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Effect of selection for reduced residual feed intake on composition and quality of fresh pork

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Effect of selection for reduced residual feed intake on composition and quality of fresh pork

by

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GENERAL INTRODUCTION

The investigation of pork quality and the factors which influence it is important in order to minimize variation and optimize consumer satisfaction of the product. Pork quality traits are complex and influenced by both antemortem and postmortem factors (Huff-Lonergan et al., 2002). An animal's genetics, diet, environment, and handling pre-slaughter can alter the process of the conversion of muscle to meat. Altering the events which occur during the conversion of muscle to meat, such as the rate of temperature decline, rate and extent of pH decline, and postmortem proteolysis, are important in developing quality attributes such as pH, color, and water holding capacity. In addition, the manifestation of a given quality attribute is often dependent on the development of other quality traits. Clearly, there are significant links between muscle growth, muscle metabolism, and meat quality.

The pork industry has been primarily focused on improving the economic returns of livestock. In response to rising feed costs, it has become increasingly important to produce more efficient, faster growing pigs. Selection methods have been highly successful in completing this task. Selection that focused on performance traits such as increased growth efficiency produced pigs which had improved feed conversion, decreased backfat, and increased muscle (Cameron et al., 1999; Kuhlers et al., 2003). However, the dramatic increase in the occurrence of pale, soft, and exudative (PSE) pork, coupled with consumer's negative perception of fresh pork products, made it evident that these intense selection methods were altering fresh pork quality (Lonergan et al., 2001; Suzuki et al., 2005). In addition, the discovery of the halothane (Cheah and Cheah, 1976; Fujii et al., 1991) and the Rendement Napole (RN) (Milan et al., 2000; Monin and Sellier, 1985) genes furthered the

understanding of the negative impact selection can have on quality attributes such as pH and water holding capacity. Studies therefore began to focus more on the impacts of selection on fresh pork quality and composition.

A selection method that has gained more interest in swine is selection for reduced residual feed intake (RFI). RFI is a measure of feed efficiency and represents the fraction of total feed intake that cannot be explained by average requirements for maintenance and growth. Pigs selected for reduced RFI can show improved carcass composition through reduction in backfat, but the effects of selection on overall meat quality are less clear. Cai et. al (2008) found that selection for reduced RFI significantly decreased the amount of feed required for a given rate of growth and backfat, without affecting loin pH, color, and marbling. Alternatively, Gilbert et al. (2007) determined that selection for reduced RFI resulted in loins with lower pH values, lighter colored gluteus medius muscles, and overall lower meat quality. Given the lack of agreement of these studies, determining what the relationships are between RFI and quality traits will give insight into how intense selection for reduced RFI might affect pork quality.

The objective of this study was to determine the extent to which selection for reduced residual feed intake (RFI) affects pork composition and quality. In order to achieve this, differences in quality traits were compared between a line selected for reduced RFI and a randomly selected control line. In addition, residual correlations were determined between measured RFI and pork composition and quality. Knowing how selection for reduced RFI influences fresh pork quality will determine whether it is a practice that will be a benefit to the pork industry.

Thesis Organization

This thesis is organized into the alternate style format. The arrangement consists of a general introduction, review of literature, a publishable paper, and a concluding general summary. The paper was prepared according to the Journal of Animal Science Style and Form guide and includes an Abstract, Introduction, Materials and Methods, Results and Discussion, Implications and Literature Cited.

REVIEW OF LITERATURE

Introduction

Jul (1981) defined meat quality as the total degree of satisfaction that meat gives the consumer. Consumers ultimately drive the market, and they demand consistent, high quality pork products. Studying and evaluating pork quality is important in order to meet these consumer demands. In order to evaluate pork quality, several attributes need to be assessed. These attributes may include pH, water-holding capacity, color, biochemical properties, and sensory characteristics. These pork quality traits are complex, and it is impossible to attribute poor overall quality to a single quality trait. In addition, quality attributes are also influenced by external factors. These factors include both pre and post slaughter conditions. Postmortem events such as rate of chilling and rate and extent of pH decline are important variables to overall pork quality. The environment that the live animal is exposed to, its genetics, diet, and any stress it may encounter prior to slaughter also play a large role in the development of acceptable quality. Identification of the sources of variation in pork quality will provide insight into more efficient methods of producing higher quality pork.

Conversion of muscle to meat

Meat differs from muscle because of a series of biochemical and biophysical changes that are initiated in muscle upon the death of the animal (Lawrie, 2006). Mechanisms controlling pork quality development are often associated with altered postmortem muscle metabolism (Ryu and Kim, 2005). Understanding this conversion of muscle to meat is necessary in understanding meat quality traits. At death, animals are first rendered unconscious and then exsanguinated. The body responds to this loss of blood pressure by constricting the blood vessels to try and save blood volume. Eventually, the vast majority of

the blood is lost the body temperature starts to rise but muscle metabolism continues. Creatine phosphate within the muscle supplies the energy for metabolism. After the blood oxygen supply has been depleted, the muscle is unable to utilize aerobic metabolism to make ATP, and the tissue reverts to anaerobic metabolism to replace ATP reserves. Anaerobic metabolism is carried out through glycogenolysis and glycolysis. Glycogenolysis breaks down the stored glycogen in the muscle into glucose using glycogen phosphorylase, glycogen debranching enzyme, and phosphoglucomutase (Scheffler and Gerrard, 2007). Then, glucose is metabolized further into pyruvate through glycolysis. At this point, the tissue is no longer able to get rid of waste products due to the complete loss of the circulatory system. In addition, the removal of blood also eliminates the oxygen supply and forces muscles to operate anaerobically. Under anaerobic conditions such as those in postmortem muscle, lactate dehydrogenase converts pyruvate to lactate using NADH, with the ultimate product being lactic acid. Lactic acid that is produced from anaerobic glycolyis now builds up in the muscle and gradually drops the pH. Glycolysis continues until glycogen is completely depleted or until the pH of the muscle is acidic enough to inactivate the glycolytic enzymes (Price, 1987). The pH of the muscle now remains constant, and metabolism no longer occurs.

Throughout this process, the muscle becomes increasingly inextensible until rigor mortis sets in (Lawrie, 2006). There is a direct relationship between the disappearance of ATP and the onset of rigor (Bate-Smith and Bendall, 1949, 1947; Scheffler and Gerrard, 2007). As ATP is depleted, actin and myosin form crossbridges to form rigid actomyosin bonds, which results in the stiffening of muscle postmortem (Bate-Smith and Bendall, 1947). The formation of actomyosin bonds begins slowly during a phase known as the delay period,

then accelerates rapidly during the fast phase (Lawrie, 2006). Once all of the stored energy has disappeared, the muscle has fully entered rigor and the muscle becomes completely inextensible.

Technical Meat Quality

Effects of pH on meat quality

Measurements of pH are fundamental to the study of pork quality. The rate of metabolism is a major factor influencing the rate of postmortem pH decline. The rate and extent of postmortem pH decline has a profound effect on water holding capacity, color, and protein proteolysis. Genetics, pre-slaughter stress, and carcass handling postmortem all can affect the rate of metabolism. Also, the diet of an animal before slaughter will affect the extent of metabolism by altering the amount of stored glycogen (Rosenvold and Andersen, 2003). The amount of stored glycogen in the muscles will determine the extent of postmortem metabolism and pH decline (Rosenvold and Andersen, 2003). Postmortem handling of carcasses can also alter the conversion of muscle to meat through environmental conditions in the plant such as chilling rate. Altering the rate and extent of metabolism can dramatically affect meat quality. The effects of metabolism on quality attributes will all be discussed within this literature review.

Muscle pH in pork usually drops from 7.4 to 5.6-5.7 within 6-8 hours postmortem (Briskey and Wismer-Pedersen, 1961). The ultimate pH is reached at 24 hours postmortem. According to the National Pork Producers Council (1998), ideal pork quality is an ultimate pH between 5.6 and 5.9. If this ultimate pH is reached at a faster rate, major quality defects can occur. A more rapid postmortem pH decline can result in the occurrence of pale, soft, and exudative (PSE) pork. A faster pH decline is associated with a rapid rate of glycolysis,

which results in the pH falling to below 6.0 within the first hour postmortem (Scheffler and Gerrard, 2007). While the ultimate pH of muscles that exhibit a rapid pH decline is normal (5.3-5.7), the pH is more acidic while the temperature within the muscle is still high. The warmer temperatures within the muscle coupled with the acidic pH can cause denaturation of key sarcoplasmic and myofibrillar proteins (Scheffler and Gerrard, 2007). Denaturation of myofibrillar proteins such as myosin can affect the meat's ability to bind water. Also, a greater precipitation of soluble sarcoplasmic proteins such as, phosphorylase and creatine kinase, are responsible for paler colored pork (Joo et al., 1999). The phenomenon known as acid meat is another quality problem that is caused by the extent of postmortem pH decline. In this instance, pH declines at a normal rate, but an excess amount of glycogen in the tissue causes the pH to decline to a very low ultimate pH of 5.3-5.55 (Scheffler and Gerrard, 2007). An opposite effect of this is the incidence of dark, firm, and dry (DFD) meat. When the muscle contains low amounts of glycogen prior to death, the muscle is less able to form lactate postmortem and therefore results in a less acidic ultimate pH (Bendall and Swatland, 1988). Generally DFD pork is characterized as having a pH higher than 6.1 (Bendall and Swatland, 1988). The result is meat that has a very dark appearance, and a firm texture which is due to enhanced water holding capacity.

Importance and effects of water holding capacity

The ability of meat to retain water during application of external forces is defined as water holding capacity (Bertram et al., 2004). Water holding capacity is one of the most important attributes of fresh pork. Pork that has poor water holding capacity is unappealing to consumers, and is less tender, less flavorful and less juicy after cooking (Huff-Lonergan and Lonergan, 2005a). Water holding capacity is dependent on several factors. Postmortem

pH is the most important variables in determining water holding capacity. In fact, Bidner et al. (2004) concluded that 26% of the variation found in drip loss is explained by ultimate pH. The isoelectric point of major muscle proteins, such as myosin (pI=5.4), and the ultimate pH of normal muscle are very close (Huff-Lonergan and Lonergan, 2005a). Since these values are so similar, the proteins attain a net charge of zero and lose their ability to attract and bind water (Huff-Lonergan and Lonergan, 2005b). Within the myofibril, electrostatic forces help to maintain myofilament spacing. As proteins within the myofibril become reduced to their isoelectric points, these forces lessen, and can cause the filaments to collapse and pack together, creating less space for water within the myofibril. The water is pushed in to the extramyofibrillar space and then is more easily expelled from the muscle cell altogether (Huff-Lonergan and Lonergan, 2005b). Muscles with accelerated pH decline or a low ultimate pH have been shown to have low water holding capacity. With the case of PSE pork, the muscle reaches its ultimate pH very rapidly while the muscle is still warm. This can cause protein denaturation of key myofibrillar proteins such as myosin. Denaturation of these proteins causes shrinkage of the actomyosin cross bridges between the thick and thin filaments and results in less available space for water within the myofibril (Huff-Lonergan and Lonergan, 2005b).

Effects of Postmortem Protein Proteolysis

Postmortem protein degradation is an important event in the development of fresh pork quality. Like most other quality traits, proteolysis is related to other changes in the muscle. Degradation of certain muscle proteins is positively correlated with greater tenderness and increased water holding capacity. Endogenous proteases that make up the calpain system are responsible for regulating degradation of proteins in postmortem muscle.

