Influence of selection for improved growth rate on pork quality

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Influence of selection for improved growth rate on pork quality

By

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GENERAL INTRODUCTION

Pork quality can be defined as the properties of fresh pork that includes things such as color, texture or tenderness, and water-holding capacity that ultimately influences consumer acceptance of the product. It is affected by many interacting factors such as genetics, feeding, pre-slaughter handling, and storage conditions (Rosenvold and Andersen, 2003; van der Wal et al., 1997) that in turn influence factors of importance in the postmortem conversion of muscle to meat such as the rate and extent of pH decline, temperature decline, and postmortem proteolysis of muscle proteins (Huff-Lonergan and Lonergan, 2005; Schafer et al., 2002; van Laack et al., 2001; Warner et al., 1997). Therefore, both pre-slaughter factors and postmortem factors are of significant importance in determining pork quality, illustrating the important link between muscle metabolism and meat quality.

High quality pork is very important to consumers which in turn means it is important to livestock producers and pork manufacturers to produce product of acceptable quality. As consumers become more discriminating towards their acceptance of inferior quality pork, the onus shifts towards the livestock producers and the processing plants to provide a large quantity of high quality product (Cassens, 2000). When considering the availability of alternatives to pork in the marketplace as well as the high feed costs as a result of the increased popularity and production of biofuels, producers and processors must continue to add value, and not lose value, to fresh pork. In response to these issues, pig breeding companies are now paying more attention to meat quality and are including quality traits as integral parts of selection programs (Plastow et al., 2005). In addition, breeders continue to develop selection programs that minimize the known negative influence on pork quality associated with genes known to provide benefits in pork production, such as the halothane
gene and the Rendement Napole (RN-) gene (Brewer et al., 2002; Channon et al., 2000; Copenhafer et al., 2006). The implementation of these selection practices has the potential to significantly influence fresh pork quality and consumer acceptance.

One such selection strategy that has previously been investigated is selection for improvements in lean growth efficiency (Lonergan et al., 2001). In this study, selection for improved lean growth efficiency resulted in carcasses that had lower backfat composition and higher percentage of lean pork cuts in the carcass. However, meat quality significantly declined as a result of the selection practice. Loin chops from the selected line were tougher and had poor water-holding capacity, as evidenced by higher Warner-Bratzler shear force values and higher drip losses. It was also apparent that selection for lean growth efficiency altered the process of the conversion of muscle to meat in the selected pigs. Selected pigs had higher early postmortem pH values and did not exhibit as much postmortem proteolysis of the muscle protein troponin-T which led to the differences in pork quality. It is therefore obvious that selection for improved lean growth negatively influences pork quality, yet questions still arise as to the influence of selecting for improvements in things such as growth rate on meat quality. Selection for improved growth rate likely influences early postmortem changes in pork quality traits and ultimately translates to differences in pork quality, in addition to changing the relationships of pork quality traits with each other in terms of accounting for variations in pork quality.

The hypothesis of the present study was that selecting sires based on their Estimated Breeding Value (EBV) for growth rate will influence early postmortem changes in pork quality traits and translate into differences in pork quality between the progeny of the selected sires. This will also potentially influence the relationship between pork quality traits
with respect to postmortem factors such as pH and muscle protein proteolysis that can be beneficial in explaining and controlling the variation in pork quality and consumer acceptance.

**Thesis Organization**

This thesis is organized to an alternate style format. Arrangement begins with a general introduction, followed by a review of literature, two publishable papers, and a concluding general summary. References cited within each chapter are listed at the end of that chapter. The papers will be submitted to Meat Science and thus follow formatting and citation guidelines of Meat Science. The general introduction and literature review follow Journal of Animal Science citation guidelines.

