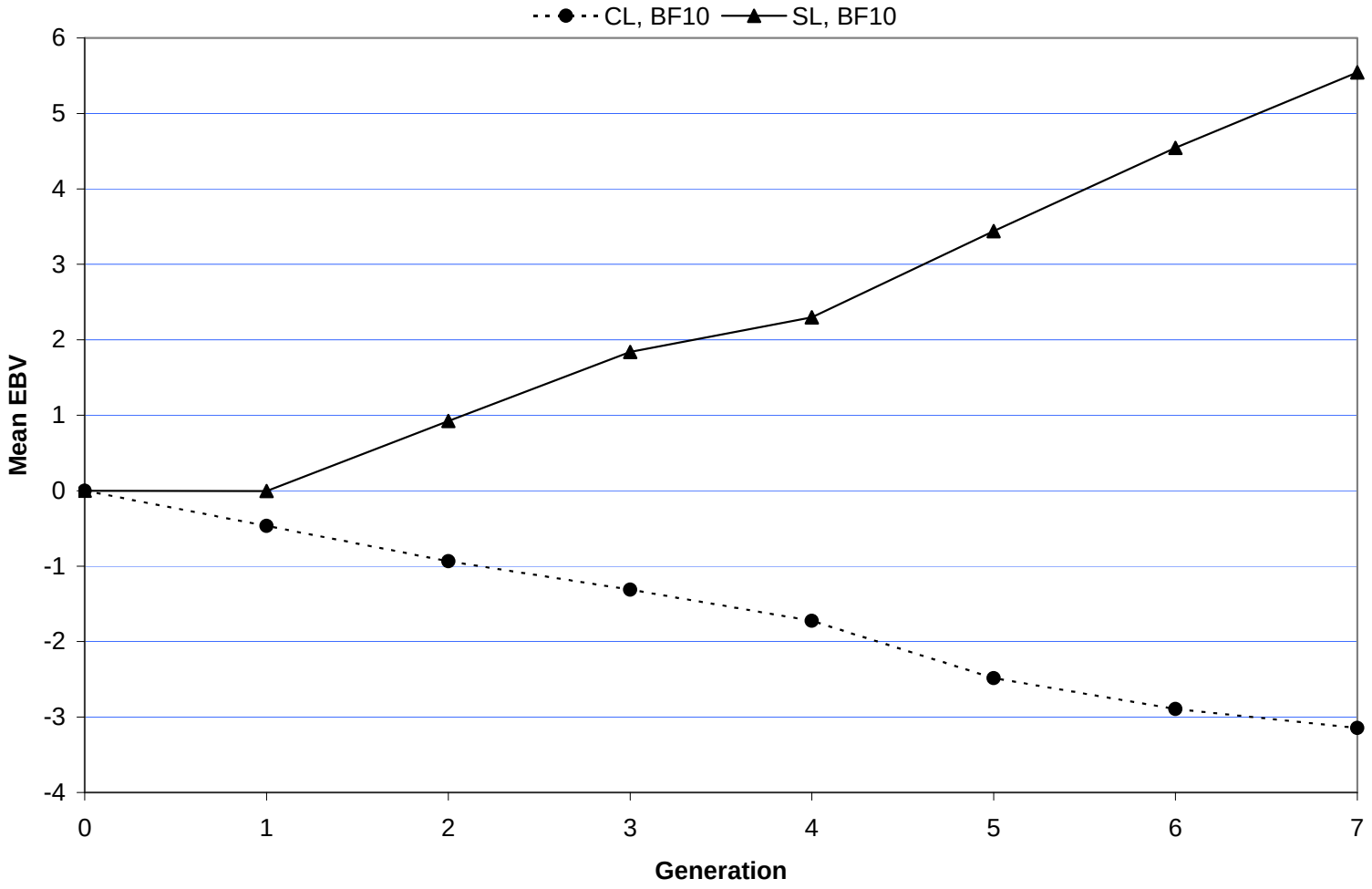

Figure 1. Genetic trends for tenth-rib backfat (BF10, mm) for select (SL) and control (CL) lines of a population of purebred Duroc pigs selected for IMF

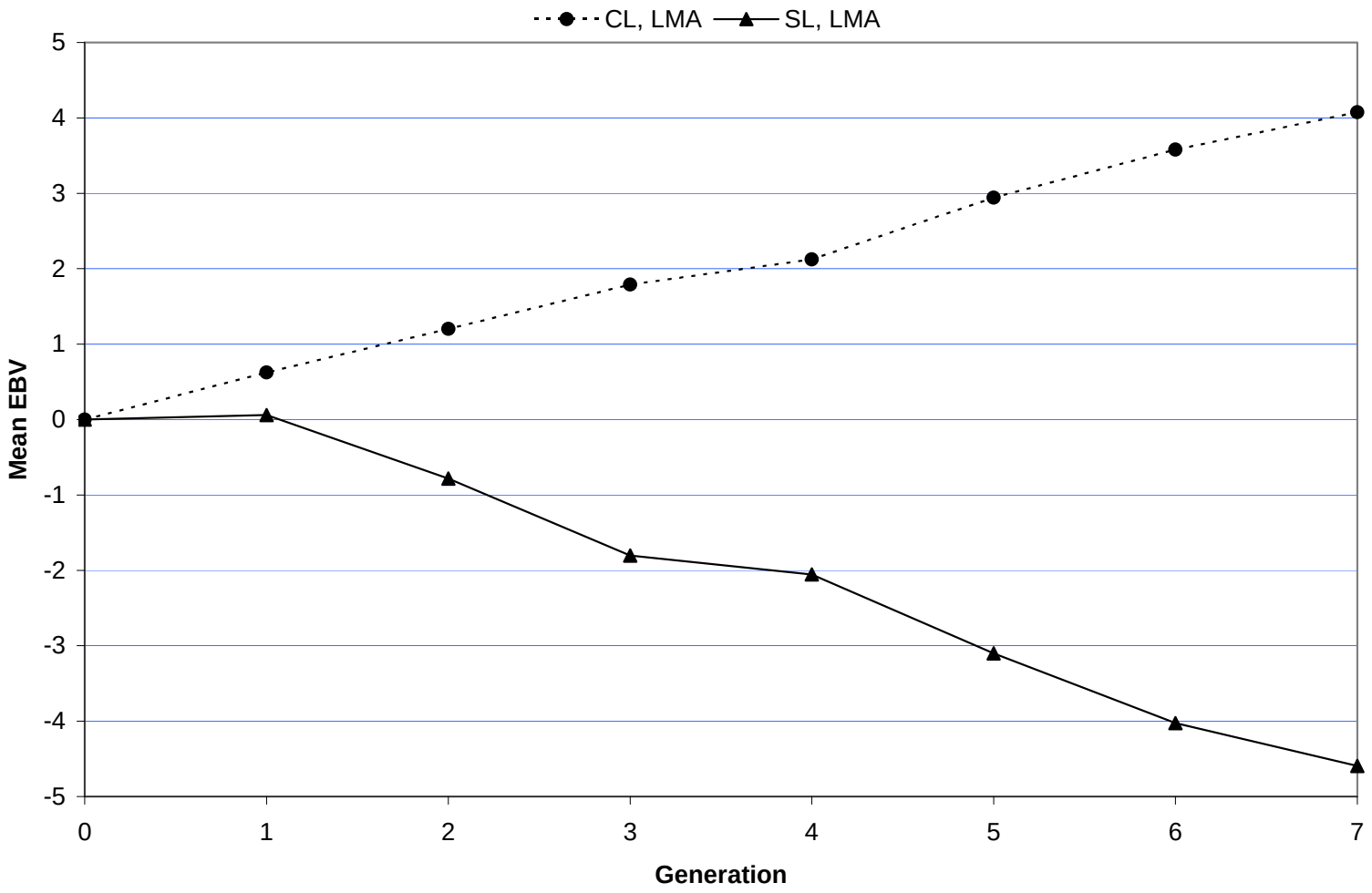

Figure 2. Genetic trends for loin muscle area (LMA, cm^2) for select (SL) and control (CL) lines of a population of purebred Duroc pigs selected for IMF