Some of the enzymes that make up this system are μ-calpain, m-calpain, and their inhibitor, calpastatin. During the conversion of muscle to meat, the amount of free calcium available in muscle dramatically increases. After death, calcium begins to leak from the sarcoplasmic reticulum into the muscle cells. This elevation in free calcium activates both the calpains and calpastatin (Koohmaraie, 1991). At 24 h postmortem, the calpains have been working on degrading proteins such as the proteins within intermediate filaments and costameres. This early activation is important because both μ-calpain and m-calpain are susceptible to inhibition by calpastatin, and their activity is compromised by the low pH and changing ionic strength over time (Huff-Lonergan and Lonergan, 2005b). Calpain activity is optimum at neutral pH (Koohmaraie and Geesink, 2006). While both μ-calpain, m-calpain degrade the same specific set of proteins, it is possible that the activation of μ-calpain is the most important for enhancing fresh pork quality (Bee et al., 2007). One reason is μ-calpain is still active at pH of 6.0 while m-calpain is not (Maddock et al., 2005).

μ-Calpain is responsible for degrading several muscle proteins, most importantly desmin, vinculin, and talin (Huff-Lonergan et al., 1996). The degradation of these key proteins is related to enhanced water holding capacity. The intermediate filament protein desmin, ties the myofibril to the cell membrane and also to other myofibrils. Degradation of desmin is especially important in increased water holding capacity and tenderness in fresh pork. Under optimum conditions, desmin is degraded as early as 45 min postmortem (Melody et al., 2004). During the conversion of muscle to meat, as the muscle begins to set into rigor, the muscle cell will shrink and force the water held within the extracellular space to be pushed out. If desmin and other intermediate filaments are degraded within the first 24-48 h postmortem, more space exists within the cell to retain water. In fact, the amount of

desmin degradation at 1 day postmortem has explained up to 24% of variation in purge loss (Huff-Lonergan and Lonergan, 2005a). In addition to desmin, costamere proteins such as talin and vinculin are also linked to water holding capacity. The degradation of these proteins can be seen 24-48 h postmortem (Melody et al., 2004). In postmortem muscle, a low pH decreases the opportunity of activation of μ-calpain. The rate of activation of μ-calpain is linked to the extent of degradation of proteins such as desmin and talin (Bee et al., 2007).

While the degradation of proteins such as desmin and talin are beneficial to the overall quality of fresh pork, the degradation of some proteins can be detrimental. For example, postmortem degradation of integrin can actually decrease water holding capacity (Zhang et al., 2006). The degradation of integrin is negatively correlated to drip loss during postmortem storage (Zhang et al., 2006). The explanation for this could be because the degradation of integrin causes drip channels to form between the cell membrane and cell body that work to push water out and increase the amount of drip loss (Lawson, 2004; Zhang et al., 2006). Postmortem protein degradation is important for development of fresh pork quality. However, the specific proteins that are degraded by the calpain system are the most important variable. Simply targeting for increased proteolysis could result in some negative effects on quality attributes such as water holding capacity. Therefore, understanding the location and function of proteins which make up the muscle structure is vital in order to continue to improve fresh pork quality.

Sensory Quality

In the past, studies that investigated fresh pork quality, focused primarily on technical quality problems such as pH and water holding capacity and less on sensory quality. In

addition, studies focusing on selection for faster growth rates and improved efficiency that resulted in increased economic returns became a major focus of the pork industry. Intensified selection for improved growth and leanness has been associated with unfavorable changes in overall quality. Consumers began to have a negative perception of fresh pork products. It's because of this that studies focusing on improving the eating quality of pork have gotten more attention in the past decade. According to consumer studies, tenderness, juiciness, and flavor are the three main components of eating quality (Wood et al., 1998).

Sensory tenderness

It is generally known that a major problem facing the meat industry is inconsistency in tenderness. Variation in tenderness cannot be attributed to just one mechanism. Several mechanisms, which can be related to each other, play very important roles in determining fresh meat tenderness. According to Koohmaraie et al. (2002), meat tenderness can be considered as a function of three main factors; connective tissue, sarcomere length, and postmortem changes in the myofibrillar protein structure. Marbling also plays a role in tenderness and other sensory traits, which will be discussed in a later section. When looking at a particular muscle, probably the most important mechanism of these three is the changes that take place to the myofibrillar protein structure.

Variation in tenderness mainly occurs due to postmortem changes in the myofibrillar protein structure. The onset of rigor plays a major role in muscle structure changes. As muscle continues to metabolize after death, ATP is eventually used up and rigor bonds are formed. The development of rigor bonds (actomyosin crossbridges) are responsible for the increase in toughness that occurs during the first 24 h postmortem (Taylor et al., 1995).

The majority of changes that take place in the myofibrillar structure are the result of proteolysis of key proteins by the calpain system. Goll (1992) suggested that the calpains are responsible for 90% or more of the tenderization that occurs during postmortem storage. During postmortem storage, calpains degrade muscle proteins which results in fragmentation of the myofibrils and allows for meat to be more easily broken down in the mouth (Wood et al., 1998). The calpains are able to disrupt the muscle structure near the Z-disks and degrade important structural myofibrillar proteins without disrupting myosin and actin (Goll et al., 2003). Proteins that are susceptible to degradation are involved in inter-myofibril linkages (desmin and vinculin), intra-myofibril linkages (titin and nebulin), linking myofibrils to the sarcolemma by costameres (vinculin and dystrophin), and attaching muscle cells to the basal lamina (laminin and fibronectin) (Koohmaraie et al., 2002). Calpain degrades titin and nebulin where these proteins enter the Z-disk. Calpain also degrades desmin and filamin, which surround the myofibril at the Z-disk. The degradation of these proteins releases alpha-actinin, a principal Z-disk protein, from the myofibril (Goll et al., 2008). This results in thin filaments being released from the surface of the myofibril. The degradation of desmin also breaks the bonds held between myofibrils, and allows them to move apart from each other. Calpains also degrade troponin-T, tropomyosin, and titin. The degradation of these proteins, disrupt the attachment of the thick filament to the myofibril (Goll et al., 2008). Because the sarcomere has now been disrupted and not held as tightly together, the breakdown of these proteins by the calpain system will increase tenderness.

Sarcomere length is also a varying factor in tenderness. It can be affected by temperature during the onset of rigor mortis. Sarcomeres can be severely shortened if they are subjected to very low temperatures before rigor has set in. The muscles remain in the

contracted state, making them very tough. This problem is more prevalent in beef; however sarcomere length can affect the tenderness of pork as well. Sarcomere length explained 40% of the combined variation in tenderness within the longissimus dorsi, biceps femoris, semimembranosus, semitendinosus, and the triceps brachii of pork (Wheeler et al., 2000). The average sarcomere length for pork longissimus is 1.83 μm (Devol et al., 1988). It was determined that if sarcomere length is extended to at least 2.0μm, muscle will be tender no matter what the collagen content is (Wheeler et al., 2000). The effects of collagen content on tenderness will be discussed in a later section. While the effects of sarcomere length are more evident in beef, understanding and realizing the potential effects in pork will help to explain variation in tenderness.

Ultimate pH is also related to tenderness. Eikelenboom (1996) found that ultimate pH was strongly correlated (r=0.78) with tenderness and negatively correlated (r=-0.78) with shear force. Huff-Lonergan (2002) also had similar results with ultimate pH being positively correlated to sensory tenderness and negatively correlated to star probe. However, the findings of the influence of pH on tenderness are not consistent. Dransfield (1985) showed that shear force values were maximum at a pH of 6.0 when investigating a range of pH 5.3 to 7.1. This same study hypothesized that tenderness is greatest in meat with pH values greater than 6.0. A higher ultimate pH corresponds to greater water holding capacity. This relationship might explain the correlations observed between pH and tenderness. After cooking, if meat holds more water, and is therefore also juicier, than it could be perceived to be more tender.

Sensory juiciness

The feeling of moisture in the mouth during chewing is defined as juiciness (Aaslyng et al., 2003). Juiciness is associated with several quality attributes such as water holding capacity and lipid content. Water holding capacity affects meat's behavior during cooking and juiciness on mastication (Lawrie, 2006). As was discussed earlier, water holding capacity is dependent upon pH decline and degradation of myofibrillar proteins. Studies have determined that pork with higher ultimate pH values and lower percentages of moisture loss are the most juicy (Davis et al., 1975; Devol et al., 1988). If meat has a high water holding capacity, it has the capability to retain more water during cooking. Water loss during cooking is often most associated with unacceptable juiciness.

Flavor

Consumers have complained that modern lean pork is very bland compared to meat that was produced several years ago (Wood et al., 1998). Selection for lean growth could be to blame for this. As pigs have become leaner over the last few years, the amount of intramuscular lipid within meat has decreased. It is generally accepted that lipids provide flavor and aroma volatiles that impact meat flavor. Cooked meat flavors are also produced by reactions between carbohydrates and proteins, and from the breakdown products of these compounds (Wood et al., 1998). Selection practices that change the composition of muscle can therefore change the flavor of cooked meat. Flavor can also be influenced by changes in the postmortem conversion of muscle to meat. When muscle glycogen is depleted, off flavors can be intensified due to the low pH of the meat (Dransfield et al., 1985). When muscle glycogen has been utilized before death due to stress or other environmental factors,

the occurrence of dark cutting meat increases. Dransfield (1985) also suggested that the high

water content from dark pork causes a poor development of flavor.

Fresh meat color

      Fresh meat color is one of the most important traits that influence consumers

purchasing decisions. Despite how tender or juicy a product may be, if the color is

undesirable, the consumer will choose not to purchase the product. The color of meat

depends on the pigment myoglobin. There are three main forms of myoglobin which each

produce a distinct color. Deoxymyoglobin, the reduced form, is a purple color,

oxymyoglobin, the oxygenated form, is a bright red color, and metmyoglobin, is the

oxidized-iron pigment that is a brown color (Price, 1987). The quantity of myoglobin, the

type and the chemical state of the myoglobin molecule, and also the chemical and physical

condition of other meat components influence the appearance of the meat surface (Lawrie,

2006). The quantity of muscle myoglobin varies between species with pork having less

myoglobin than beef and lamb (Table 1). The quantity of myoglobin also varies between

muscles (Table 2).

Table 1. Myoglobin content within species

Species	Myoglobin Content
Beef	4-10 mg/g
Lamb	2.1-2.5 mg/g
Pork	0.6-0.9 mg/g

(Newcom et al., 2004; Price, 1987; Sanudo et al., 2000)

Table 2. Myoglobin content within different porcine muscles

Muscle	Myoglobin (% of wet weight)
Longissimus dorsi	0.044
Psoas major	0.082
Triceps	0.089

(Lawrie, 2006)

Active muscles used primarily for locomotion contain greater amounts of myoglobin than muscles used for posture and support. Pork ultimate pH plays a large role in the development of fresh pork color. The surface of normal pork which has been exposed to oxygen consists of oxymyoglobin and has a pinkish red color. In the case of DFD meat, which was previously discussed, the ultimate pH is higher, water is more tightly held within the muscle, and the color is much darker than normal pork. Since the water is so tightly held within the muscle fibers, a barrier preventing oxygen diffusion is formed and oxygen-scavenging enzymes are able to survive longer (King and Whyte, 2006). Deoxymyoglobin is then favored over oxymyoglobin and the meat appears to be a much darker deep red color. The opposite effect is seen in the case of PSE pork. In pork with very low pH, myoglobin can be denatured causing the color to be lighter. Also, when the rate of pH decline is very rapid or the ultimate pH is very low, myoglobin is oxidized to metmyoglobin, which has low color intensity (Lawrie, 2006). In addition to the low color intensity, the muscle structure is open, and light is scattered when it hits the meat surface, which gives PSE meat its pale color (Lawrie, 2006).

Composition and Growth

Muscle growth and composition are also important factors that influence meat quality. The histochemical and biochemical properties of muscle, such as fiber type composition, oxidative and glycolytic potential, and lipid content, all effect fresh meat quality (Karlsson et al., 1999). Muscle fibers are influenced by selection practices, genetics, and are also very adaptable to functional demands and hormonal signals during growth. This makes it difficult to pinpoint the exact cause of variation in quality that occurs between and within muscles and animals. This further reiterates the importance of understanding the relationship between meat quality and the physical and biochemical factors that influence it.