**Literature Cited**


Acceptable quality pork is very important because in the present global economy, meat quality takes on considerable importance for segments of the industry from producer to consumer. Consumers are becoming more discriminating and will no longer accept pork of inferior quality. Thus, live animal producers and meat producers must pay attention to the quality of meat being produced in addition to the quantity they produce (Cassens, 2000). The increased consumer demand for lean meat has led to carcass pricing systems that discriminate in favor of high lean meat content. Thus, an important goal of the pork industry has been to increase the quantity of high-quality lean meat without decreasing either the efficiency of growth or meat quality (Mason et al., 2005). It is also important to consider the effect of biofuels production in that with the increased cost and competition for grain and feed from biofuel byproducts, we must continue to add value and not lose value in fresh meat pork. Combining this knowledge with the knowledge that the availability of alternatives to pork such as plants and poultry that are usually less expensive have grown (Cassens, 2000) and it is evident that good quality pork continues to be of the utmost importance.

What exactly is pork quality? Different definitions of pork quality exist and have been used that can help derive a solid, general definition. One definition describes pork quality as a combination of different properties of fresh meat that concern both consumer acceptance and technological aspects such as color, water-holding capacity, and texture (van der Wal et al., 1997). Rosenvold and Andersen (2003) define pork quality as the inherent properties decisive for the suitability of the meat for further processing and storage, with the main attributes of interest being water-holding capacity, color, fat content and composition,
oxidative stability, and uniformity. Though different, these two definitions cover the important aspects of pork quality. From these definitions, one can derive the very basic definition being those properties of fresh pork that influence consumer acceptance and technological quality such as color, texture, and water-holding capacity.

Pork quality can be influenced by many interacting factors. These factors include animal breed and genotype, feeding, pre-slaughter handling, and storage conditions (Rosenvold and Andersen, 2003). These factors are all important by themselves, but can interact with each other in numerous ways that can have both positive and negative impacts on determining ultimate pork quality as it is perceived by the consumer (Rosenvold and Andersen, 2003; van der Wal et al., 1997; Wood et al., 2004). However, there are also interacting postmortem factors that are important once the pig has been slaughtered. These include things like the rate and extent of pH decline, temperature decline, and the postmortem proteolysis of muscle proteins (Huff-Lonergan and Lonergan, 2005; Schafer et al., 2002; van Laack et al., 2001; Warner et al., 1997). What is interesting about pork quality, though, is that the pre-slaughter factors can influence the postmortem factors and therefore both are of significant importance in determining pork quality. This illustrates the important link between muscle metabolism and meat quality. For example, genetic background of the pig, such as its susceptibility to the porcine stress syndrome, can influence the proteolytic solubility and degradation of muscle proteins (Boles et al., 1992) and influence consumer acceptance of pork (Brewer et al., 2002). In addition, pig breed, diet, and environment can also influence the eating quality of pork (Wood et al., 2004). Pork quality is therefore a result of many pre-slaughter and postmortem factors that can interact with each other to ultimately influence the consumer acceptance of fresh pork products.
One such factor that has been thought to directly influence the consumer acceptance of fresh pork is that of intramuscular lipid or fat content in relation to improving sensory quality and tenderness (Fernandez et al., 1999; Lonergan et al., 2007; van Laack et al., 2001). The results of studies that have investigated this factor have demonstrated mixed results, however. Some studies have found a positive relationship between lipid content and sensory quality in that there is a certain level of intramuscular lipid that must be met in order to attain acceptable sensory quality and tenderness (Devol et al., 1988). Other studies, though, have found a minimum contribution of an increasing lipid content leading to improved sensory quality (Fernandez et al., 1999). Some studies have also found the relationship between intramuscular fat or lipid and tenderness to be dependent on genetic type of the animal, meaning that increasing levels of intramuscular lipid will not necessarily improve pork tenderness (van Laack et al., 2001). It is therefore likely that this factor is another interacting factor in pork quality, as it can be dependent on other factors such as genetics as well as pH. Lonergan et al. (2007) investigated the influence of intermuscular lipid content at differing pH levels on sensory quality. The results of this study demonstrated that lipid content can minimally improve pork sensory quality only at intermediate pH values (pH 5.50-5.80), and it was clear that increasing lipid content would not consistently improve the quality of low pH (pH<5.50) pork which has poor sensory quality, or high pH (pH>5.80) pork that has superior sensory quality. These results demonstrate that lipid is an important factor in determining pork quality, yet it is still a factor that can be dependent on other factors and is likely not an independent source of contributing to pork quality variation and other factors likely have a greater influence.
This literature review will focus on many of these factors in relation to their role in determining pork quality. The conversion of muscle to meat will be discussed and will outline many of these factors of importance. Also, the role of the postmortem proteolysis of muscle proteins will be reviewed with particular focus on those proteins that are important for water-holding capacity and tenderness of fresh pork. Finally, the impact of pig genetics on pork quality will be discussed, specifically looking at genes of interest and how different selection practices can ultimately influence pork quality.