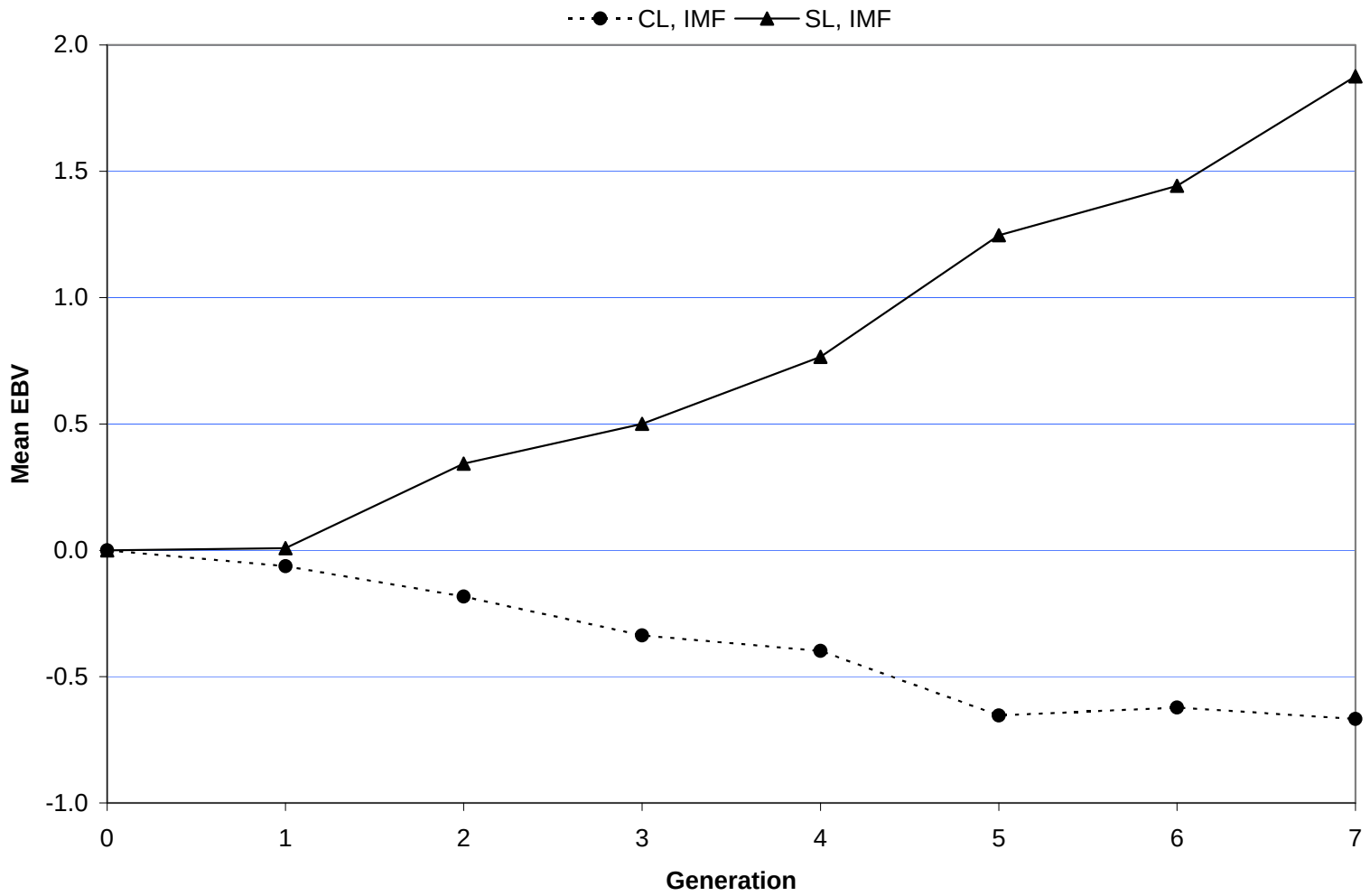

Figure 3. Genetic trends for intramuscular fat (IMF, %) for select (SL) and control (CL) lines of a population of purebred Duroc pigs estimated selected for IMF

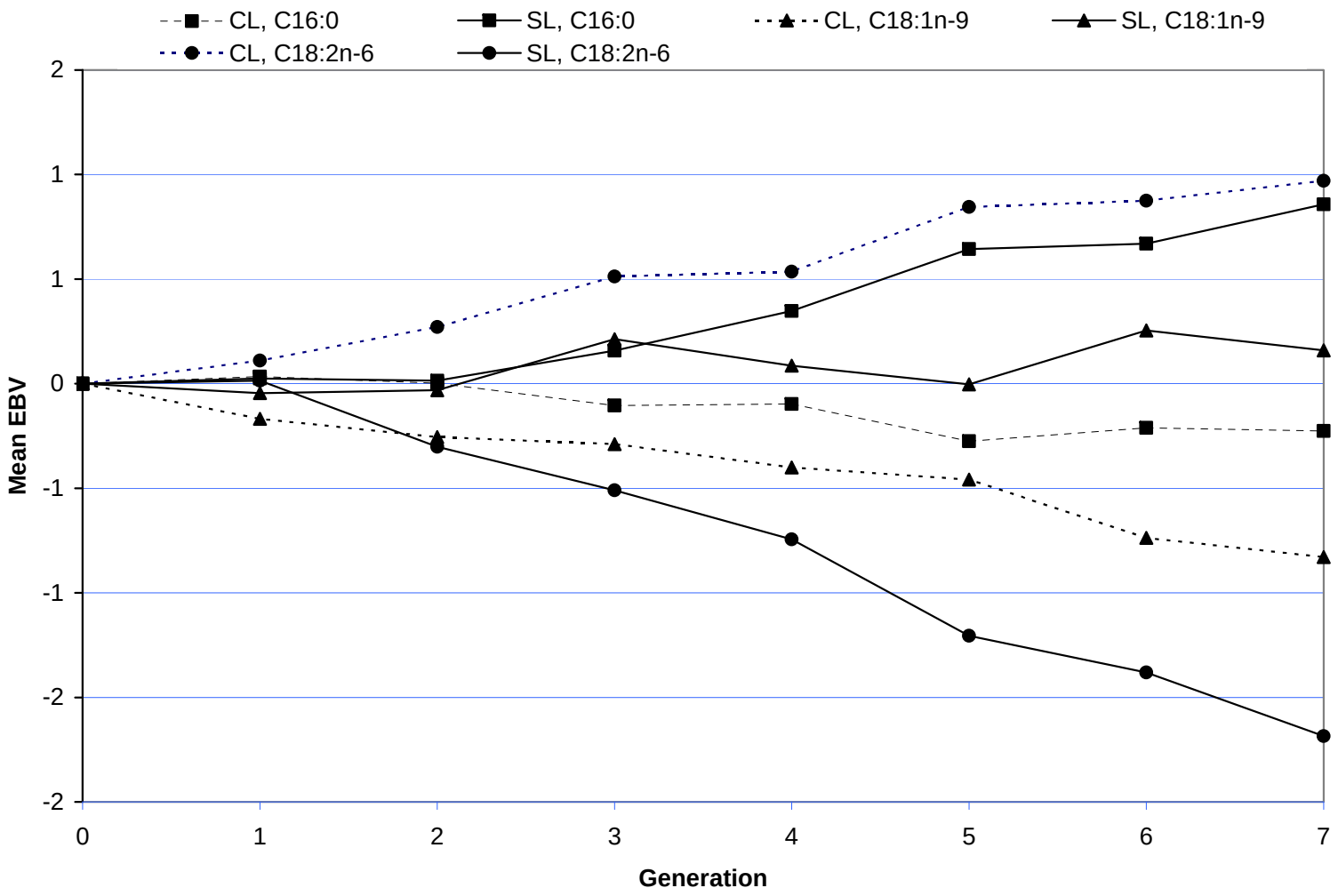

Figure 4. Genetic trends for palmitic acid (C16:0), oleic acid (18:1), and linoleic acid (18:2) for select (SL) and control (CL) lines of a population of purebred Duroc pigs selected for IMF