Fiber Type Composition

Skeletal muscle is made up of a heterogeneous mixture of muscle fibers that differ in their structural, contractile and metabolic properties (Bottinelli et al., 1994). Fiber types are most often classified by myosin heavy chain (MHC) isoforms. The different fiber types which exist based on the MHC isoforms found in adult mammalian skeletal muscle include: type I, type IIA, type IIB, and type IIX (Pette and Staron, 2000). Type I, or red muscle fibers, are small in diameter and are rich in myoglobin and mitochondria, whereas type II, or white muscle fibers, are larger in diameter and contain less myoglobin and mitochondria (Lawrie, 2006). Type I muscle fibers are more oxidative in nature, are able to work for long periods of time without rest, and have low glycogen content. In addition, type I fibers have greater vascularization and are able to maintain aerobic metabolism longer. Type II muscle fibers can be classified as either intermediate fibers known as type IIA or type IIX, or as fast glycolytic fibers known as type IIB. Type IIB fibers are fast twitch fibers, are more glycolytic in nature, and have a greater glycogen content than type IIA fibers. They utilize

anaerobic metabolism and operate in short, fast bursts with frequent periods of rest (Lawrie, 2006). The intermediate fiber, type IIA, is known as a fast oxidative-glycolytic fiber. In general, type IIA fibers are most closely related to type I fibers, while type IIX are more closely related to type IIB fibers.

The ratios of these different fiber types vary across muscles. Muscles that primarily function for posture or support generally have more oxidative fibers, whereas muscles that function for rapid and forceful contractions have more glycolytic fibers (Lawrie, 2006). At birth, the majority of fibers are oxidative, and as animals age, fibers differentiate into type-I and type-II fibers (Bee, 2004). The different MHC isoforms are responsible for the muscles' ATPase activity and can therefore affect the conversion of muscle to meat and ultimately meat quality. Without realizing it, as producers selected for leaner pigs, they were also selecting for the larger muscle fibers of type IIB (Klont et al., 1998). At slaughter, type IIB fibers have a higher capacity for the rapid production of lactate because of their significant glycogen content and glycolytic enzymatic activity. The fast metabolism of type IIB fibers could contribute to a fast pH decline and be related to the occurrence of PSE. Increasing the percentage of type IIB fibers in pork resulted in an increasing rate of muscle pH decline, drip loss, and lightness (Ryu and Kim, 2005). Chang (2003) concluded that oxidative and intermediate fiber types are more advantageous for meat quality due to their darker color characteristics, higher ultimate pH, increased water holding capacity, and better tenderness measurements. Fiber types are able to adapt to physical activity and growth, and so simply selecting for more oxidative fibers won't entirely work. Also, muscles are composed of a mixture of fiber types and no one muscle is composed of just one type of fiber. This is why

there is such variation in quality traits across different muscles. Understanding the cause of these variations will ultimately help to produce pork that is more consistent in meat quality.

Meat Composition

The overall composition of meat can be an important influence on meat quality. Meat is approximately made up of 75% water, 19% protein, 3.5% soluble, non-protein substances, and 2.5% fat (Lawrie, 2006). Changes in the composition of meat can greatly affect the nutritional value and also the overall quality. It has previously been discussed how proteins affect meat quality through their structure and postmortem degradation. The influence of connective tissue and fat content are important components of meat quality that have not been thoroughly discussed.

Connective tissue

Connective tissue is important in the framework of the muscle structure. Sheaths of connective tissue make up the epimysium, perimysium, and endomysium and surround the entire muscle, the muscle bundles, and the individual muscle fibers, respectively (Lawrie, 2006). These connective tissue sheaths are composed of the proteins collagen and elastin. The amount and nature of connective tissue can have adverse effects on meat quality, and has the greatest effects on tenderness and eating quality. Connective tissue is a contributing factor to toughness of meat. The percent of soluble collagen is significantly related to the contribution of connective tissue to toughness (Cross et al., 1973). In addition, Koohmaraie et al. (2002) explained that during periods of aging, connective tissue determines "background toughness" and accounts for only some of the variation in fresh meat tenderness because the amount of connective tissue does not change during postmortem storage. In pork, collagen content predicted 7% of the variation within the semimembranosus, and 4% of

the variation within the longissimus dorsi (Wheeler et al., 2000). Muscle from young animals has a greater concentration of connective tissue content than older animals, but the nature of the connective tissue is different. Young animals have muscles that contain few cross-links between the polypeptide chains of collagen (Lawrie, 2006). The cross-links that do exist can be broken down by heat during cooking. As animals age, thermally stable cross links form that are more difficult to break down during heating. In addition, connective sheaths thicken during the aging process. The thickening of the perimysium level contributes most to the increased shear force values seen in older animals (Fang et al., 1999).

Lipids

Meat is often identified as having a high fat content and an undesirable balance of fatty acids. However, through selection for increased lean growth, pork has become a very lean meat with a desirable balance between polyunsaturated and saturated fatty acids (Wood and Enser, 1997). The influence that fat has on pork quality is an ongoing debate. Several studies have concluded that pork which receives higher marbling scores (3-5) is juicier, more tender, and has better flavor than pork which receives low marbling scores (1-2) (Davis et al., 1975; Devol et al., 1988; Hodgson et al., 1991). However, other studies have shown that the relationship between marbling and eating quality of pork is variable (Lonergan et al., 2007; Rincker et al., 2008). These differing results could stem from the fact that there are several factors which influence palatability, as has been discussed previously. It has been proposed that a threshold of lipid content exists in which sensory traits are optimized and consumer acceptance is still high. Fernandez et al. (1999) concluded that the texture and taste of pork was improved at intramuscular fat levels up to 3.25% and consumers still recognized this level as acceptable.

Increased marbling could also have other positive effects on meat quality. Marbling is significantly correlated with firmness, drip loss, and percentage cook loss (Huff-Lonergan et al., 2002). According to Saffle (1959), muscles that have more marbling tend to have higher water holding capacities. The reasoning behind this is unknown. One hypothesis is that more intramuscular fat loosens the microstructure of the meat and allows more water to be held within the structure (Lawrie, 2006). An association between marbling and meat quality does exist, but more research needs to be done in order to fully understand the extent of this relationship.

How genetics affect meat quality

Pork quality is affected by several factors. One of the most important of these factors is the genetics of the animal. Genetics can cause differences between breeds or between animals within the same breed. For example, the Duroc breed is included as a terminal sire type because it is known to produce lean, high quality pork (Cameron et al., 1999). Contrasting this, selection studies focusing on increasing efficiency utilizing the Duroc breed have resulted in lines producing poor quality meat (Lonergan et al., 2001). Genetic differences can be caused by the combined effects of a large number of genes, known as polygenic effects (Rosenvold and Andersen, 2003). Meat quality can also be linked to large monogenic effects from major genes. Over the last several years, selection practices have been linked to detrimental quality and further investigation has linked these quality problems to specific genes. Understanding the relationship between genetics and fresh pork quality will provide the industry with more insight on how to provide consumers with a more consistent, high quality product.

Selection methods

Selection practices that improve the economic returns of livestock have been widely used for many years. Over the last decade, selection processes have dramatically changed the pork industry. Selection for increased growth, better feed efficiency, and carcass leanness has been the main focus of industry selection programs (Barbut et al., 2008). However, it became apparent that meat quality was being compromised in exchange for this increase in lean growth. As a result, the industry has seen a dramatic increase in the development of pale, soft, and exudative (PSE) pork. This has led to more studies focused on the influence of selection methods and genetics on pork quality.

Influence of selection for lean growth on meat quality

Within the last twenty years, the introduction of a grid-based marketing system has increased the percentage of pigs sold on a carcass merit base from 28% in 1988 to 83% in 2002 (Schwab et al., 2006). With leaner hogs receiving more economic returns, producers made great changes in selection practices to select for leaner hogs. Selection for increased lean growth is effective in increasing lean content and thereby improving lean cut yield (Cameron and Curran, 1995). Nevertheless, as selection for lean carcasses became more intense, consumers became increasingly dissatisfied with the decreased quality of the final product. The discovery of the halothane and RN genes helped to explain some of the quality defects associated with meat from animals that had been selected for increased lean growth. However, a study by Lonergan et al. (2001) showed that even normal Duroc pigs that were selected for increased lean growth, produced poorer quality pork compared to a randomly selected control line. Loin chops from pigs in the lean growth efficiency line had greater Warner-Bratzler Shear values, lower subjective firmness scores, and poorer water-holding

capacity (Lonergan et al., 2001). While differences between lines did not exist for ultimate pH, differences in the rate of pH decline did exist, which could very well explain the quality differences observed. These results demonstrate that selection for increased lean growth can significantly alter the response of muscle to the process of conversion of muscle to meat. Eliminating target genes such as the halothane and RN gene is effective; however there may be more genes that are also important. Therefore, more work needs to be done to determine exactly how selection alters fresh meat quality.

Influence of selection for increased efficiency traits on meat quality

With the ever-rising cost of feed, it has become increasingly important to more produce more efficient pigs that will be market ready in a shorter period of time. Selection methods for increased growth rates have focused on increasing daily gains and reducing daily feed intake. Not unlike selection for increased lean growth, selection for increased growth rates can negatively affect fresh meat quality. Selection for increased daily gain can result in meat with a softer texture, lower ultimate pH, and decreased tenderness (Suzuki et al., 2005). The same study, however, showed that drip loss actually decreased over generations (Suzuki et al., 2005). This finding contradicts the known relationship between water holding capacity and ultimate pH, but the higher intramuscular fat content could have influenced the increased water holding capacity. Another study by van Wijk (2005) also concluded that selection for increased daily gain resulted in paler colored pork with a lower ultimate pH, and decreased water holding capacity.

Another selection method for increased efficiency that recently received more attention is selection for reduced residual feed intake (RFI). RFI is the measure of feed efficiency that represents the fraction of total feed intake that is unexplained by average

requirements for maintenance and average requirements for growth and backfat. In an ongoing study at Iowa State, selection for reduced RFI has significantly decreased the amount of feed required for a given rate of growth and backfat (Cai et al., 2008). Few studies have focused on selection for residual feed intake in swine, and therefore little is known about its influence on pork quality. A divergent selection study for reduced RFI by Gilbert (2007) demonstrated that reduced RFI decreases pork quality through lower ultimate pH and paler colored meat. However, these conclusions were based on genetic correlations of the difference between a high RFI and low RFI line and a meat quality index. There is a need for further research to fully understand the affects that selection for reduced RFI can have on fresh pork quality.