**Postmortem Conversion of Muscle to Meat**

Meat can be thought of as the postmortem state of muscle, since it largely reflects the chemical and structural properties of the muscles from which it arises. However, meat differs from muscle as a result of a series of biochemical and biophysical changes initiated in muscle at the death of the animal (Lawrie, 2006). It is generally influenced by many factors such as genetics, nutrition, preslaughter handling and stress, and type of muscle (Lawrie, 2006; Rosenvold and Andersen, 2003; van der Wal et al., 1997). There are many common processes that will be described below, such as glycogen storage, pH decline and ultimate pH, and temperature. The following will review key events and processes such as death of the animal, postmortem glycolysis, onset of rigor and rigor development, and the denaturation of proteins and proteolysis. However, these processes are not all-inclusive, as other factors exist that influence how muscle is converted to meat.

**Death of the animal initiates the conversion to meat**

The conversion of muscle to meat is initiated by the death of the animal, which for the pig is initiated by bleeding the animal after they have been immobilized through the use of electrical stunning or by anaesthetization with carbon dioxide (Lawrie, 2006). One of the
problems associated with the use of electrical stunning is the occurrence of blood splash, the appearance of numbers of small dark red areas in the muscles, which may be alleviated with the use of carbon dioxide stunning (Lawrie, 2006). Carbon dioxide stunning is an effective alternative to electrical stunning when the gas concentration is between 65-70% which is has been found to somewhat relax the muscles of the pig and result in an ultimate pH that is slightly lower and less variable than electrical stunning (Lawrie, 2006). CO₂ anaesthesia was also found to be associated with a slower rate of postmortem glycolysis and less fluid loss than with electrical stunning (Bertram et al., 2004).

Bleeding of the animal should be performed as soon as possible after stunning regardless of the method used in order to ensure the animal’s welfare is not compromised, and it is recommended that the stun to stick ratio with electrical stunning should not exceed 15 seconds when electrical stunning is applied (Anil, 1991). The loss of blood and subsequent stoppage of blood circulation throughout the body at the time of death initiates a complex series of changes in muscular tissue (Lawrie, 2006) that can be considered the point at which the conversion to meat really starts to take place. Many of the changes associated the conversion to meat are a result of the muscle continuing metabolism. Though muscle is not contracting, energy is being used as a means to maintain temperature as well as maintain cell organizational integrity against spontaneous break down (Lawrie, 2006). The most immediate change as a result of blood loss is the elimination of blood-born oxygen being supplied to the muscles. When this occurs, the oxidation-reduction potential of muscle falls, via a decrease in oxidative phosphorylation, which means the resynthesis of ATP from this method is impossible. This is important because oxidative phosphorylation is a means by which ATP can be generated through aerobic metabolism, and it is also the most efficient
means of producing ATP. However, since it requires oxygen to function, muscle can no longer produce ATP by its most effective means (Lawrie, 2006). That means muscle must produce ATP by some other method, such as creatine phosphate (CP) or anaerobic metabolism. CP can be used to make ATP, but it is the most rapidly consumed and is thus effective during a very short term period. Thus, muscle will use anaerobic metabolism, also inefficient like CP, as a means to generate ATP as ATP level is slowly depleted. Since oxygen is not being supplied to muscle, anaerobic glycolysis takes place, though as has already been stated it cannot maintain ATP levels that are produced with an available supply of oxygen. This leads to the formation of actomyosin and subsequent development of rigor mortis. The lowered availability of ATP leads to the accumulation of lactic acid which has been produced by glycogen during anaerobic glycolysis and causes a lowering of pH. As pH is lowered and ATP is depleted, the ability of proteins to maintain their structural integrity is decreased which makes them more susceptible to denaturation (Lawrie, 2006). These concepts will be discussed in subsequent sections.