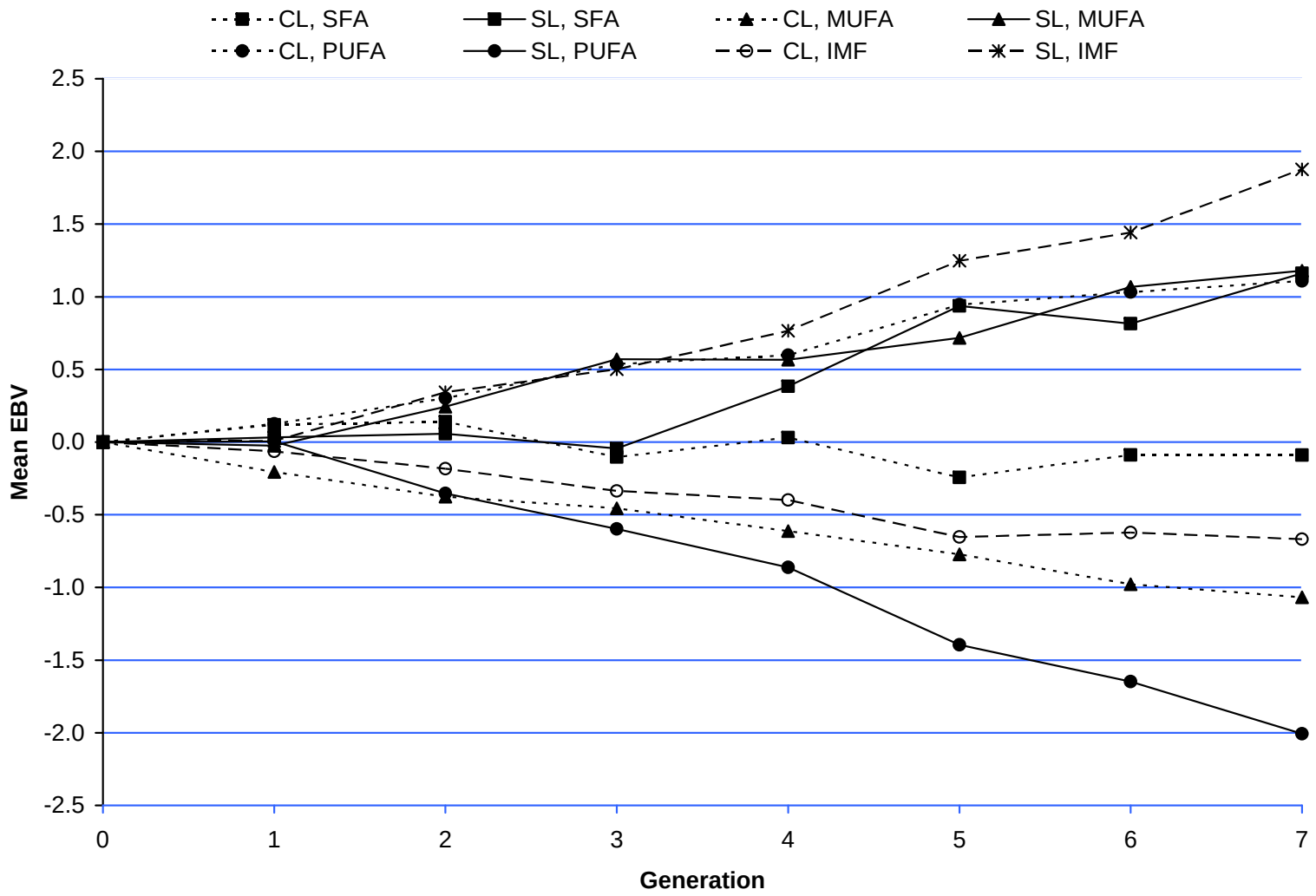

Figure 5. Genetic trends for saturated fat (SFA), monounsaturated fat (MUFA), polyunsaturated fat (PUFA), and intramuscular fat (IMF) for select (SL) and control (CL) lines of a population of purebred Duroc pigs selected for IMF

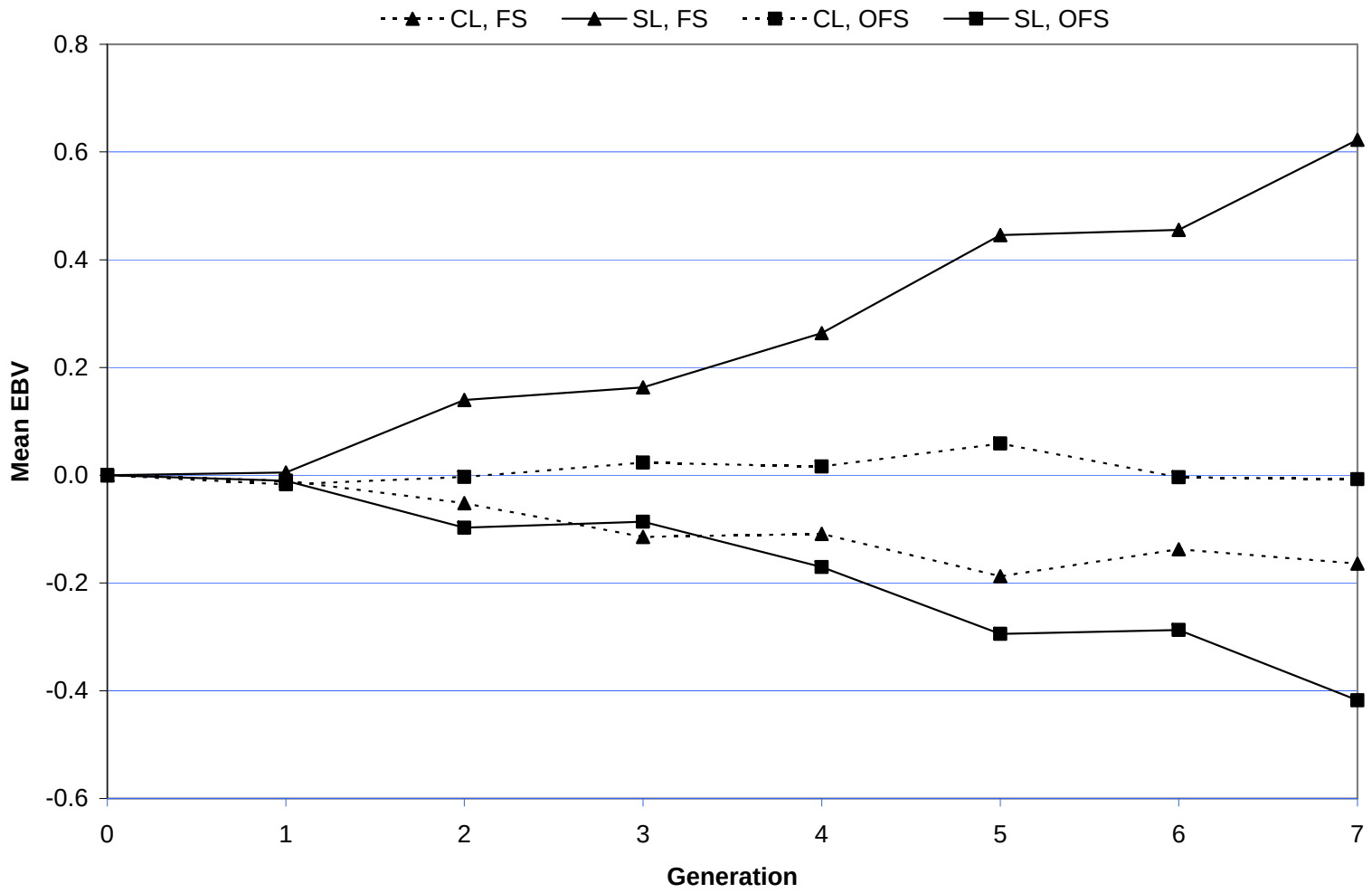

Figure 6. Genetic trends for sensory panel evaluations of flavor (FS) and off-flavor (OFS) for select (SL) and control (CL) lines of a population of purebred Duroc pigs selected for IMF

CHAPTER 7.