Halothane gene

One of the major genes that has been identified as having severe detrimental effects on pork quality is the halothane gene. The halothane gene is also referred to as the porcine stress syndrome (PSS), which is a condition that is equivalent to malignant hyperthermia in humans (Scheffler and Gerrard, 2007). It is generally known that PSS is associated with the development of PSE pork and therefore it has been closely studied. In the 1960s certain breeds of swine and certain strains within breeds were noted as being more prone to PSE, while other breeds were virtually free of the defect (Rosenvold and Andersen, 2003). Poland China, Hampshire, Landrace, and Pietran breeds were identified as being much more susceptible to PSE. It was also noted that pigs that were more susceptible to PSE were commonly the heaviest muscled animals. Pigs which possess the mutant recessive halothane allele are generally leaner, faster growing, and have better feed conversion efficiencies, which explains how the gene became incorporated into breeds (Fisher et al., 2000). The

negative effects that this genotype has on pork quality, however, far outweigh the benefits (Table 3). Eikelenboom (1974) demonstrated that when some pigs were exposed to the anesthetic halothane they exhibited rapid metabolism, elevated body temperature, muscle rigidity, and sometimes even death. Since this discovery, exposure to halothane gas has been used to screen for stress susceptible pigs. The halothane gene has a normal dominant allele and a mutant recessive allele (Scheffler and Gerrard, 2007). A single point mutation within the skeletal muscle ryanodine receptor leads to an alteration in the amino acid sequence and is responsible for the formation of the mutant allele (Fujii et al., 1991). As a result of this mutation, the muscle's ability to adequately regulate the release of calcium is severely altered. The ryanodine receptor is responsible for releasing calcium that is stored in the sarcoplasmic reticulum into the sarcoplasm to initiate contraction (Scheffler and Gerrard, 2007). Pigs with the mutation in the ryanodine receptor gene (genotype nn) are extra sensitive to factors that cause the channels to open and release calcium at a rate that is equivalent to twice that of normal muscle (Cheah and Cheah, 1976). The increase in sarcoplasmic calcium activates and accelerates muscle metabolism, which in turn accelerates lactate production. Pigs with the mutation in the ryanodine receptor gene are susceptible to stress, especially pre-slaughter stress. The effects of accelerated muscle metabolism and stress prior to slaughter have been previously discussed. The rapid metabolism prior to slaughter depletes energy resources and accelerates lactic acid build up. This in turn accelerates the decline of pH postmortem. During this time of rapid pH decline, the temperature of the muscle remains at physiological levels. The combination of low pH and warmer muscle temperature results in PSE meat. As previously discussed, PSE meat is coupled with extremely poor water holding capacity, pale color, and poor sensory

characteristics. In addition, PSE meat has very poor functionality when used in further

processed products.

Table 3. Meat quality traits of halothane positive (nn) and halothane negative (NN) genotypes

Traits	Halothane genotype		
	NN	Nn	P-value
Glycogen content (mmol/kg)	232	136	<0.01
Lactate content (mmol/kg)	90	165	<0.001
Exsanguination pH	6.62	6.32	<0.001
Ultimate pH	5.54	5.49	>0.1
Drip Loss (%)	2.4	5.3	<0.001

(Essengustavsson et al., 1992)

RN gene

Another major gene that has been identified as being directly related to pork quality is

the RN gene. As the Hampshire breed began to be used more and more in crossbreeding

practices, it was noted that carcasses from Hampshires pigs and their crosses had a high

occurrence of meat that was pale and had poor water holding capacity.   However, the

occurrence of the mutation in the ryanodine receptor in Hampshires is essentially zero

(Monin and Sellier, 1985). Monin (1985) observed that muscle from Hampshire pigs had a

greater glycogen content and a lower ultimate pH than most other breeds. The term

glycolytic potential was consequently established which encompasses a muscle's

concentration of glycogen, glucose, glucose 6-phosphate, and lactate at the time of slaughter

(Monin and Sellier, 1985). By grouping these metabolites into a single term, the muscle's

capacity for extended postmortem glycolysis can be indicated. Hampshire pigs were

identified as having a very high glycogen potential. It was hypothesized that there was

another major gene that was causing this increased muscle glycogen storage. LeRoy et al. (1990) confirmed the existence of the major gene that was responsible for what became known as the Hampshire effect. The gene was named the Rendement Napole (RN) gene because of it effects on the Rendement Technology Napole measure of cured-cooked ham processing yield (Lebret et al., 1999). The RN gene has different alleles. The dominant RN$^-$ allele is responsible for increasing the glycogen content of muscle which causes the occurrence of acid meat (Estrade et al., 1993). Muscles in pigs with the RN$^-$ gene contain about 70% more glycogen content than other animals (Monin and Sellier, 1985). As was discussed earlier, glycolytic potential is very important for meat quality. At death, muscle will continue to metabolize until stored glycogen is used up. In the case of the RN gene, meat has a normal rate of pH decline. It is due to the large amount of glycogen that the muscle continues to generate lactic acid for much longer than normal muscle. This causes the pH of the meat to continue to fall to much lower values than normal. The low pH causes the pale colored meat that is sometimes observed and inferior water holding capacity.

For several years, it was not understood what caused this genetic mutation. Pigs which have the RN$^-$ allele had leaner carcasses. Like the halothane gene, it is expected that the occurrence of the gene increased because of increased selection for growth and carcass traits. More recently, Milan et al. (2000) have linked the RN gene to the R200Q substitution in the PRKAG3 gene (protein kinase, AMP-activated, gamma-3-subunit). The PRKAG3 gene encodes a muscle specific isoform of the regulatory γ subunit of adenosine monophosphate activated protein kinase (AMPK) (Milan et al., 2000). This mutation causes defects in glucose metabolism, which explains the large amount of stored glycogen in Hampshire pigs possessing the mutation in the RN gene.

In addition to the R200Q substitution, three other PRKAG3 allelic variations have been identified. These allelic variations include the T30N, G525, and I199V substitutions (Ciobanu et al., 2001). Ciobanu (2001) also found that the I199V substitution showed the most significant effects for glycogen and lactate content, glycolytic measures, and also meat quality traits. While investigating the I199V substitution, the 199I allele was actually associated with improved meat quality had lower glycogen, lactate, and glycolytic potential, with higher pH and color values (Ciobanu et al., 2001). The 199I allele is always with the 200R variant, while the 199V is found with both the 200R and the 200Q variant (Ciobanu et al., 2001). The 199V-200R haplotype is associated with higher glycogen content that leads to a lower postmortem ham and loin pH (Table 4). It is believed that the substitution at codon 199 has an effect on glucose metabolism, which increases the muscle glycogen content. In addition, the 199V-200Q haplotype confers the RN$^-$ phenotype, has a greater effect on glycogen content, and is dominant over the other haplotypes (Ciobanu et al., 2001). This led to the conclusion that the RN$^-$ genotype is actually caused through a combined effect of the 199V-200Q haplotype instead of only the R200Q substitution (Ciobanu et al., 2001). Understanding what gene is responsible and where the mutation is located will ultimately lead to being able to select against the gene and avoiding the quality problems it causes.

Table 4. PRKAG3 Genotypes at the I199V substitution site and meat quality traits least square means

Traits	I199V		
	II	**IV**	**VV**
Average glycogen	8.01a	9.10b	9.37b
Average lactate	84.83a	86.83a	90.54b
Average glycolytic potential	100.84a	105.02b	109.28c
24 h Loin pH	5.86c	5.80b	5.77a
24 h Loin Hunter	46.56a	47.07ab	47.70b

Traits with different subscripts are significantly different (P<0.05).

(Ciobanu et al., 2001)

MC4R

As science advances, the discovery of specific genes which influence performance traits and meat quality will dramatically affect selection practices. The halothane and RN genes became more prevalent simply due to the selection of pigs which exhibited exceptional growth and efficiency. The ability that geneticists now have to test for certain genes have enabled negative genotypes to be eliminated from populations. Specific genes can now be targeted for selection to improve performance traits. While this knowledge is valuable from a selection aspect, it is still important to investigate how these genes could potentially alter meat quality.

One gene that has also received attention for its role in growth is the melanocortin-4 receptor (MC4R) gene. The MC4R gene has been shown to play a role in feeding behavior and body weight in humans and mice. Studies focusing on obesity have linked MC4R mutations to dominantly inherited obesity in humans (Vaisse et al., 1998; Yeo et al., 1998).

Based on this information, Kim (2000) investigated the MC4R gene as a possible candidate

gene that could used as a genetic marker for important growth and performance traits in pigs.

The porcine MC4R has an Asp298Asn missense mutation that is significantly associated with

fatness, daily gain, and feed intake (Kim et al., 2000). The receptor for MC4R is expressed

in the region of the brain that regulates appetite and the receptor works to regulate feed intake

and energy balance (Van den Maagdenberg et al., 2007). Asp298 is the wild-type allele and

is required for signaling, while Asn298, the mutated allele, works to decrease the signaling of

MC4R which results in effect on average daily growth, feed intake, lean growth, and carcass

fat (Kim et al., 2000; Van den Maagdenberg et al., 2007). The Asp298 allele (GG genotype)

is associated with less backfat, slower growth, and less feed intake, while the Asn298 allele

(AA genotype) is associated with more backfat, faster growing, and greater feed intake (Kim

et al., 2000). The finding by Kim (2000) demonstrates the effectiveness of using the MC4R

gene to explain variation in fat, growth, and feed intake but very few studies have focused on

the effects MC4R has on meat quality. One study that focused on the affects of MC4R on

meat quality determined that post mortem pH, drip loss, and color were not affected by

MC4R, but the loins from the faster growing, fatter genotype pigs had more tender meat,

which could be attributed to the greater amount of intramuscular fat (Table 5) (Van den

Maagdenberg et al., 2007). These data suggest that selection using this marker could

significantly improve performance and not affect meat quality.

Table 5. Meat quality of MC4R genotypes

Trait	MC4R genotype		
	GG	**GA**	**AA**
Fat thickness (mm)	13.46[b]	13.91[a]	14.58[a]
IMF (%)	1.06	1.13	1.17
pH (24 h)	5.53	5.53	5.53
L*	53.53	53.87	53.84
Drip Loss (mg)	64.19	64.81	61.47
Shear Force (kg)	35.71[b]	34.85[a]	34.78[ab]

Traits with different superscripts are significantly different ($P<0.05$)

(Van den Maagdenberg et al., 2007)

Summary

This literature review addressed the topics of meat quality and the influences of meat composition and animal genetics. It is clear that pork quality is affected by many factors and that there is still more to be learned. Understanding the relationships between quality attributes and the factors that influence them is important in order to be able to control variation. With rising costs of feed, it has become increasingly important to produce more efficient pigs. New selection practices and the discovery of new genes related to increased growth and efficiency could introduce problems with overall quality. Investigating the effects on meat quality is vital in order to ensure these practices can be applied without causing detrimental effects on fresh pork quality

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EFFECT OF SELECTION FOR REDUCED RESIDUAL FEED INTAKE ON COMPOSITION AND QUALITY OF FRESH PORK

A paper to be submitted to Journal of Animal Science

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Abstract

Selection for improved growth efficiency has the potential to alter meat composition and meat quality. The objective of this study was to determine the extent to which selection for reduced residual feed intake (RFI) affects pork composition and quality. In order to achieve this, pork composition and meat quality traits were compared between a line selected for reduced RFI over five generations (select) and a randomly selected control line (control). Residual correlations between RFI and pork composition and quality traits were also evaluated. In the evaluated group of Yorkshire gilts (select = 80, control = 89), gilts from the select line had 0.052 kg lower RFI per day. Gilts were harvested at ~114 kg, and the boneless loins were collected at 24 h postmortem. Back fat and loin eye depth were collected off the midline at the last rib region using the Fat-O-Meater. Quality attributes were measured at 2 d postmortem. Drip loss and water holding capacity were measured in duplicate. Hunter L, a, and b values were measured in triplicate on two chops. Quality scores were assigned by a 3 member panel. Intramuscular lipid and moisture content were determined. Desmin degradation was measured at 2 and 7 d postmortem. Purge, cook loss, sensory traits, and star probe texture were measured at 7-10 d postmortem on cooked chops.