**Postmortem glycolysis and rigor development: key aspects in muscle to meat conversion**

*Postmortem glycolysis and pH decline*

During the first 24-36 h postmortem, the dominant mechanism taking place is postmortem glycolysis, the conversion of glycogen to lactic acid, which will culminate with the development of ultimate pH (Lawrie, 2006). This conversion of lactic acid from glycogen will continue until it reaches a pH when the enzymes effecting glycogen breakdown become inactivated, typically around pH 5.4-5.5 (Bate-Smith, 1948). All of the glycogen will generally be used up and no residual glycogen will remain if the pH does not fall to 5.4-5.5
Glycogen has been found to exist in multiple forms in muscle, distinguished by structure and/or their susceptibility to metabolic change (Lawrie, 1955). Glycogenesis in muscle is initiated by the protein glycogenin (Lawrie, 2006) whose availability is likely the major factor that limits glycogen storage in muscle (Alonso et al., 1995). Regardless of how much glycogen is stored in muscle, the breakdown of glycogen to form lactic acid is very important to the conversion of muscle to meat, as evidenced by the confirmation that lactic acid production is virtually the only event causing pH decline during postmortem glycolysis (Lundberg et al., 1986). Nevertheless, pH decline is an important factor in the conversion of muscle to meat. As has previously been stated, pH decline will continue until it reaches a final pH of approximately 5.4-5.5 which is referred to as the ultimate pH (Lawrie, 2006). An ultimate pH of 5.4-5.5 is very close to the isoelectric point (pI) of many proteins of muscle, such as myosin whose pI = 5.4. At the isoelectric point, the positive and negative charges of the protein are essentially equal and the net charge of the protein is zero. This means that the positive and negative charges on the proteins are attracted to each other which means they will not bind or be attracted to the negative charge on the dipolar water molecule. Thus, less water can be attracted and held within the protein. In addition, the diminishment in net negative and positive charges as the charge approaches zero means that there is less repulsion among like structures with similar charges within the myofibril. As a result, these structures can pack more closely together and reduce space within the myofibril and thus water-holding capacity of muscle with proteins near their isoelectric point is lower (Huff-Lonergan and Lonergan, 2005). This highlights why there is quality problems associated with muscle and it
also shows why pH decline and ultimate pH are important properties in the development of meat from muscle.

In addition to the extent that pH declines, i.e. ultimate pH, the rate it declines is also important and both can be influenced by many intrinsic factors such as species, genetics, muscle type, stress and environment, and temperature (Lawrie, 2006; Rosenvold and Andersen, 2003; van der Wal et al., 1997). The effect of temperature on postmortem glycolysis and thus pH decline can be somewhat perplexing, as postmortem glycolysis has been shown to increase with increasing temperatures, i.e. a faster pH decline at elevated temperatures after death (Bate-Smith and Bendall, 1949), but the rate of postmortem glycolysis has also been shown to increase as temperature falls from about 5-0°C (Lawrie, 2006), meaning that pH decline can also increase at common storage temperatures if ultimate pH has not been reached. One of the most common quality problems associated with an accelerated rate of pH decline early postmortem is the development of meat that is considered pale, soft, and exudative (PSE) (Lawrie, 2006). Pigs that produce PSE meat exhibit an accelerated pH decline to about 5.4 within 40-45 minutes postmortem that is likely associated with and reflects a high temperature early postmortem (Briskey and Wismer-Pedersen, 1961; Cheah and Cheah, 1976). Therefore, pH decline plays a very important part in the conversion of muscle to meat. It is a result of the production of lactic acid from glycogen during postmortem glycolysis and is a key element in many of the quality aspects of pork.