EVALUATION OF CANDIDATE GENES FOR USE IN SELECTION PROGRAMS AIMED AT CHANGING FATTY ACID COMPOSITION AND INCREASING INTRAMUSCULAR FAT IN DUROC SWINE[1]

A paper to be submitted to the Journal of Animal Breeding and Genetics

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ABSTRACT: Sufficient levels of intramuscular fat (IMF) are needed to enhance consumer acceptance of pork. The overall fatty acid composition of fat (IMF) plays an important role not only in fat quality, but ultimately, overall pork quality. As a result, IMF has recently received greater attention for overall consumer health and is being implemented in many genetic improvement programs. An examination of previously described and novel genetic variants within candidate genes for intramuscular fat deposition and fatty acid composition was performed to evaluate the potential use of genetic markers in marker-assisted selection (MAS) schemes. Biological candidate genes implicated to play a role in fatty acid synthesis and interconversion, as well as adipogenesis, within purebred Duroc pigs examined in this study were: Fatty acid synthase (*FASN*), stearyl-CoA desaturase (*SCD*), and acetyl-CoA carboxylase (*ACC*). There was no difference between genotypes for the three markers in *ACC* and *FASN* genes for IMF, saturated fatty acids, monounsaturated fatty acids, or polyunsaturated fatty acid concentrations. A substantial amount of phenotypic variation in palmitic acid, stearic acid, and total SFA content of IMF was described by the *SCD* haplotypes. Polymorphic sites within the four *SCD* variants were significantly associated with fatty acids in the population. Results from this study suggest that the *SCD* gene could be utilized in selection programs focusing on changing the concentration of saturated fatty acids in IMF. This is beneficial from a health standpoint where the intake of saturated fatty acids has been shown to be undesirable.

Key words: Duroc, genetic markers, linkage, meat quality, pigs selection

INTRODUCTION

The fatty acid composition of meat is of great interest due to its impact on human health. There are benefits to the human consumer of increasing the degree of unsaturation of

pig meat (COMA, 1984). It has been reported that diet has a dramatic effect on the fatty acid composition of fat of pigs and to a lesser extent, genetics (Cameron et al., 2000). However, the fatty acid profile of the resulting fat may not totally reflect that of dietary fat as the pattern of fatty acid incorporation may change by site as well as fatty acid interconversions after de novo synthesis (Wiseman and Agunbiade, 1998).

Typically, pork has been viewed as unhealthy because of its high concentration of SFA, which can result in elevated plasma cholesterol, and ultimately contribute to cardiovascular disease (Bronte-Stewart et al., 1956). Of the SFA, lauric acid (C12:0), myristic acid (C14:0), and palmitic acid (C16:0) are considered to have the most harmful effects (Keys et al., 1974), whereas stearic acid (C18:0) is believed to be neutral in its effect (Bonanome and Grundy, 1988). Monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) increase hepatic low density lipoprotein (LDL) receptor activity, thereby decreasing the circulating concentration of LDL-cholesterol (Woollett et al., 1992; Rudel et al., 1995).

The fatty acid composition of pork can be influenced by dietary manipulation, however, results from Burkett et al. (2009) have shown that purebred Duroc pigs have differing fatty acid profiles when pigs were selected for IMF and fed similar diets. This suggests that there may be differences in the key lipogenic enzymes and transcription factors in the fatty acid synthesis pathway of pigs. Biological candidate genes that may play a role in meat and fat quality were identified as fatty acid synthase (*FASN*), stearoyl-CoA desaturase (*SCD*), and acetyl-CoA carboxylase (*ACC*).

The interconversion of fatty acids from their saturated to unsaturated form is solely controlled by the *SCD* gene. Studies have shown that differences in MUFA percentage were correlated with *SCD* activity in cattle (Sturdivant et al., 1992; Laborde et al., 2001). Results

from these studies suggest that genotyping of the *SCD* gene could be a useful tool for selection of pork with more healthful fatty acid composition.

Fatty acid synthase (FAS) is a multifunctional enzyme complex that catalyzes the synthesis of long-chain saturated fatty acids. It is a homodimer of two identical subunits containing seven different catalytic sites. In contrast to the intense attention placed on the effect of the *SCD* gene on fatty acid composition, the investigation of the *FASN* gene has focused primarily on the effect of fat accumulation (Moon et al., 2002; Wang et al., 2004). To our knowledge, there have been no previous studies that have focused on the association of polymorphisms of the *FASN* gene with fatty acid composition in pork.

Acetyl-CoA carboxylase-1 catalyzes the formation of malonyl-CoA, an intermediary substrate for FAS, from acetyl-CoA and bicarbonate in de novo fatty acid biosynthesis. There is considerable evidence that this enzyme has a key role in the regulation of fatty acid biosynthesis in animal tissues and may catalyze the rate-limiting step in the lipogenic pathway (Numa et al., 1970).

Within pig breeding populations, molecular markers that have an influence on meat quality, fatty acid composition, and eating quality will receive added attention because these traits are often lowly heritable, difficult to measure in the live animal, hard to measure in harvested progeny, and difficult to make progress in through conventional selection methodology. Independent of backfat thickness and intramuscular fat composition, genetic variation between specific genotypes seems to exist for the synthesis and incorporation of individual fatty acids, which deserve more attention at the molecular level. Therefore, the objective of this study was to identify novel sites of genetic variation within candidate genes

implicated to be associated with fatty acid composition and intramuscular fat (IMF) in purebred Duroc swine.

MATERIALS AND METHODS

Animals

Experimental protocols for the study were approved by the Iowa State University Institutional Animal Care and Use Committee. A purebred Duroc population was initiated in 1998 to evaluate selection for intramuscular fat (IMF) in Duroc swine using real-time ultrasound. After two generations of random mating, a line selected for IMF (SL) and a control line (CL) were created and selection began as described by Schwab et al. (2009a). Selection was based on breeding values for IMF estimated by fitting a two-trait (IMF measured on the carcass and IMF predicted via real-time ultrasound) animal model in MATVEC (Wang et al., 2003). Details of this selection, breeding value estimation, mating procedures, and responses after 6 generations are reported by Schwab et al. (2009a).

Finishing pigs were housed in fully slatted, mechanically ventilated, curtain-sided finishing buildings and were provided a minimum of 0.77 m^2 of floor space with 20 to 25 pigs per pen from 34 kg until they reached an average off test weight of 110 kg. Upon completion of the performance test period, all available barrows and randomly selected gilts were harvested at a commercial abattoir (Hormel Foods, Austin, MN). Carcass measurements were obtained by Iowa State University personnel 24 h post-mortem. Standard carcass collection procedures as outlined in Pork Composition and Quality Assessment Procedures (NPPC, 2000) were followed to obtain measurements of 10^{th} rib backfat (BF10) and loin muscle area (LMA). A section of bone-in *longissimus dorsi* containing the 10^{th} to 12^{th} ribs was excised from the carcass and transported to the Iowa State

University Meat Laboratory. A 3.2 mm slice from the 10th rib face was utilized for lipid content analysis. Additionally, a loin sample from each pig was retained for DNA analysis. Loin samples or ear tissue from all pigs in the study were collected to identify each pigs' genomic DNA. Ear tissue samples were collected using the TypiFixTM ear tag system (Agrobiogen, Thalmannsdorf, Germany). Porcine genomic DNA was isolated from tissue samples (ear or loin) using the Nexttec^{TM} DNA isolation system (Nexttec GmbH Biotechnologie, Agrobiogen, Thalmannsdorf, Germany), adhering to the manufacturer's protocol.

Fatty acid analysis

Trimmed loin samples (generations 3 through 6) from the *longissimus dorsi* at the 10-11th rib were utilized for fatty acid determination. Total lipid was extracted from the IMF samples with a chloroform and methanol (2:1, vol:vol) mixture and quantified gravimetrically (Folch et al., 1957). Triacylglycerols (TAG) were separated from phospholipids (PL) by thin-layer chromatography with hexane and ethyl acetate (4:1, vol:vol). Fatty acids in each lipid were derivatized to methyl esters according to Lepage and Roy (1986). Fatty acid methyl esters (FAME) from IMF were analyzed by gas chromatography (GC; model 3400, Varian, Palo Alto, CA) equipped with a Supelco SP-2560 column (100 m x 0.25 mm x 0.2 μm film thickness) and a flame ionization detector. The column started at a temperature of 100°C and was increased to 170°C at a rate of 2°C per min, followed by an increase to 180°C at 0.5°C per min and to 250°C at 10°C per minute. Total run time was 77 min and the detector was maintained at 220°C. Based on the fatty acid composition, the atherogenic index (AI) was calculated following Ulbricht and Southgate (1991):

$$AI = \frac{C12:0 + (4 \times C14:0) + C16:0}{\Sigma MUFA + \Sigma PUFA}.$$

Candidate genes and restriction fragment length polymorphism (RFLP) screening

A description of the genes (*SCD*, *FASN*, *ACC*) chosen for investigation along with published conditions of polymerase chain reaction (PCR) and restriction endonuclease digestions are presented in Table 1. Sequencing of pooled PCR products from eight pigs representing varying levels of IMF was conducted using an ABI sequencer 377 (Applied Biosystems, Foster City, CA, USA). The sequences were compared using Sequencher software version 3.0 (Gene Codes, Ann Arbor, MI, USA) to detect SNP.