The model included fixed effects of line, slaughter date, MC4R genotype, barn group, line by slaughter date, genotype by line interactions, a covariate for off-test weight, and sire, pen, and litter fitted as random effects. Compared to the control line, carcasses from the select line tended to have less (P=0.09) backfat (15.2 ± 0.9 vs. 17.3 ±0.7 mm), greater (P<0.05) loin depth, and greater (P<0.05) calculated percentage of fat free lean (56.5% vs. 54.8%). Select line chops tended to have greater water holding capacity (P=0.07). Loin chops from the select line had less (P<0.01) intramuscular lipid content (1.14% vs. 1.67%) and lower subjective marbling scores (P<0.05) than control chops. Loin chops from the select line carcasses also had a greater (P<0.01) percentage of moisture than the control chops. There were no differences between lines for hot carcass weight, pH, drip loss, Hunter L and a values, subjective color, firmness, and wetness scores, amount of intact desmin at 2 or 7 d, any sensory traits, or star probe values. Within lines, RFI was positively correlated (r=0.24, P<0.01) with tenderness and negatively correlated (r= -0.26, P<0.01) with star probe. The residual correlation of intact desmin at 2 d postmortem with RFI was not significant, but RFI was correlated (r= -0.18, P=0.02) with the amount of intact desmin at 7 d postmortem. RFI was also correlated (r= -0.15, P<0.05) with chewiness and tended to be correlated (r=0.15, P=0.06) with the percentage of intramuscular lipid. Selection for reduced RFI has the potential to improve carcass composition with few effects on selected measures of meat quality such as pH and water holding capacity. Reduced RFI could negatively affect eating quality due to decreased lipid content and postmortem protein degradation. This work was funded by the National Pork Board.

Keywords: Carcass composition, pork quality, sensory, residual feed intake

Introduction

With the rising cost of feed, it has become increasingly important to emphasize production efficiency. Selection for increased lean growth efficiency may, however, have the unintended consequence of altering composition and quality of fresh pork (Lonergan et al., 2001). A measure of efficiency that has gained interest in swine is residual feed intake (RFI). RFI represents the fraction of total feed intake that cannot be explained by average requirements for maintenance, growth, and backfat. Cai et al. (2008) showed that selection for reduced RFI in a selection experiment in Yorkshire pigs significantly decreased the amount of feed required for a given rate of growth and backfat without affecting loin pH, color, and marbling. In a similar selection experiment, Gilbert et al. (2007), however, found that selection for reduced RFI resulted in loins with lower pH values, lighter colored gluteus medius muscles, and overall lower meat quality. Thus, the effects of selection on overall meat quality are of some dispute. Determining relationships between RFI and quality traits will give insight into how intense selection for reduced RFI might affect pork quality. Knowing how selection for reduced RFI influences fresh pork quality will determine its usefulness to the pork industry. Therefore, the objective of this study of this study was to determine the extent to which selection for reduced residual feed intake (RFI) affects pork composition and quality.

Materials and Methods

Animals

For this study, the gilts from the fifth generation of pigs in the Iowa State residual feed intake study were utilized (Cai et al., 2008). The melanocortin-4 receptor genotype was sequenced in these animals using the method described by Kim et al. (2000). This

population consists of two lines: a select line (n=80) which was selected for reduced residual feed intake and a randomly selected control line (n=89). Pigs were harvested at 114 kg in three slaughter groups over an 8 week period (July-September). Pigs were rendered unconscious through carbon dioxide stunning. Hot carcass weight and Fat-O-Meat'er fat depth (SFK Technology A/S, Herlev, Denmark) and loin muscle depth were collected off the midline of the posterior part of the loin. Carcass composition data were used to calculate percent lean using the following equation: 58.86 - (fat depth (mm) x 0.61) + (loin depth (mm) x 0.12). The boneless loins were removed from the carcass at 24 h postmortem, vacuum packaged, and shipped on ice to the ISU Meat Laboratory.

Loin separation

Boneless loins were separated into 2.54 cm chops starting at the blade end cutting toward the sirloin end at 48 h postmortem at the ISU Meat Laboratory. Approximately 12.54 cm were first removed from the blade end and discarded and then as chops were cut from the loins, they were assigned to quality traits in the same order for each loin in order to eliminate any variation caused by location effects (Figure 1). Loin chops that were to be used for sensory and star probe analysis were vacuum packaged and held for 7 to 10 d postmortem at 4˚C. Samples to be used for biochemical analysis were vacuum packaged and held at 4˚C until they were frozen at either 2 d or 7 d postmortem.

pH measurements

Boneless loins were separated into 2.54 cm chops and the ultimate pH of one chop from each loin was measured at 48 hours postmortem. A Hanna 9025 pH/ORP meter (Hanna Instruments, Woonsocket, RI) with a penetration probe was used to take the measurements.

The pH meter was calibrated to the temperature of the chops using two buffers (4.2 and 7.10) and monitored every five chops.

Meat quality traits

Loin quality scores were evaluated at 48 hours postmortem by a trained panel (n=3). Subjective scores assigned consisted of color, firmness, wetness, and marbling. Firmness and wetness were evaluated on three point scales (1=soft and wet, 3=firm and dry). Color scores (1 = pale, 6 = dark) and marbling scores (1 = no marbling, 10 = high marbling) were assigned based on National Pork Board standards. Loin chops were also evaluated for intramuscular lipid (AOAC, Hexane extraction) and moisture content (AOAC, 1993). Hunter L, a, and b values were determined on two chops in triplicate at 1 d postmortem using a calibrated Hunter Labscan colorimeter. The six color values were used to calculate the average value for each color measurement for each chop. A calibrated Hunter Labscan colorimeter (Hunter Association Laboratories, Inc.; Reston, VA) utilized a C10 illuminant to obtain color scores using a 10° observer, and 1.27 cm aperture.

Water Holding Capacity

Loin chops were evaluated for water holding capacity using different methods. Drip loss was determined at 3 d postmortem on two chops per animal. The chops were trimmed of external fat, weighed, and stored in a sealed plastic bag at 4°C. After 24 h of storage, the liquid lost was removed from each bag, and the chops were blotted of excess moisture and re-weighed. Drip loss was recorded as a percentage of the original weight of the chop by the following equation: [(initial weight – final weight)/initial weight] x 100. Water holding capacity was also assessed using a centrifugation method at 3 d postmortem. Duplicate 10g minced samples taken from one chop per loin were placed into centrifuge tubes and spun for

10 minutes at 40,000 x g. After centrifugation, the liquid was removed and the sample meat re-weighed. Water lost was also recorded as a percentage of the original weight of the chop using the same equation as used for drip loss. The amount of purge loss and cook loss was also determined on chops used for sensory analysis. Purge loss was recorded as a percentage of water lost during the aging time. The purge present in the vacuum packaged bag was weighed as well as the chop. The percentage of purge loss was calculated using the following equation: [weight of purge / (purge + chop)] x 100. Prior to cooking the chops to be used for sensory analysis, the raw chop was weighed. After cooking to an internal temperature of 70°C, the cooked chop was then weighed and cook loss was recorded as a percentage of the raw weight of the chop using the following equation: [(raw weight-cooked weight) / raw weight] x 100.

Star probe

Chops aged 7-10 d postmortem were cooked on clamshell grills to an internal temperature of 70°C. The temperature of each chop was monitored individually using thermocouples (Omega Engineering, Inc. Stamford, CT). The chops were then cooled to room temperature prior to analysis. Star probe is an instrumental measure of texture which calculates the amount of force necessary to compress the sample to 80% of its height. A circular, five-pointed star probe that measures 9 mm in diameter with 6 mm between each point was attached to an Instron Universal Testing Machine (Model 5566, Instron, Norwood, MA). Each chop was punctured at a crosshead speed of 3.3 mm/second. Each chop was punctured three times and the average of the three values determined the overall value (Lonergan, 2002).

Sensory Panels

A trained sensory panel (n=4) evaluated sensory traits on loin chops aged 7-10 d postmortem. The chops were cooked on clamshell grills to an internal temperature of 70˚C. Four cubes were cut from the center of the chop and each panelist evaluated the samples for juiciness, tenderness, chewiness, pork flavor, and off-flavor. An unanchored, fifteen unit scale (Figure 2) was used with a term that represented a low degree of juiciness, tenderness, chewiness, pork flavor, and off-flavor on the left and a term that represented a high degree on the right side of the scale.

Whole-muscle sample preparation for gel electrophoresis

Samples to be used for SDS-PAGE analysis and Western blotting of desmin degradation were prepared from muscle taken at either 2 d or 7 d postmortem. Frozen loin chops were minced, frozen with liquid nitrogen, and then ground to a powder in order to ensure a uniform sample and remove any variation caused by location effects within the chop. Whole-muscle protein extraction and sample preparation for gel electrophoresis was then conducted using 0.4 g of powdered sample (buffer consisting of 10mM sodium phosphate and 2% [vol/vol] SDS; pH 7.0) according to the method described by Lonergan et al. (2001). Protein concentration was determined using premixed DC assay reagents (Bio-Rad Laboratories, Hercules, CA). SDS-PAGE gel sample preparation was conducted according to (Lonergan et al., 2001). Gel samples (4 µg/ml protein) were frozen and stored at -20˚C until used for analysis. The relative protein concentration of the gel samples was checked using fiften percent polyacrylamide separating gels (acrylamide:bisacrylamide = 100:1 [wt/wt], 0.1% [wt/vol] SDS, 0.05% [vol/vol] TEMED, 0.05% [wt/vol] APS, 0.5 M Tris·HCl, pH 8.8) and five percent polyacrylamide stacking gels (acrylamide:bisacrylamide =

100:1 [wt/wt], 0.1% [wt/vol] SDS, 0.125% [vol/vol] TEMED, 0.075% [wt/vol] APS, and

0.125 M Tris·HCl, pH 6.8). 40 µg of protein per lane were loaded onto the gel and they were

run using the same conditions described below.

Gel electrophoresis and Western blotting

Ten percent polyacrylamide separating gels (acrylamide:bisacrylamide = 100:1

[wt/wt], 0.1% [wt/vol] SDS, 0.05% [vol/vol] TEMED, 0.05% [wt/vol] APS, 0.5 M Tris·HCl,

pH 8.8) were used for the determination of the relative amount of desmin at 2 d and 7 d of

storage. Five percent polyacrylamide gels (acrylamide:bisacrylamide = 100:1 [wt/wt], 0.1%

[wt/vol] SDS, 0.125% [vol/vol] TEMED, 0.075% [wt/vol] APS, and 0.125 M Tris·HCl, pH

6.8) were used as the stacking gels.

Gels (10 cm wide x 8 cm tall x 1.5 mm thick) for the analysis of desmin were run on

Hoefer Mighty Small II SE 250/SE 260 electrophoresis units (Hoefer Scientific Instruments,

San Francisco, CA). The gels were loaded with 40 µg of total protein per lane, and the same

reference was loaded onto each gel. A constant voltage of 120V was applied to the gels for

approximately 2.5 h.

Gels were transferred to polyvinylidene (PVDF) membranes (Millipore Corporation,

Bedford, MA) using a Hoefer TE22 Mighty Small transfer tank electrophoresis unit (Hoefer

Scientific Instruments) by a constant voltage of 90V for 1.5 h. The transfer buffer used

consisted of 25 mM Tris, 192 mM glycine, 2 mM EDTA and 15% [vol/vol] methanol. A

circulating water bath (Ecoline RE 106; Laura Brinkman, Westbury, NY) maintained the

temperature of the transfer buffer between 4°C and 8°C.

Western blotting and chemiluminescent detection were done according to Melody et

al. (2004). After transfer, membranes were incubated at room temperature for 1 h in a PBS-

Tween blocking solution (80mM disodium hydrogen orthophosphate, 20 mM sodium dihydrogen orthophosphate, 100 mM sodium chloride, 0.1% [vol/vol] polyoxyethylene sorbitan monolaurate [Tween 20]) and 5% (wt/vol) nonfat dry milk. The blots were then incubated overnight at 4˚C with a primary polyclonal rabbit anti-desmin antibody (No. V2022; Biomeda, Foster City, CA) which was diluted 1:20,000 with PBS-Tween. The next day, the blots were rinsed three times (10 min per rinse) in PBS-Tween at room temperature. The blots were then incubated for 1 h in a secondary goat anti-rabbit-HRP IgG antibody (81-6120; Zymeda Laboratories, San Francisco, CA) which was diluted 1:10,000 in PBS-Tween. In order to remove any unbound secondary antibody, the blots were again rinsed three times (10 min per rinse) with PBS-Tween. Protein bands labeled for desmin degradation were detected using a chemiluminescent detection kit (ECL Plus) as described by the supplier (ECL, Amersham Pharmacia Biotech). The density of the immunoreactive desmin bands were quantified by densitrometry using ChemiImager 5500 (Alpha Innotech, San Leandro, CA) and Alpha Ease FC (v. 2.03; Alpha Innotech). The ratio of the amount of intact desmin was calculated as the intensity of the immunoreactive intact desmin band of each sample over the intensity of the immunoreactive desmin band of a reference sample which was loaded onto each gel (Melody et al., 2004).