Onset and development of rigor affects the conversion of muscle to meat

As postmortem glycolysis proceeds and ultimate pH is reached, muscle becomes inextensible and stiffens as rigor mortis develops (Lawrie, 2006). There is a strong
relationship between the onset of rigor and the disappearance of muscle ATP in that the absence of ATP leads to actin and myosin, the two main muscle proteins of the myofibrils, combining to form rigid actomyosin chains that results in the extensive stiffening of muscle (Bate-Smith and Bendall, 1949, 1947). It is the formation of actomyosin that reflects the loss in extensibility of muscle, therefore associating an increase in actomyosin formation with an increase in muscle inextensibility. Actomyosin formation is slow at first (delay period of rigor formation) and muscle is still extensible, but then formation rapidly increases (fast phase) and muscle extensibility will remain constantly low resulting in a high degree of inextensibility (Bate-Smith and Bendall, 1949). The relationship between ATP and rigor development is highlighted in the time between the delay phase to the onset of the fast phase of rigor formation. The time to reach the onset of the fast phase is most directly dependent on the level of ATP which is initially being lowered by the ATP-ase activity of myosin that is not forming actomyosin, but rather is attempting to maintain the structural integrity of the muscle cell in order to keep it extensible (Lawrie, 2006). The delay in onset time and actomyosin formation can be further delayed by the resynthesis and formation of ATP through creatine phosphate (CP) in addition to postmortem glycolysis, when stored CP has been used up (Lawrie, 2006), but that is not an effective source of ATP formation, as has already been pointed out, and therefore the level of ATP decreases. A low level of stored glycogen will speed up the onset of the fast phase of rigor formation, but even an abundant supply of glycogen cannot maintain a high level of ATP necessary to prevent actomyosin formation. The time frame can also be sped up as a result of the animal struggling at death which results in a lower initial pH and higher initial depletion of glycogen (Lawrie, 2006) which results in actomyosin forming sooner.
There are quality changes associated with the onset of rigor. One such change is the lowering of water-holding capacity, though this is not solely due to pH decline towards the isoelectric point of myofibrillar proteins or sarcoplasmic protein denaturation (Lawrie, 2006). Studies have shown that even when rigor forms at a high pH, there is still a loss in water-holding capacity that is associated with a depletion of ATP and subsequent formation of actomyosin (Marsh, 1952). However, the readdition of ATP at a relatively high concentration, through sarcoplasmic reticulum pumps in postmortem muscle, will cause muscle swelling and restore water-holding capacity towards levels seen pre-rigor (Lawrie, 2006). This change in water-holding capacity can be further explained when thinking of the two phases of water in muscle: bound water and free water. The majority of water in muscle exists as “free” water, meaning it is not bound to things such as proteins, but some of the water also exists as “bound” water, meaning it is bound to the likes of proteins and will not be lost. When the onset of rigor occurs the amount of “bound” in the muscle remains constant. However, there is a movement of “free” water between environments within the muscle which presumably reflects the cross-linking and formation of actomyosin (Pearson et al., 1974) and subsequent decrease in water-holding capacity.