Genetic variant within SCD

The sequence fragments containing the four detected variants within the *SCD* gene, as outlined by Ren et al. (2004a) and Ren et al. (2004b), were amplified and sequenced to validate the existence of each site of genetic variation within the population under study. Sequencing revealed four nucleotide substitutions: C/T located 233 bp upstream from the start codon in the 5'UTR (SCD1, NCBI#ss119336781), A/G located in intron 1 (SCD2, NCBI#ss119336782), C/G located 1038 bp upstream from the start codon in the 5' UTR (SCD3, NCBI#ss119336783), and A/G located on exon 6 (SCD4, NCBI#ss119336784), 2001 bp from the stop codon.

Novel genetic variant within FASN

The porcine *FASN* cDNA reported here (accession #EF589048) allowed for the identification of two single nucleotide polymorphisms on sus scrofa chromosome 12 (Munoz et al., 2003). Within intron 15 of *FASN*, SNP Y (FASN14, NCBI#ss119336785) was identified which was a C/T transition using a forward primer of 5'-

CGAGTACAGCGTCAACAACC-3' and reverse primer of 5'-GTGGGAACAGACCGTTGG-3'. This SNP creates a polymorphic *AvaII* restriction site. The second SNP identified for *FASN* (FASN24, NCBI#ss119336786) was in exon 24 (SNP R [A/G]), which resulted in an amino acid change of Asn1426Asp. Using the forward primer of 5'CTGGTGGCCCTGAAGAGGT-3' and reverse primer of 5'-GTCCCGGTAGACGTTCATCA-3' within the *FASN* cDNA (accession #EF589048), a polymorphic *Hinf1* restriction site was identified.

Novel genetic variant within ACC

Primers were designed from a *ACC* sequence (GenBank accession no. CU468157.2) found by aligning with mRNA sequence (GenBank accession no. EU168399). The primers were forward, 5'-CCCTTCATTGCCTTCTTAGG-3'; and reverse, 5'-CATGACCCAGCACATCTCAC-3', resulting in an amplified PCR product size of 369 bp. Comparative sequencing of the PCR products revealed a nucleotide substituition C/T (ACACA, NCBI#ss119336787) positioned with a *TaqI* restriction enzyme recognition site within the 3' UTR.

Statistical analysis

The PHASE software program (v2.1, Seattle, WA) was used to estimate haplotype genotype data (Stephens et al., 2001) from the current population for the *SCD* SNPs. Differences between genotypes and haplotypes for meat quality, carcass composition, and fatty acid composition phenotypic measures were assessed with use of the PROC MIXED procedure in SAS (SAS Inst., Cary, NC). Least squares means and corresponding SE were computed using a model that included fixed effects of sex, contemporary group, genotype (or

haplotype), generation, and line, and a covariate of hot carcass weight. Random effects of sire nested within line and dam nested within sire and line were also included in the analysis.

This model is the result of a stepwise process of fitting all two-way interactions between fixed effects, along with second- and third-order polynomial effects of the covariate hot carcass weight, and subsequently removing non-significant ($P > 0.05$) individual effects sequentially. The Chi-Squared test was used to compare the observed allele and genotype frequencies with Hardy-Weinburg equilibrium values.

RESULTS AND DISCUSSION

Genotype and allele frequencies

Number of observations for each genotype of the identified markers is presented in Table 2. The distribution of allele and genotype frequencies for each of the genes evaluated in the current study did not differ ($P > 0.05$) within line from Hardy-Weinberg equilibrium (Table 3). These results suggest that factors such as random genetic drift or selection did not have a significant impact on allele frequencies in the population. Similarly, Schwab et al. (2009b) reported no differences in allele frequencies for *MC4R, FABP3*, *DLK1*, and *TCF7L2* in the same population.

Least squares means for carcass traits and fatty acid composition of intramuscular fat by *ACC-Taq1* genotype are presented in Table 4. There was no effect of genotype for *ACC-Taq1* on carcass traits ($P > 0.05$). Pigs with genotype TT for *ACC-Taq1* had the highest concentration of C16:1*n*7 present in the total lipid fraction of IMF. Means between *ACC-Taq1* genotypes for SFA, MUFA, and PUFA were not different ($P > 0.05$).

Least squares means for carcass traits and fatty acid composition of intramuscular fat by FASN14 and FASN24 are presented in Table 5. There were no differences ($P > 0.05$) in fatty acid composition or carcass traits between genotypes for FASN14 or FASN24.

Least squares means of the effect of *SCD* variants on fatty acid composition of intramuscular fat are presented in Table 6. A trend for an under dominance effect was found for *SCD1-PfLF1* ($P = 0.078$) and *SCD4-BstUI* ($P = 0.076$) for IMF. Polymorphisms in the *SCD* gene resulted in an additive effect for C16:1, C18:0, SFA, and MUFA.

Stearoyl-CoA desaturase (*SCD*), or Δ^9-desaturase, catalyzes the conversion of C16:0 and C18:0 to C16:1 and C18:1, the 2 major MUFA of pork lipids (Warnants et al., 1996). This conversion is the terminal step in the desaturation of these saturated fatty acids to their respective monounsaturated form. In the current study, polymorphisms for SCD SNPs were additive for the interconversion of C16:0 to C16:1 and C18:0 to C18:1. These ratios are an indicator of the activity of Δ^9-desaturase on the interconversions of fatty acid from their saturated to monounsaturated forms (Table 6). Several studies have reported differences in desaturase enzyme activity in Wagyu beef cattle with excessive amounts of IMF as an explanation of the increase in MUFA present in the lipid fraction (Sturdivant et al., 1992; Cameron et al., 1994). Results of mRNA concentrations and enzyme activities were not significantly different between Angus and Wagyu beef cattle, and thus could not explain the higher MUFA concentration in samples from Wagyu cattle. Potential allelic frequency differences in a *TaqI* restriction fragment length polymorphism in Japanese beef cattle could be one explanation for the difference in MUFA concentration (Wilson et al., 1993). Little information regarding Δ^5-desaturase or Δ^6-desaturase activity, responsible for the desaturation steps in longer chain fatty acids (C20-C24) in pigs, has been reported.

Least squares means for carcass traits and fatty acid composition of intramuscular fat by *SCD* haplotype combination are presented in Table 7. Haplotypes with very few observations ($n < 20$) in the current population were removed from the analysis resulting in three major haplotype combinations. These three haplotype combinations were significantly different for their association with several fatty acids and ratios of fatty acids. Pigs homozygous for *SCD* haplotype CCGG had a greater concentration of C16:0, C18:0, and total SFA present in the total lipid fraction of intramuscular fat ($P < 0.0001$). Additionally, pigs homozygous for *SCD* haplotype TGAA had the greater concentrations of total MUFA ($P < 0.0001$), while also having greater calculated iodine value ($P = 0.0005$). The effect of the *SCD* haplotype combinations for LMA, BF10, and IMF did not differ ($P > 0.05$).

Other studies have shown that increased Δ^9-desaturase activity has resulted in increased C16:1 concentration between breeds of beef cattle (Sturdivant et al., 1992; Laborde et al., 2001). Zhang et al. (2007) conducted a multibreed study in pigs and utilized 3 different ratios for estimating Δ^9-desaturase activity. Similar indexes were calculated in the current study in order to estimate the activity of Δ^9-desaturase on overall fatty acid concentration. Greater index values mean greater desaturase activity (Table 7). The Δ^9-desaturase (C16) index, which is an indicator of the *SCD* influence on the conversion of C16:0 to C16:1, was different ($P < 0.0001$) between *SCD* haplotype combinations in this current study. However, the Δ^9-desaturase (C18) index, which is an indicator of the influence of *SCD* activity and conversion of C18:0 to C18:1, did not differ ($P > 0.05$).