Statistical analyses

Data was analyzed using Mixed procedure in SAS (Version 9.1; SAS Inst., Inc., Cary, NC). The model included fixed effects of line, slaughter date, MC4R genotype, barn group, line by slaughter date, genotype by line interactions, covariate of off-test weight, and sire, pen, and litter fitted as random effects. For sensory traits, an additional fixed effect of sensory analysis day was added. Least square means for line, slaughter date, and MC4R

genotype were computed. A mixed model using a single trait binary analysis with a normal distribution for RFI was used to analyze color, firmness, wetness, and marbling scores. To enable the GLIMMIX procedure to converge, firmness and wetness scores were merged into class <1 or >1, color scores were merged into class <3 or >3, and marbling scores were merged into class <1 or >1. Classes were determined based on the number of scores in each class.

Results & Discussion

Suboptimal growth efficiency of swine limits the productive competitiveness of the U.S. meat industry. The swine industry has made efficient production a high priority and, as a result, has realized rapid improvements in the lean growth of market pigs (Cameron and Curran, 1995). Unfortunately, improvement in efficiency of swine production through intensive genetic selection has been shown to be accompanied by a decrease in the functional and sensory characteristics of fresh pork (Cameron et al., 1999; Lonergan et al., 2001). What is not known is just how present day industry selection practices that focus heavily upon improvement in growth efficiency will affect future pork quality and value. The current experiment aims to fill this gap in our understanding of the complex relationships among muscle growth, muscle metabolism, and meat quality.

Selection for reduced RFI affected carcass composition (Table 1). Select line pigs, which were selected for reduced RFI, had significantly greater loin eye depths and percentage lean, and also tended to have less backfat than the control line pigs. The decrease in backfat is consistent with previous studies (Cai et al., 2008; Gilbert et al., 2007).

Few studies have focused on RFI in swine production (Cai et al., 2008; Hoque et al., 2009; Johnson et al., 1999; Nguyen et al., 2005) and even fewer have investigated the

influence of selection for reduced RFI on meat quality. Gilbert et al. (2007) reported that the longissimus dorsi of low RFI pigs had lower ultimate pH values and also lighter colored meat in the gluteus medius. However, Cai et al. (2008) showed no differences between lines for ultimate pH or color of the loin. In the current study, loin muscle ultimate pH also did not differ across lines (Table 2), consistent with results obtained by Cai et al. (2008) in generation four of this selection experiment. Loin chop drip loss, purge loss, or cook loss also did not differ between lines. Loin chops from the select line did tend to lose less water than chops from the control line during the centrifugation test (Table 2). Hunter L and a values were not different between select and control line chops. However, Hunter b values tended (P=0.08) to be lower for chops from select line carcasses, indicating a lesser degree of yellowness, or discoloration (Table 2). Marbling can affect objective color measurements. Chops from select line carcasses contained a lower amount of marbling than chops from control line carcasses. This greater amount of marbling could explain the tendency for higher b values in chops from control line carcasses. Loin chops from the select lines contained significantly less lipid and more moisture than loin chops from the control line (Table 2).

Selection for reduced RFI did not result in differences in loin chop color, firmness, or wetness scores, but did result in lower marbling scores compared to loin chops from control line pigs. In addition, chops from select line carcasses has less intramuscular lipid and select line carcasses tended to have less backfat than control line carcasses (Table 1). The differences between lines for lipid content are consistent with what is known about RFI. Cai et al. (2008) and Gilbert (2007) found significant genetic correlations between selection for

RFI and backfat. Moreover, selection for reduced RFI in pigs results in decreased backfat and less overall lipid content (Cai et al., 2008; Hoque et al., 2009; Johnson et al., 1999).

There were no significant differences between lines for the sensory traits of juiciness, tenderness, chewiness, pork flavor, and off flavor. There were also no differences between lines for star probe values (Table 3).

There were no differences observed between select and control lines chops in the amount of intact desmin at day 2 postmortem. In addition, no differences were observed between lines for the amount of intact desmin at day 7 postmortem (Table 4, Figure 3).

The MC4R gene was investigated in this study for its known relationship to feed intake and lean growth (Kim et al., 2000). Significant differences were observed for backfat and also percentage of lean. The 11 and 12 genotype had significantly less backfat than the 22 genotype, while the 11 genotype also tended to have less backfat than the 12 genotype (Table 5). These differences are to be expected based on previous findings (Guimaraes et al., 2006; Van den Maagdenberg et al., 2007). Since the calculation of percentage of lean is dependent on backfat, this explains the differences observed between MC4R genotypes in which the 11 genotype had the greatest percentage of lean while the 22 genotype had the lowest. The relationships between MC4R and meat quality traits observed in this study agree with previous studies that have concluded that the effects of MC4R on meat quality are of little importance (Ovilo et al., 2006; Van den Maagdenberg et al., 2007).

Few line differences were observed for meat quality traits however, selection for reduced RFI could alter meat quality across lines. Table 6 lists the maximum, minimum, and average individual RFI values within both lines. The overall average RFI value for the select line pigs was lower than the control line pigs (0.065 kg/d vs. 0.108 kg/d). However, the

highest RFI value within the select line was 0.36 kg/d which was only 0.079 kg/d less than the highest value within the control line. In addition, the difference between the lowest RFI values for both lines were only 0.037. The variation that exists across lines in RFI values suggests that line differences alone may not fully reveal the effect of selection on quality attributes. Calculating correlations between quality traits and the actual individual RFI values could provide further insight as to whether or not RFI affects meat quality.

In this study, correlations using residual values were calculated in order to reduce variation and only investigate correlations between traits of interest. Residual correlations are not affected by variation accounted for by fixed and random effects that are included in the model. The residual correlations between carcass composition traits and RFI were not significant (Table 7).

Percent lean was negatively correlated with backfat depth and positively correlated with loin eye depth. Percent lean is calculated using an equation which includes both backfat and loin eye depth, and therefore these correlations are to be expected. Hot carcass weight was significantly correlated with loin eye depth and tended to be negatively correlated (P=0.077) with star probe values. Backfat depth was negatively correlated with percent moisture, and tended to be negatively correlated (P=0.08) with star probe. Loin eye depth was positively correlated with percent moisture and negatively correlated with pH and percent lipid. In addition, loin eye depth was also negatively correlated with the sensory attributes of tenderness and pork flavor and tended to be positively correlated with chewiness (P=0.056) and off flavor (P=0.054) . The correlations with loin eye depth indicate that a greater amount of muscle results in more moisture, a lower ultimate pH, less intramuscular lipid, and greater sensory tenderness scores. Carcass composition has a major influence on

overall meat quality. Selection practices primarily alter carcass composition which has in turn adversely affected meat quality (Cameron et al., 1999; Lonergan et al., 2001). The results from the current study suggest that leaner, heavier muscled carcasses produce meat that has a lower ultimate pH, is less tender, and has a less characteristic pork flavor. In this instance, carcasses from the select line were leaner and heavier muscled. Continued intense selection for reduced RFI will likely continue to alter carcass composition and ultimately negatively affect fresh pork quality.

Residual correlations for quality and sensory attributes are in Tables 8 and 9. The residual correlations explain relationships between quality traits that are important to note. The measures of water holding capacity, including drip loss, centrifugation loss, purge loss, and cook loss were all negatively correlated with pH. Chops with a lower ultimate pH lose a greater percentage of water and thereby could be expected to have a lower water holding capacity. This influence of pH on water holding capacity in pork has been widely documented (Bendall and Swatland, 1988; Huff-Lonergan and Lonergan, 2005a; Melody et al., 2004; Offer and Trinick, 1983).

Star probe is an instrumental measure of texture which is not as commonly used as Warner-Bratzler shear force. Star Probe was found to be strongly negatively correlated to sensory tenderness scores, indicating good agreement between the two measures. Greater star probe values correspond to lower tenderness scores from sensory panelists.

The amounts of intact desmin at 2 and 7 d postmortem were both positively correlated with drip loss. During the conversion of muscle to meat, as the muscle begins to set into rigor, the muscle cell will shrink and force the water held within the extracellular space to be pushed out. If desmin is degraded, more space exists within the cell to retain water, and this

results in a greater water holding capacity of the product (Melody et al., 2004; Zhang et al., 2006). The amount of intact desmin at 2 and 7 d postmortem was also related to star probe and to the sensory traits of tenderness and chewiness.

Postmortem proteolysis by the calpain system disrupts the muscle structure and causes tenderization during aging. The degradation of desmin allows thin filaments to be released from the surface of the myofibril, and also breaks the bonds held between myofibrils, allowing them to move apart from each other (Goll et al., 2008). A greater amount of intact desmin will therefore correspond to lower sensory tenderness scores, higher chewiness scores, and also higher star probe values (Table 9).

RFI was positively correlated with tenderness and negatively correlated with star probe (Table 9). Reduced RFI was also related to greater chewiness scores. Pigs with low RFI values, therefore, produced meat that was tougher, chewier, and had greater star probe values. RFI was also negatively correlated with purge loss. A lower RFI value relates to a greater amount of water loss as purge during aging. While direct line comparisons did not reveal these differences among sensory traits, the residual correlations suggest that selecting for reduced RFI can potentially cause detrimental effects on sensory quality and also water holding capacity. These relationships can possibly be explained by the negative correlation between RFI and the amount of intact desmin at 7 d postmortem.   A greater amount of intact desmin suggests that the loins from lower RFI carcasses experienced decreased protein degradation during aging. Postmortem degradation of the protein desmin improves tenderness and also water holding capacity (Melody et al., 2004). The relationships observed in this study between intact desmin at 2 and 7 d postmortem with tenderness, chewiness, star probe, and measures of water holding capacity further support this conclusion. If the loins

from pigs with low RFI values experienced less protein degradation during the aging period, it is very likely that the chops lost more water and was tougher than chops from pigs with higher RFI values. These results are consistent with recent observations in a different trial where muscle from select line pigs had higher calpasatin activity than muscle from control line pigs (personal communication from Nick Boddicker). Calpastatin inhibits the calpain system from degrading proteins. A greater amount of calpastatin activity would help explain the greater amount of intact desmin in lower RFI pigs.

In addition to desmin degradation, RFI also tended to be positively correlated with marbling and with the percentage of intramuscular lipid, indicating that selection for reduced RFI will result in lower intramuscular fat content. The lower amount of intramuscular lipid could be another explanation for the lower tenderness, and greater chewiness and higher star probe values. The relationship between lipid content and pork quality is of some dispute. Several studies have shown that pork with more marbling is juicier, more tender, and has better flavor (Davis et al., 1975; Devol et al., 1988; Hodgson et al., 1991; Huff-Lonergan et al., 2002) while other studies have found that no consistent relationships exist between lipid content and tenderness (Blanchard et al., 2000; Rincker et al., 2008). In the current study, percent lipid tended to be positively correlated with pork flavor and also tended to be negatively correlated with star probe values. While these are not strong correlations, they help to support the hypothesis that the lower lipid content in low RFI pigs may help explain the noted correlations in sensory scores to RFI.