Another quality change is a decrease in meat tenderness, or an increase in toughness, associated with rigor shortening (Koohmaraie et al., 1996; Koohmaraie and Geesink, 2006; Koohmaraie et al., 1995; Taylor et al., 1995). Rigor shortening is similar to contraction, except it likely does not involve all muscle fibers and is irreversible (Lawrie, 2006). Shortening can occur at different temperature ranges which gives rise to different types of shortening. One type is “rigor shortening” which has been shown to increase at temperatures above 20°C and the other is “cold shortening” which increases at temperatures below 10-
15°C if the pH is still fairly high at around 6.0-6.2 (Honikel et al., 1983). This contractile shortening is also likely to be stimulated as ATP decreases and calcium ions are leaked back into the sarcoplasm through the sarcoplasmic reticulum (Lawrie, 2006). Increased shortening leads to an increase in muscle toughness but this is likely not due solely to actomyosin formation. Increased meat toughness is likely also result of sarcomere shortening in the myofibril that leads to more actomyosin cross-bridges, as longer sarcomeres have been associated with increased meat tenderness and less actomyosin cross-bridging (Koohmaraie et al., 1996; Taylor et al., 1995). Muscle toughening does not have to be a result of rigor onset, as Koohmaraie et al. (1996) showed that it can be prevented if muscle fibers are not allowed to shorten during rigor development.

It is evident that postmortem glycolysis and rigor development play key roles in the conversion of muscle to meat. Both processes result in key factors that have roles in meat quality attributes. It is at this point that meat can be considered to have been converted from muscle, however there are still other factors of influence and important, such as protein denaturation.

**Muscle protein denaturation influences muscle structure and meat quality**

As muscle pH declines and lactic acid accumulates, structural proteins become much more capable to denature, which is frequently accompanied by a loss in their ability to bind water, and also potentially makes them liable to attack by muscle proteases (Lawrie, 2006). Protein denaturation can be prevented if energy, such as ATP, is available to preserve protein structure, however as has already been discussed, ATP is not available after death of the animal. Protein denaturation can be thought of as a physical or intramolecular rearrangement which does not involve hydrolysis of the chemical bonds linking the protein chains’ amino
acids (Lawrie, 2006). Denaturation is generally accompanied by a loss of enzymatic activity in muscle, a change in molecular shape or size, and a decrease in solubility. Proteins can more easily be denatured if they are subjected to pH levels below those in vivo, to temperatures either above 25°C or below 0°C, or non-physiological salt concentrations (Lawrie, 2006) which is why they are commonly denatured in processed meat products.

During the postmortem storage or aging period of meat, myofibrillar and sarcoplasmic proteins are those proteins most commonly denatured, each at varying degrees (Lawrie, 2006). First considering myofibrillar protein, a combination of rigor onset and high ionic strength leads to a 75% decrease in extractability of myofibrillar protein immediately postmortem. However, extractability of myofibrillar protein will rise to levels even beyond what is observed initially during storage at 2°C (Lawrie, 2006). The importance of this is that in this instance, when actomyosin is predominant, other myofibrillar proteins such as α-actinin, troponin, and tropomyosin are extractable (Taylor et al., 1995). This also means that during the aging period, actin filaments detach from the Z-line due their interaction with tropomyosin being weaker than their interaction with myosin (Huxley, 1963). The actin filaments then collapse on to myosin filaments, leading to a lengthening of the A-band. This also results in an increased weakening of the sarcomere at the A-I band junction and leads to an increased gap between the A and I bands of the sarcomere (Taylor et al., 1995; Wheeler et al., 2000). Thus, myofibrillar protein denaturation can influence things like tenderness due to changes in muscle structure.

Myofibrillar protein extractability is also influenced by pH and temperature. A high ultimate pH leads to greater extractability while a high temperature leads to less extractability (Lawrie, 2006). An important aspect of myofibrillar protein changes, reflected in their
tenderness extractability, is their degree of shortening during the onset of rigor (Koohmaraie et al., 1996; Wheeler and Koohmaraie, 1994). In muscle that enters rigor in an extended (somewhat relaxed) state there may possibly be a larger degree of actin and myosin filament overlap and a smaller degree of actin-myosin cross-linking which results in less formation of actomyosin and ultimately in tender meat upon cooking. However, when muscle enters rigor in a contracted state, there is a large degree of cross-bridging between actin and myosin which leads to a higher degree of actomyosin formation and muscle shortening increases which results in meat that is tough when cooked (Koohmaraie et al., 1996; Lawrie, 2006; Taylor et al., 1995; Wheeler et al., 2000). Thus, myofibrillar protein denaturation interacts with the degree of muscle shortening and abundance of actomyosin formation which can greatly influence meat tenderness.