Results from this study suggest that the *SCD* gene could be utilized in selection programs focusing on changing the level of saturation in IMF. This is beneficial from a human health standpoint where the intake of saturated fats has shown to be undesirable

because of the implications with atherosclerosis. Additionally, when emphasis is placed on saturation of fat as a measure of pork quality, *SCD* could be a beneficial marker to utilize to improve selection for fat quality since fatty acids are typically lowly heritable and difficult to measure. At the current time, information on expressed genes that are involved in fatty acid synthesis and metabolism is too limited to explain between-animal genetic variability in fatty acid composition. Further investigation into possible genotype differences for genes responsible for transport and synthesis of fatty acids is warranted.

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Table 1. Description of the genes and marker polymorphisms from Duroc pigs after six generations of selection for increased IMF.

Marker	Gene name/Gene	Chromosome/ Polymorphism	Primer set	Restriction enzyme	T_A[1]	PCR-RFLP Fragments (bp)[2]	DNA test description
SCD1	Stearyl-CoA desaturase (delta-9-desaturase) (SCD) NCBI#ss119336781	SSC14 5' UTR (-233) Y[C/T]	F: 5'-CGG GAG TGG AGT TGT GCG TA-3' R: 5'-CTT TGC ACG TTG GGT CG-3'	PFlf1	60	Allele 1: 686 Allele 2: 589/97	(Ren et al., 2004a)
SCD2	Stearyl-CoA desaturase (delta-9-desaturase) (SCD) NCBI#ss119336782	SSC14 Intron 1 (+70) R[A/G]	F: 5'-AAC TCC TCC CTG AAG TCT C-3' R: 5'-CCC AAA TTA CAA TCC ACA TTC C-3'	BsrI	59	Allele 1: 241 Allele 2: 122/119	(Ren et al., 2004a)
SCD3	Stearyl-CoA desaturase (delta-9-desaturase) (SCD) NCBI#ss119336783	SSC14 5' UTR (-1038) S[C/G]	F: 5'-CTG GGC TTG CCT AGT AGC TG-3' R: 5'-CCC TGG AAG AGG AAG AGG AC-3'	MspA1I	61	Allele 1: 454 Allele 2: 374/80	(Ren et al., 2004b)
SCD4	Stearyl-CoA desaturase (delta-9-desaturase) (SCD) NCBI#ss119336784	SSC14 3' UTR Exon 6 (+2001) R[A/G]	F: 5'-AGC TTC CTC TCC CAC AGT CA-3' R: 5'-GTC TTG GCC TCT TGT GCT TC-3'	BstUI	58	Allele 1: 426 Allele 2: 354/72	(Ren et al., 2004b)
FASN14	Fatty acid synthase (FASN) NCBI#ss119336785	SSC12[3] Intron 15 Y[C/T]	F: 5'-CGA GTA CAG CGT CAA CAA CC-3' R: 5'-GTG GGA ACA GAC CGT TGG-3'	AvaII	59	Allele 1:257,259 Allele 2: 257/196/63	
FASN24	Fatty acid synthase (FASN) NCBI#ss119336786	SSC12[3] Exon 24 Asn1426Asp R[A/G]	F: 5'-CTG GTG GCC CTG AAG AGG T-3' R: 5'-GTC CCG GTA GAC GTT CAT CA-3'	Hinf1	60	Allele 1: 534 Allele 2: 419/115	
ACACA	Acetyl-Coenzyme A carboxylase alpha (ACACA) NCBI#ss119336787	SSC12 3'UTR (+48) Y[C/T]	F: 5'-CCC TTC ATT GCC TTC TTA GG-3' R: 5'-CAT GAC CCA GCA CAT CTC AC-3'	TaqI	58	Allele 1: 213/156 Allele 2: 156/127/86	

[1] T_{ann} = Annealing temperature (ºC).
[2] Size of RFLP fragments produced from allele 1 and allele 2, heterozygote produces fragment lengths listed for both alleles 1 and 2.
[3] Assigned to pig chromosome 12 by physical and linkage mapping (Munoz et al., 2003).

Table 2. Number of observations for different markers from Duroc pigs selected for IMF quantity for six generations.

	Generation												
	3			4			5			6			
Gene	**11**	**12**	**22**	**11**	**12**	**22**	**11**	**12**	**22**	**11**	**12**	**22**	**Total**
SCD1-PFlf1													
Control	4	29	45	0	5	24	1	26	70	0	16	59	279
Select	8	31	22	2	8	11	5	29	32	7	31	30	216
Total	12	60	67	2	13	35	6	55	102	7	47	89	**495**
SCD2-BsrI													
Control	45	25	3	23	6	0	72	24	2	57	14	0	271
Select	22	29	6	12	10	1	31	33	5	32	25	5	211
Total	67	54	9	35	16	1	103	57	7	89	39	5	**482**
SCD3-MspA1I													
Control	5	27	43	0	6	22	3	24	71	0	15	56	272
Select	8	32	23	1	9	11	5	31	32	6	30	30	218
Total	13	59	66	1	15	33	8	55	103	6	45	86	**490**
SCD4-BstUI													
Control	3	31	46	0	5	24	2	23	72	0	16	60	282
Select	8	32	22	2	10	11	6	28	29	5	30	31	214
Total	11	63	68	2	15	35	8	51	101	5	46	91	**496**
FASN14-AvaII													
Control	4	17	52	0	8	19	2	34	59	1	29	43	268
Select	3	18	40	1	6	12	0	27	40	5	14	42	208
Total	7	35	92	1	14	31	2	61	99	6	43	85	**476**
FASN24-Hinf1													
Control	22	35	22	4	13	11	21	57	17	16	40	20	278
Select	6	31	26	4	12	4	22	23	17	17	31	11	204
Total	28	66	48	8	25	15	43	80	34	33	71	31	**482**
ACACA-TaqI													
Control	0	14	59	0	10	18	2	21	74	1	12	62	273
Select	0	9	51	0	3	17	0	4	63	0	0	61	208
Total	0	23	110	0	13	35	2	25	137	1	12	123	**481**

Table 3. Number of observations by genotype and allele frequency as a percentage of the total number of alleles for markers from Duroc pigs after six generations of selection for increased quantity of intramuscular fat.

	Genotype[1]			Allele frequency (%)		HWE[2]
Marker	**11**	**12**	**22**	**1**	**2**	***P-value*[3]**
SCD1-PFlf1-control line[4]	5	76	198	15.4	84.6	ns
SCD1-PFlf1-select line[5]	22	99	95	33.1	66.9	ns
SCD2-BsrI-control line[4]	197	69	5	85.4	14.6	ns
SCD2-BsrI-select line[5]	97	97	17	69.0	31.0	ns
SCD3-MspA1I-control line[4]	8	72	192	16.2	83.8	ns
SCD3-MspA1I-select line[5]	20	102	96	32.6	67.4	ns
SCD4-BstUI-control line[4]	5	75	202	15.1	84.9	ns
SCD4-BstUI-select line[5]	21	100	93	33.2	66.8	ns
FASN14-AvaII-control line[4]	7	88	173	19.0	81.0	ns
FASN14-AvaII-select line[5]	9	65	134	20.0	80.0	ns
FASN24-Hinf1-control line[4]	63	145	70	48.7	51.3	ns
FASN24-Hinf1-select line[5]	49	97	58	47.8	52.2	ns
ACACA-Taq1-control line[4]	3	57	213	11.5	88.5	ns
ACACA-Taq1-select line[5]	0	16	192	3.8	96.2	ns

[1]Genotypes are defined as follows:

SCD1-PFlf1 - allele 1 is allele T, allele 2 is allele C.
SCD2-BsrI - allele 1 is allele G, allele 2 is allele A.
SCD3-MspA1I - allele 1 is allele G, allele 2 is allele C.
SCD4-BstUI - allele 1 is allele A, allele 2 is allele C.
FASN14-AvaII - allele 1 is allele C, allele 2 is allele T.
FASN24-Hinf1 - allele 1 is allele A or amino acid Asn, allele 2 is allele G or amino acid Asp.
ACACA-Taq1 - allele 1 is allele T, allele 2 is allele C.

[2]HWE = Hardy-Weinberg equilibrium

[3]Significant *P*-values indicate a discrepancy from HWE; ns = not significant.