It has been proposed that there is a threshold of intramuscular lipid content above which sensory traits are optimized (Fernandez et al., 1999). Consumer sensory scores were highest for pork that had an intramuscular fat content of 2.5% to 3.5%, above this percentage

there were no real differences and there was a negative association with the observable fat (Fernandez et al., 1999). All the pigs utilized in this study have low percentages of overall lipid. Chops from select line carcasses contained only 1.14% intramuscular fat and chops from the control line had only 1.67% intramuscular fat. The earlier suggested threshold was not met in this study and could explain why direct line differences for sensory traits were not found. In conclusion, lower RFI was associated with less proteolysis and less overall lipid content. The effects of both of these factors combined conspire to decrease sensory quality.

Implications

Selection for reduced RFI has the potential to be a viable selection method that could reduce feed intake, improve carcass composition, and have few detrimental effects on selected measure of pork quality. However, low RFI pigs may present some quality challenges. Correlations observed between RFI, sensory traits, and star probe values indicated that the response to selection for lower RFI is predicted to decrease fresh pork sensory traits. The explanation for this response to lower RFI is a related reduction in intramuscular lipid and a decrease in postmortem proteolysis of key myofibrillar proteins such as desmin.

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Table 1. Effect of selection for reduced RFI on carcass composition

Trait	Select (n=80)	Control (n=89)	P-value
Hot carcass weight, kg	87.0	85.9	0.15
SE	1.3	1.1	
Loin eye depth, mm	57.5	54.7	<0.05
SE	1.1	0.8	
Backfat depth, mm	15.2	17.3	0.09
SE	0.9	0.7	
Percentage lean	56.48	54.85	<0.05
SE	0.60	0.45	

Upper row = LS Means
Bottom row = SE (pooled standard error)

Table 2. Effects of selection for reduced RFI on technical quality traits.

Trait	Select (n=80)	Control (n=89)	P-value
pH, 48 h	5.55	5.54	0.71
SE	0.02	0.01	
Drip Loss, %[1]	1.41	1.39	0.91
SE	0.13	0.12	
Centrifugation Loss, %[2]	6.28	6.95	0.07
SE	0.30	0.25	
Purge Loss, %[3]	1.99	2.01	0.34
SE	0.17	0.14	
Cook Loss, %[4]	17.19	16.98	0.31
SE	0.48	0.41	
Hunter L	45.83	45.97	0.74
SE	0.30	0.26	
Hunter a	2.37	2.67	0.13
SE	0.15	0.12	
Hunter b	7.41	7.67	0.08
SE	0.11	0.08	
% Lipid[5]	1.14	1.67	<0.01
SE	0.09	0.08	
% Moisture[5]	74.35	73.78	<0.01
SE	0.07	0.06	

Upper row = LS Means

Bottom row = SE (pooled standard error)

[1]Weight lost during 24 h gravitational test.

[2]Weight lost after being centrifuged at 40,000 x g for 10 minutes.

[3]Weight lost after 7-10 days of aging.

[4]Weight lost during cooking to 70ºC.

[5]Percent loin composition

Table 3. Sensory and star probe values for select and control lines

Trait	Select (n=80)	Control (n=89)	P-value
Juiciness[1]	9.87	9.93	0.51
SE	0.21	0.18	
Tenderness[1]	10.09	9.99	0.15
SE	0.22	0.19	
Chewiness[1]	2.97	3.09	0.21
SE	0.16	0.14	
Pork Flavor[1]	2.49	2.66	0.91
SE	0.14	0.12	
Off Flavor[1]	2.19	2.02	0.99
SE	0.24	0.20	
Star Probe, kg[2]	5.19	5.29	0.54
SE	0.11	0.09	

Upper row = LS Means
Bottom row = SE (pooled standard error)
[1]Sensory score based on an unanchored, fifteen unit scale with a greater value representing a greater degree of juiciness, tenderness, chewiness, pork flavor, or off flavor.
[3]Force necessary to compress a pork loin to 20% of its initial height.

Table 4. Biochemical measurements of pork quality for select and control lines

Trait	Select (n=80)	Control (n=89)	P-value
Intact Desmin D 2[1]	1.01	0.97	0.42
SE	0.04	0.03	
Intact Desmin D 7[1]	0.79	0.78	0.66
SE	0.03	0.03	

Upper row = LS Means

Bottom row = SE (pooled standard error)

[1]Ratios were calculated as the intensity of the intact desmin band in each sample over the intensity of the intact desmin band in the internal designated densitometry sample

Table 5. Effects of MC4R genotype on pork composition, quality, sensory, and biochemical traits

Trait	11 (n=40)	12 (n=75)	22 (n=54)	P-value
Hot Carcass Weight, kg	190.2	190.8	190.7	0.95
SE	1.6	1.1	1.3	
Loin eye depth, mm	56.2	55.9	56.1	0.92
SE	1.0	0.8	0.9	
Backfat depth, mm	15.1[b]	16.1[a]	17.7[b]	<0.01
SE	0.7	0.6	0.7	
Percentage Lean	56.37[a]	55.75[a]	54.86[b]	<0.01
SE	0.47	0.40	0.43	
pH, 48 h	5.53	5.55	5.56	0.31
SE	0.02	0.01	0.01	
Drip Loss, %[1]	1.60	1.28	1.31	0.14
SE	0.16	0.12	0.13	
Centrifugation Loss, %[2]	6.89	6.37	6.59	0.46
SE	0.37	0.27	0.30	
Purge Loss, %[3]	1.83	1.99	2.18	0.38
SE	0.20	0.15	0.17	
Cook Loss, %[4]	17.17	17.32	16.76	0.56
SE	0.54	0.42	0.47	
Hunter L	46.03	46.11	45.56	0.35
SE	0.37	0.26	0.30	
Hunter a	2.46	2.48	2.62	0.62
SE	0.16	0.12	0.14	
Hunter b	7.47	7.57	7.58	0.71
SE	0.12	0.09	0.10	
% Lipid[5]	1.30	1.48	1.43	0.16
SE	0.09	0.07	0.08	
% Moisture[5]	74.17	74.06	73.97	0.16
SE	0.08	0.06	0.07	
Juiciness[6]	9.84	9.67	10.19	0.16
SE	0.26	0.19	0.21	
Tenderness[6]	9.87	9.86	10.39	0.15
SE	0.27	0.20	0.22	
Chewiness[6]	3.07	3.11	2.91	0.64
SE	0.20	0.15	0.16	
Pork Flavor[6]	2.56	2.71	2.45	0.17
SE	0.15	0.12	0.13	
Off Flavor[6]	2.28	2.06	1.98	0.68
SE	0.29	0.22	0.24	
Star Probe, kg[7]	5.25	5.28	5.2	0.83
SE	0.13	0.09	0.11	
Intact Desmin Day 2[8]	0.98	1.02	0.96	0.27
SE	0.04	0.03	0.03	
Intact Desmin Day 7[8]	0.81	0.79	0.77	0.78
SE	0.04	0.03	0.03	

Upper row = LS Means

Bottom row = SE (pooled standard error)

[a-b]Means within a row lacking a common superscript differ (P<0.05)

Table 5. (continued)

[1]Weight lost during 24 h gravitational test.

[2]Weight lost after being centrifuged at 40,000 x g for 10 minutes.

[3]Weight lost after 7-10 days of aging.

[4]Weight lost during cooking to 70ºC.

[5]Percent loin composition

[6]Sensory score based on an unanchored, fifteen unit scale with a greater value representing a greater degree of juiciness, tenderness, chewiness, pork flavor, or off flavor.

[7]Force necessary to compress a pork loin to 20% of its initial height.

[8]Ratios were calculated as the intensity of the intact desmin band in each sample over the intensity of the intact desmin band in the internal designated densitometry sample

Table 6. Low, average, and high RFI values (kg of feed/d) within each line

	Select	Control
Low RFI	-0.207	-0.237
Average RFI	0.065^a	0.108^b
High RFI	0.360	0.439

Upper row = LS Means
Bottom row = SE (pooled standard error)
[1]Values with unlike subscripts within rows are significantly different (P<0.05)

Table 7. Residual correlations between RFI values, carcass composition, quality, sensory, and biochemical traits

	HCW[1]	BF	LE	% Lean
BF[1]	0.185 0.016			
LE[1]	**0.422** <.0001	-0.072 0.351		
% Lean	-0.055 0.477	**-0.960** <.0001	**0.350** <.0001	
RFI[1]	-0.018 0.818	-0.022 0.782	-0.083 0.282	-0.002 0.980
pH	-0.098 0.205	0.032 0.678	**-0.168** 0.029	-0.078 0.315
Drip Loss, %	0.084 0.278	-0.062 0.421	0.039 0.610	0.069 0.371
Centrifugation Loss, %	0.054 0.487	0.026 0.737	0.079 0.310	-0.002 0.977
Hunter L	0.108 0.162	-0.036 0.638	0.083 0.284	0.057 0.458
Hunter a	-0.001 0.989	-0.020 0.800	-0.001 0.988	0.019 0.810
Hunter b	0.032 0.683	-0.055 0.474	0.047 0.548	0.065 0.400
Purge Loss, %	-0.065 0.402	**-0.131** 0.090	0.034 0.662	**0.132** 0.086
Cook Loss, %	**-0.128** 0.098	-0.104 0.179	-0.054 0.487	0.082 0.289
Juiciness	0.005 0.945	0.002 0.984	0.034 0.662	0.008 0.917
Tenderness	-0.084 0.278	0.030 0.701	**-0.177** 0.022	-0.077 0.317
Chewiness	0.080 0.298	-0.023 0.767	**0.147** 0.056	0.063 0.417
Pork Flavor	-0.041 0.595	0.079 0.309	**-0.193** 0.012	**-0.128** 0.098
Off-Flavor	0.007 0.932	-0.107 0.167	**0.148** 0.054	**0.142** 0.066
Star Probe, kg	**-0.137** 0.077	**-0.135** 0.080	0.014 0.852	**0.131** 0.090
% Lipid	0.065 0.400	**0.125** 0.107	**-0.139** 0.071	**-0.156** 0.043
% Moisture	-0.055 0.475	**-0.288** 0.000	**0.143** 0.063	**0.310** <.0001
Desmin Day 2	-0.006 0.935	**-0.136** 0.077	0.062 0.425	**0.145** 0.060
Desmin Day 7	-0.018 0.814	-0.076 0.328	0.019 0.805	0.076 0.325

Upper row = residual correlations, bold value indicate significant correlations or trends.

Bottom row = P-values

[1]HCW = hot carcass weight, BF = backfat depth, LE = loin eye depth, RFI = residual feed intake

Table 7. (continued)

[2]Weight lost during 24 h gravitational test.

[3]Weight lost after being centrifuged at 40,000 x g for 10 minutes.

[4]Weight lost after 7-10 days of aging.

[5]Weight lost during cooking to 70ºC.

[6]Percent loin composition

[7]Sensory score based on an unanchored, fifteen unit scale with a greater value representing a greater degree of juiciness, tenderness, chewiness, pork flavor, or off flavor.

[8]Force necessary to compress a pork loin to 20% of its initial height.