[4]Control line = randomly mated, unselected population

[5]Select line = selected for 6 generations for increased intramuscular fat based on a 2 trait- animal model that included carcass IMF and ultrasonically predicted IMF values.

Table 4. Effect of *ACC-Taq1* polymorphism on fatty acid composition of *longissimus dorsi* intramuscular fat from purebred Duroc pigs selected for IMF quantity for six generations.[1]

	Genotype			
Marker	**TT**	**TC**	**CC**	**P-Value**
ACC-Taq1				
IMF, (%)	3.03 ± 0.81	3.52 ± 0.22	3.90 ± 0.16	0.0922
C14:0	24.57 ± 1.64	25.42 ± 0.40	26.19 ± 0.24	0.0850
C16:0	4.08[a] ± 0.33	3.30[b] ± 0.08	3.43[ab] ± 0.05	0.0197
16:1*n*7	12.06 ± 0.95	13.22 ± 0.22	13.24 ± 0.13	0.4584
C18:0	42.41 ± 3.31	42.47 ± 0.77	42.51 ± 0.44	0.9984
C18:1*n*9	8.02 ± 1.08	8.22 ± 0.28	7.72 ± 0.19	0.1326
C18:2*n*6	38.83 ± 2.11	40.98 ± 0.51	41.71 ± 0.31	0.1398
SFA	50.73 ± 2.12	47.95 ± 0.50	48.32 ± 0.30	0.3581
MUFA	8.67 ± 1.25	10.02 ± 0.33	9.42 ± 0.22	0.0629

[1]Presented as g of fatty acid / 100 g of total lipid.

Table 5. Effect of *FASN* polymorphisms on fatty acid composition of *longissimus dorsi* intramuscular fat from purebred Duroc pigs selected for IMF quantity for six generations.[1]

	Genotype[2]			
Marker	**11**	**12**	**22**	**P-Value**
FASN14-AvaII				
IMF, (%)	3.94 ± 0.37	3.81 ± 0.18	3.74 ± 0.16	0.8109
C14:0	1.60 ± 0.08	1.44 ± 0.03	1.43 ± 0.03	0.0971
C16:0	27.30 ± 0.75	26.20 ± 0.31	25.84 ± 0.25	0.1153
16:1*n*7	3.49 ± 0.15	3.40 ± 0.06	3.43 ± 0.05	0.7820
C18:0	12.61 ± 0.14	13.19 ± 0.17	13.24 ± 0.14	0.3330
C18:1*n*9	41.79 ± 1.44	42.46 ± 0.56	42.53 ± 0.45	0.8815
C18:2*n*6	7.54 ± 0.49	7.82 ± 0.23	7.83 ± 0.20	0.8374
SFA	42.38 ± 0.95	41.68 ± 0.39	41.38 ± 0.32	0.4890
MUFA	48.06 ± 0.93	48.08 ± 0.37	48.39 ± 0.30	0.6850
PUFA	9.10 ± 0.58	9.55 ± 0.26	9.57 ± 0.23	0.7179
FASN24-HinfI				
IMF, (%)	3.71 ± 0.19	3.73 ± 0.15	3.70 ± 0.18	0.9743
C14:0	1.49 ± 0.03	1.43 ± 0.03	1.41 ± 0.03	0.0965
C16:0	26.45 ± 0.33	25.89 ± 0.25	25.91 ± 0.31	0.2144
16:1*n*7	3.44 ± 0.07	3.40 ± 0.05	3.46 ± 0.06	0.6708
C18:0	13.27 ± 0.18	13.17 ± 0.14	13.10 ± 0.17	0.7472
C18:1*n*9	41.36 ± 0.60	42.83 ± 0.45	42.26 ± 0.56	0.0723
C18:2*n*6	7.80 ± 0.24	7.86 ± 0.19	8.00 ± 0.23	0.7296
SFA	42.09 ± 0.41	41.34 ± 0.31	41.34 ± 0.38	0.1790
MUFA	47.64 ± 0.40	48.34 ± 0.30	48.14 ± 0.37	0.2425
PUFA	9.56 ± 0.28	9.61 ± 0.22	9.73 ± 0.27	0.8474

[1]Presented as g of fatty acid / 100 g of total lipid.

[2]Genotypes are defined as follows:

FASN14-AvaII - allele 1 is allele C, allele 2 is allele T.

FASN24-Hinf1 - allele 1 is allele A or amino acid Asn, allele 2 is allele G or amino acid Asp.

Table 6. Effect of *SCD* polymorphisms on fatty acid composition of *longissimus dorsi* intramuscular fat from purebred Duroc pigs selected for intramuscular fat quantity for six generations.[1]

	Genotype[2]			
Marker	**11**	**12**	**22**	**P-Value**
SCD1-PfLF1				
IMF, (%)	3.56 ± 0.03	3.93 ± 0.17	3.65 ± 0.16	0.0783
C16:0	25.62 ± 0.58	25.77 ± 0.28	26.28 ± 0.26	0.1577
C16:1	3.87^{a} ± 0.11	3.56^{b} ± 0.05	3.24^{c} ± 0.05	<0.0001
C18:0	11.87^{c} ± 0.31	12.81^{b} ± 0.15	13.70^{a} ± 0.13	<0.0001
C18:1	43.37^{ab} ± 1.09	42.97^{a} ± 0.51	41.84^{b} ± 0.46	0.0744
SFA	39.62^{b} ± 0.72	40.88^{b} ± 0.34	42.34^{a} ± 0.32	<0.0001
MUFA	50.68^{a} ± 0.69	48.94^{b} ± 0.32	47.23^{c} ± 0.29	<0.0001
C16:1 / C16:0	0.139^{a} ± 0.003	0.121^{b} ± 0.001	0.110^{c} ± 0.002	<0.0001
C18:1 / C18:0	3.77^{a} ± 0.11	3.40^{b} ± 0.05	3.12^{c} ± 0.05	<0.0001
SCD2-BsrI				
IMF, (%)	3.74 ± 0.17	3.91 ± 0.17	4.07 ± 0.33	0.3757
C16:0	26.34 ± 0.28	25.98 ± 0.29	25.42 ± 0.63	0.2310
C16:1	3.27^{c} ± 0.06	3.57^{b} ± 0.06	3.83^{a} ± 0.13	<0.0001
C18:0	13.72^{a} ± 0.15	12.82^{b} ± 0.15	11.77^{c} ± 0.34	<0.0001
C18:1	41.98 ± 0.50	42.88 ± 0.52	43.44 ± 1.20	0.1919
SFA	42.42^{a} ± 0.34	41.08^{b} ± 0.35	39.36^{c} ± 0.78	<0.0001
MUFA	47.32^{c} ± 0.32	48.96^{b} ± 0.33	51.02^{a} ± 0.76	<0.0001
C16:1 / C16:0	0.110^{c} ± 0.002	0.122^{b} ± 0.002	0.138^{a} ± 0.004	<0.0001
C18:1 / C18:0	3.13^{c} ± 0.05	3.40^{b} ± 0.05	3.81^{c} ± 0.12	<0.0001
SCD3-MspA1I				
IMF, (%)	3.91 ± 0.29	3.85 ± 0.16	3.65 ± 0.16	0.3053
C16:0	25.37 ± 0.57	25.81 ± 0.27	26.30 ± 0.26	0.1142
C16:1	3.78^{a} ± 0.11	3.54^{b} ± 0.05	3.23^{c} ± 0.05	<0.0001
C18:0	11.97^{c} ± 0.31	12.85^{b} ± 0.14	13.77^{a} ± 0.14	<0.0001
C18:1	43.48 ± 1.10	42.96 ± 0.50	41.91 ± 0.47	0.1093
SFA	39.54^{b} ± 0.71	40.94^{b} ± 0.33	42.42^{a} ± 0.32	<0.0001
MUFA	50.70^{a} ± 0.69	48.88^{b} ± 0.32	47.28^{c} ± 0.30	<0.0001
C16:1 / C16:0	0.135^{a} ± 0.003	0.121^{b} ± 0.002	0.110^{c} ± 0.002	<0.0001
C18:1 / C18:0	3.76^{a} ± 0.11	3.39^{b} ± 0.05	3.11^{c} ± 0.05	<0.0001
SCD4-BstUI				
IMF, (%)	3.79 ± 0.30	3.93 ± 0.16	3.62 ± 0.16	0.0764
C16:0	25.45 ± 0.59	25.82 ± 0.27	26.25 ± 0.26	0.1954
C16:1	3.84^{a} ± 0.11	3.59^{b} ± 0.05	3.22^{c} ± 0.05	<0.0001
C18:0	11.87^{c} ± 0.31	12.76^{b} ± 0.14	13.74^{a} ± 0.13	<0.0001
C18:1	43.53^{ab} ± 1.10	42.96^{a} ± 0.49	41.82^{b} ± 0.45	0.0653
SFA	39.50^{b} ± 0.72	40.87^{b} ± 0.33	42.33^{a} ± 0.31	<0.0001
MUFA	50.78^{a} ± 0.69	48.94^{b} ± 0.31	47.19^{c} ± 0.29	<0.0001
C16:1 / C16:0	0.137^{a} ± 0.003	0.122^{b} ± 0.002	0.110^{c} ± 0.002	<0.0001
C18:1 / C18:0	3.83^{a} ± 0.11	3.42^{b} ± 0.05	3.12^{c} ± 0.05	<0.0001

[1]Presented as g of fatty acid / 100 g of total lipid.

[2]Genotypes are defined as follows:

SCD1-PFlf1 - allele 1 is allele T, allele 2 is allele C.
SCD2-BsrI - allele 1 is allele G, allele 2 is allele A.
SCD3-MspA1I - allele 1 is allele G, allele 2 is allele C.
SCD4-BstUI - allele 1 is allele A, allele 2 is allele C.

Table 7. Least squares means (±SE) for carcass traits and fatty acid composition of intramuscular fat by *SCD* haplotype combinations from pigs in generations 3 through 6 of a selection project for intramuscular fat in Duroc swine.[1]

	SCD Haplotype Combinations			
Trait	**TGAA/TGAA**	**TGAA/CCGG**	**CCGG/CCGG**	**P-value**
LMA, (cm^2)	41.90 ± 1.09	40.94 ± 0.60	40.55 ± 0.59	0.3868
BF10, (cm)	22.51 ± 1.29	22.71 ± 0.70	22.23 ± 0.69	0.6796
IMF, (%)	4.03 ± 0.33	3.94 ± 0.18	3.67 ± 0.17	0.1335
C16:0	25.31 ± 0.62	25.92 ± 0.29	26.38 ± 0.27	0.1126
16:1*n*7	3.74 ± 0.12	3.58 ± 0.06	3.23 ± 0.06	<0.0001
C18:0	11.96 ± 0.34	12.79 ± 0.15	13.69 ± 0.15	<0.0001
C18:1*n*9	43.10 ± 1.18	42.88 ± 0.53	41.97 ± 0.50	0.2297
C18:2*n*6	7.72 ± 0.43	7.68 ± 0.22	7.79 ± 0.21	0.8614
SFA	39.43 ± 0.78	41.01 ± 0.36	42.43 ± 0.34	<0.0001
MUFA	50.67 ± 0.73	48.98 ± 0.33	47.32 ± 0.31	<0.0001
PUFA	9.39 ± 0.51	9.42 ± 0.26	9.52 ± 0.25	0.9027
PUFA:SFA[2]	0.24 ± 0.01	0.23 ± 0.01	0.23 ± 0.01	0.5111
Δ^9-desaturase (C16) index[3]	12.88 ± 0.42	12.15 ± 0.20	11.03 ± 0.19	<0.0001
Δ^9-desaturase (C18) index[4]	75.91 ± 1.94	76.69 ± 0.87	75.66 ± 0.82	0.5250
Δ^9-desaturase (C16+C18) index[5]	54.84 ± 1.28	54.37 ± 0.57	53.07 ± 0.54	0.0686
Iodine Value[6]	59.50 ± 0.84	58.08 ± 0.41	56.87 ± 0.39	0.0005
AI[7]	0.52 ± 0.04	0.55 ± 0.02	0.57 ± 0.02	0.2212

[1]Presented as g of fatty acid / 100 g of total lipid.
[2]The ratio of total PUFA to total SFA.
[3]Calculated as 100 × [C16:1n7/(C16:1n7 + C16:0)].
[4]Calculated as 100 × [C18:1n9/(C18:1n9 + C18:0)].
[5]Calculated as 100 × [(C16:1n7 + C18:1n9)/(C16:1n7 + C16:0 + C18:1n9 + C18:0)].
[6]Iodine Value =(C16:1*n*7*0.95) + ((C18:1*n*9+18:1*n*7)*0.86) + (C18:2*n*6*1.732) + ((C18:3*n*3+C18:3*n*6)*2.616) + (C20:1*0.785) + (C22:1*0.723).
[7]Atherogenic index, calculated as (C12:0 + 4 × C14:0 + C16:0)/(∑ MUFA + ∑ PUFA).

CHAPTER 8.

GENERAL SUMMARY

Due to increased demand for pork products with superior meat quality, increased emphasis has been placed on breeding programs that focus on traits that influence meat quality. At the present time, several studies have been conducted to increase marbling (IMF) in pork; however, very few have focused on the health implications that may be associated with selection for increased quantities of IMF. To understand the physiological changes that occur during the deposition of IMF, one must begin to understand the fatty acid composition of this fat depot.

Fatty acids play in integral role, not only in fat quality, but ultimately overall eating quality of pork. Because a minimal level of IMF is required to maintain a pleasurable eating experience, further investigation into fatty acid composition of IMF is no doubt warranted. Based on the findings in the current study, the fatty acid composition of pork is a correlated response to selection for IMF.

Pigs in the current study that were selected for increased IMF had a greater concentration of saturated fatty acids in both IMF and subcutaneous fat depots. This increase in saturated fatty acids can be explained by increased de novo synthesis of fat and fatty acids by pigs with the propensity to have more overall fat compositionally. This metabolic change is considered a correlated response to selection for IMF. Additionally, pigs in the control line had a more unsaturated fatty acid profile and compositionally were leaner. This increased concentration of unsaturated fatty acids suggests that the fatty acid profiles of pigs that are leaner compositionally are more influenced by the fat source in the diet than from de novo synthesis of fatty acids.

Traditionally, it has been believed that diet plays a major role in the fatty acid composition of non-ruminant animals and to a lesser extent, genetics. Findings from the current study suggest that the fatty acid composition of IMF from pork is moderate to highly heritable for total lipids. The greatest heritability estimates were for lauric acid (0.73), palmitoleic acid (0.40), stearic acid (0.36), linoleic acid (0.33) and α-linolenic acid (0.26). These heritability estimates suggest that with the genetic variation within these traits, it is possible to place selection pressure on them and expect a change phenotypically. Heritability estimates for PL and TAG were nearly zero, suggesting that there may not be enough variation in the population to detect a difference in the heritability estimates of these lipid fractions.

There were no significant genetic correlations between fatty acids and eating quality traits in the current study. However, linoleic acid was positively correlated with LMA (0.75) and negatively correlated with tenth-rib backfat (-0.62). This could be explained by the higher content of linoleic acid found in the genetically leaner pigs of the control line, for which the contribution of dietary fatty acids to total fat deposition is larger than that of de novo fatty acid synthesis. Understanding the changes in fatty acid composition as a correlated response to selection for IMF is more important than direct selection for specific fatty acids. This genetic association of production traits and linoleic acid is very complex, and it is unclear on how selection for this fatty acid may impact the overall breeding program.

This unique population of pigs allowed for identification of genes associated with IMF concentrations as well as fatty acid composition. The genes investigated in this study and identified to play a role in fatty acid synthesis and interconversion were stearoyl-CoA

desaturase (SCD), fatty acid synthase (FASN), and acetyl-CoA carboxylase (ACC). Although no significant associations were found among fatty acid composition, ACC genotypes, and FASN genotypes, SCD genotypes in this population were very informative. The SCD genotype was a significant source of variation for unsaturated fatty acid concentrations. The four genetic polymorphisms for the SCD gene were combined in a haplotype analysis that was significant for the level of unsaturation in IMF. Results from this study indicate that the use of SCD in a marker-assisted breeding program may be beneficial to change the fatty acid composition of IMF to a more unsaturated fatty acid profile. Because literature has shown that the consumption of increased amounts of saturated fatty acids can lead to health problems in humans, this may play a role in designing breeding programs to produce pork with a healthier fatty acid profile.

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