[9]Ratios were calculated as the intensity of the intact desmin band in each sample over the intensity of the intact desmin band in the internal designated densitometry sample

Table 8. Binary analysis of correlations of RFI with subjective quality data

Trait	Correlation	P-value
Firmness	-0.04	0.31
Wetness[1]	-	-
Marbling	0.1	0.13
Color	0.03	0.36

[1] Wetness data unable to converge

Table 9. Residual correlations between RFI values, quality, sensory, and biochemical traits

	RFI	pH	Drip Loss	Cent. Loss	Hunter L	Hunter a	Hunter b	Purge Loss	Cook Loss	Juic	Tend	Chew	Pork Flavor	Off Flavor	Star Probe	% Lipid	% Moist	Desmin D2
pH	-0.011																	
	0.886																	
Drip Loss, %¹	-0.038	**-0.375**																
	0.621	<.0001																
Cent. Loss, %²	-0.003	**-0.523**	**0.437**															
	0.971	<.0001	<.0001															
Hunter L	-0.023	**-0.430**	**0.298**	**0.281**														
	0.767	<.0001	<.0001	0.000														
Hunter a	**0.123**	**-0.179**	0.033	0.103	**-0.381**													
	0.112	0.020	0.670	0.183	<.0001													
Hunter b	0.107	**-0.456**	**0.293**	**0.319**	**0.374**	**0.547**												
	0.167	<.0001	0.000	<.0001	<.0001	<.0001												
Purge Loss, %³	**-0.156**	**-0.371**	**0.335**	**0.309**	**0.157**	**0.250**	**0.371**											
	0.044	<.0001	<.0001	<.0001	0.042	0.001	<.0001											
Cook Loss, %⁴	**-0.123**	**-0.340**	**0.225**	**0.221**	**0.293**	0.005	**0.173**	**0.274**										
	0.111	<.0001	0.003	0.004	0.000	0.944	0.025	0.000										
Juiciness⁵	0.111	**0.136**	-0.073	-0.032	-0.104	-0.017	-0.025	**-0.208**	**-0.537**									
	0.152	0.077	0.348	0.680	0.180	0.823	0.745	0.007	<.0001									
Tenderness⁵	**0.243**	**0.227**	**-0.145**	-0.103	**-0.186**	0.005	-0.041	**-0.275**	**-0.416**	**0.645**								
	0.002	0.003	0.061	0.184	0.015	0.953	0.592	0.000	<.0001	<.0001								
Chewiness⁵	**-0.151**	**-0.216**	**0.144**	**0.155**	**0.200**	0.043	0.089	**0.239**	**0.409**	**-0.576**	**-0.870**							
	0.052	0.005	0.062	0.044	0.009	0.579	0.249	0.002	<.0001	<.0001	<.0001							
Pork Flavor⁵	-0.108	**0.213**	**-0.216**	**-0.180**	**-0.138**	-0.040	-0.071	**-0.216**	**-0.151**	0.050	**0.235**	**-0.203**						
	0.162	0.005	0.005	0.020	0.074	0.609	0.361	0.005	0.050	0.515	0.002	0.008						
Off Flavor⁵	-0.015	**-0.372**	**0.291**	**0.305**	**0.144**	**0.161**	**0.246**	**0.269**	0.129	-0.060	**-0.169**	**0.189**	**-0.596**					
	0.843	<.0001	0.000	<.0001	0.062	0.037	0.001	0.000	0.095	0.437	0.028	0.014	<.0001					
Star Probe, kg⁶	**-0.265**	-0.064	**0.204**	0.035	0.105	-0.036	0.037	**0.333**	**0.430**	**-0.464**	**-0.571**	**0.583**	-0.109	0.108				
	0.001	0.406	0.008	0.655	0.174	0.639	0.632	<.0001	<.0001	<.0001	<.0001	<.0001	0.157	0.162				
% Lipid⁷	**0.148**	**-0.150**	0.019	0.138	**0.217**	**0.243**	**0.468**	0.117	0.023	0.060	0.100	-0.037	**0.130**	-0.049	**-0.121**			
	0.056	0.052	0.810	0.074	0.005	0.002	<.0001	0.130	0.764	0.437	0.198	0.636	0.092	0.528	0.118			
% Moist⁷	0.029	-0.028	0.067	-0.082	0.001	-0.096	**-0.178**	0.057	**0.122**	-0.008	-0.039	0.050	-0.009	-0.046	**0.155**	**-0.619**		
	0.706	0.715	0.385	0.291	0.991	0.213	0.021	0.464	0.113	0.913	0.618	0.519	0.905	0.551	0.045	<.0001		
Desmin Day 2⁸	-0.101	-0.102	**0.204**	0.094	0.055	-0.115	-0.029	0.105	**0.183**	-0.127	**-0.230**	**0.193**	0.024	0.012	**0.268**	-0.003	0.072	
	0.191	0.186	0.008	0.222	0.479	0.135	0.706	0.175	0.017	0.099	0.003	0.012	0.756	0.876	0.000	0.966	0.351	
Desmin Day 7⁸	**-0.175**	**-0.259**	**0.231**	**0.296**	**0.212**	-0.081	0.029	**0.255**	**0.290**	**-0.244**	**-0.307**	**0.350**	**-0.170**	**0.179**	**0.320**	0.033	0.013	**0.634**
	0.023	0.001	0.003	<.0001	0.006	0.295	0.713	0.001	0.000	0.001	<.0001	<.0001	0.027	0.020	<.0001	0.673	0.863	<.0001

¹Upper row = residual correlation, bold values indicate significant correlations or trends

²Bottom row = P-values

Table 9. (continued)

[1]Weight lost during 24 h gravitational test.
[2]Weight lost after being centrifuged at 40,000 x g for 10 minutes.
[3]Weight lost after 7-10 days of aging.
[4]Weight lost during cooking to 70ºC.
[5]Sensory score based on an unanchored, fifteen unit scale with a greater value representing a greater degree of juiciness, tenderness, chewiness, pork flavor, or off flavor.
[6]Force necessary to compress a pork loin to 20% of its initial height.
[7]Percent loin composition
[8]Ratios were calculated as the intensity of the intact desmin band in each sample over the intensity of the intact desmin band in the internal designated densitometry sample

Figure 1. Diagram demonstrating the location within the loin that chops were removed from for evaluation of quality traits
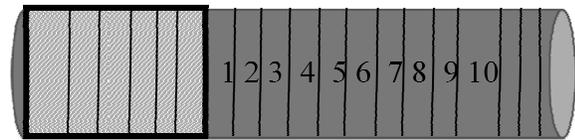
Blade   Center   Sirloin

Chop Number	Traits to be measured
1	pH and centrifugation loss
2	Hunter color and drip loss
3	Hunter color and drip loss
4	Biochemical Day 2
5	Biochemical Day 7
6	Star Probe
7	Sensory analysis
8	Proximate analysis
9	Extra
10	Extra

Figure 2. Example of fifteen unit scale used for sensory evaluation

PORK LOIN CHOPS

Date_____   **Sample**_____   **Panelist**_____

Evaluate the sample and indicate the intensity of each attribute.

Juiciness

_____

Not Juicy   Juicy

Tenderness

_____

Not Tender   Tender

Chewiness

_____

Not Chewy   Chewy

Pork Flavor

_____

None   Intense

Off-Flavor

_____

None   Intense

If an off-flavor is detected, please describe it below-

_____

Figure 3. Western blot depicting amount of intact desmin at 2 and 7 d postmortem. Lanes indicated as Day 2 corresponds to samples aged 2 days postmortem. Lanes indicated as Day 7 corresponds to samples aged 7 days postmortem. The two samples from the same pig were loaded into corresponding lanes (1 and 2, 3 and 4, etc.). Lane 5 corresponds to the internal standard (Std, porcine longissimus dorsi at 10 d postmortem). The uppermost band is the intact desmin, while the lower bands are the desmin degradation product. All lanes were loaded with 40µg of protein on 10% polyacrylamide separating gels. A primary polyclonal rabbit anti-desmin antibody diluted 1:20,000 and a secondary goat anti-rabbit HRP IgG antibody diluted to 1:10,000 were used for detection.
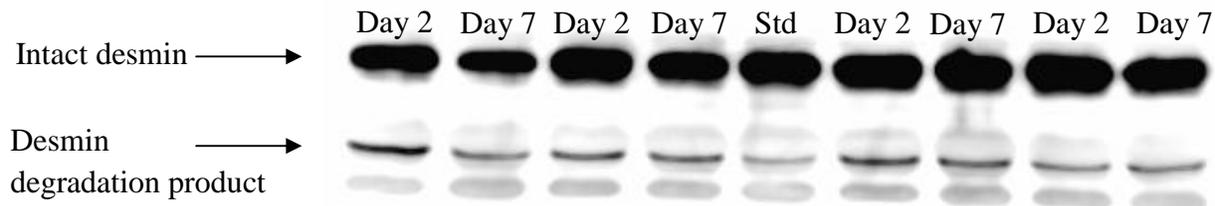
GENERAL SUMMARY

Identifying and defining the inherent relationships that regulate fresh pork quality will result in the production of higher quality, more consistent pork products. Selection practices, genetic background, and an animal's individual muscle metabolism are all important factors which affect overall pork quality. Selection for increased growth and efficiency has produced the unintended consequence of altered meat composition and poorer quality in other selection models. The purpose of the present study was to investigate how selection for reduced residual feed intake (RFI) affects fresh pork quality and composition.

Selection for reduced residual feed intake successfully reduced RFI by 0.043 kg of feed/day in the select line (P<0.05) compared to the randomly selected control line. As a result of this selection, carcass composition was affected. Select line carcasses had greater loin eye depths and greater percentages of lean. In addition, select line pigs tended to produce leaner carcasses as shown by significantly less marbling and intramuscular fat in the loin and a tendency to have less backfat than carcasses from control line pigs. While altering carcass composition has had detrimental effects on fresh pork quality in other selection models (Gilbert et al., 2007; Lonergan et al., 2001), no line differences were noted for pH, star probe, or sensory values in this study. Loin chops from select line carcasses tended to lose less water during centrifugation and have lower Hunter b values, but there were no differences between lines for measures of drip loss, Hunter L, or a values. Selection for reduced RFI could be applied as a valuable selection tool while having few detrimental effects on pork quality. However, low RFI still presents some quality challenges.

Residual correlations demonstrated some additional relationships between RFI and pork quality. Lower RFI values were related to loin chops with decreased tenderness,

increased chewiness scores, increased purge loss, and increased star probe values. These correlations revealed the interesting results that must be considered. While there were no significant line differences for quality and sensory traits, the correlations predict that continued intense selection for reduced RFI will result in a decrease in fresh pork sensory traits. An explanation for this response to lower RFI could be a related reduction in intramuscular lipid and a decrease in postmortem proteolysis of key myofibrillar proteins.

RFI was correlated to lipid content, indicating that selection for low RFI will result in lower intramuscular lipid content in the loin. Direct line differences for lipid content had these same results, with loin chops from select line carcasses having less intramuscular lipid content.

The influence of lipid on sensory attributes in pork is of some debate. In this study, lipid content tended to be positively correlated with pork flavor and star probe. The average pH range of the samples was 5.54-5.55. Lipid content influences pork sensory traits at intermediate pH values (>5.50) (Lonergan et al., 2007). This supports the hypothesis that intramuscular lipid content does play some role in the development of sensory traits.

The influence of selection for reduced RFI on pork quality traits could also be linked to postmortem protein degradation. Degradation of desmin in postmortem muscle improves water holding capacity and tenderness. Lower RFI values were related to a greater amount of intact desmin at 7 d postmortem indicating that less protein degradation occurred during aging. This greater amount of intact desmin would cause chops to be less tender and also lose a greater amount of water as purge loss. These results are further supported by a different trial (unpublished data) where calpastatin activity was higher in muscle from select line pigs than muscle from control pigs. A greater calpastatin activity would inhibit desmin

from being degraded, and would explain the greater amount of intact desmin in lower RFI pigs.

The relationships observed in this study demonstrate the complex links that exist between quality traits and the factors which influence them. Selection strategies need to be fully investigated to ensure they can be implemented without having detrimental quality effects. Selection for reduced RFI has the potential to be a viable selection method that could reduce feed intake, improve carcass composition, and have few detrimental effects on selected measure of pork quality. However, residual correlations indicated that selection for lower RFI is predicted to decrease fresh pork sensory traits. The results from the current study represent the differences observed in the pork loin. Further work could investigate the influence that selection for reduced RFI has on other pork cuts. For example, the reduction in overall lipid could especially have negative quality affects on the pork belly. Moreover, fully understanding how selection for reduced RFI influences fresh pork quality is in important in order to determine whether it is a practice that will be a benefit to the pork industry.

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