Though the denaturation of myofibrillar proteins is prevalent and can influence things such as meat tenderness, sarcoplasmic muscle proteins are the most liable to denaturation (Lawrie, 2006). Sarcoplasmic protein denaturation is commonly associated with a precipitation of sarcoplasmic proteins out of the sarcoplasm, especially in the presence of salt and as pH declines to acidic levels, as well as an indirect influence of the increased abundance of actomyosin (Lawrie, 2006). Precipitation increases as temperature increases, as evidenced by maximum precipitation occurring at all temperatures when pH is 4.8-5.2 (Scopes, 1964). Even though normal ultimate pH is approximately 5.5, there is still likely some sarcoplasmic protein precipitation occurring even though it is not at the maximum level. However, there may be additional precipitation at normal ultimate pH if high temperature is prevalent during postmortem glycolysis (Scopes, 1964). Sarcoplasmic protein denaturation occurs severely in muscles associated with the pale, soft, and exudative state in
which there is a combination of low pH and high temperature. In this instance, sarcoplasmic proteins precipitate onto myofibrillar proteins and lower their extractability and water-holding capacity (Bendall and Wismer-Pedersen, 1962).

Though tenderness variations are associated with protein denaturation (Taylor et al., 1995), perhaps the most important result is the decrease in water-holding capacity (Bendall and Wismer-Pedersen, 1962; Lawrie, 2006). As has already been reviewed, the point of lowest water-holding capacity in muscle proteins is a pH of 5.4-5.5 which is near the isoelectric point (Huff-Lonergan and Lonergan, 2005; Lawrie, 2006), and also the production of lactic acid from glycogen in normal meat will generally cause the pH to reach 5.5 and result in some fluid loss, which can be minimized at a high ultimate pH (Lawrie, 2006). Water-holding capacity is at its minimum at its ultimate pH, but will tend to increase as aging occurs. This may be due to proteolysis, which will be discussed in further detail. This idea is reinforced in the findings of previous studies that found increased proteolysis of proteins such as vinculin and desmin during postmortem aging periods and suggested that destruction of the cytoskeleton of myofibrils and muscles did not allow for the forcing of water to the exterior of the muscle cell which could lead to the observed increase in water-holding capacity over the aging period (Kristensen and Purslow, 2001). Therefore, it is important to consider the effects of proteolysis on meat quality which will be discussed further.

**Postmortem Proteolysis**

Proteolysis of myofibrillar and cytoskeletal proteins is another important process that can influence meat quality. Many myofibrillar and cytoskeletal proteins are responsible for maintaining the structural integrity of the muscle cell or myofibril. Myofibrillar proteins of interest include α-actinin (not degraded but released from the Z-line), titin, tropomyosin, and
the troponin complex such as troponin-T (Taylor et al., 1995) whose degradation has shown to positively influence meat tenderness (Huff-Lonergan et al., 1996; Lonergan et al., 2001; Melody et al., 2004). Myosin and actin are the two most important myofibrillar proteins but are not affected by proteolysis. These myofibrillar proteins are important, but will not be the main focus of this discussion. The more important proteins for this discussion are those that are important for intermediate filament structures and costameres which provide the structural framework linking myofibrils to each other and to the sarcolemma of the muscle cell. Proteins of interest for intermediate filaments and costameres include desmin, vinculin, integrin, dystrophin, synemin, and talin, among others (Barbut et al., 2007; Bee et al., 2007; Huff-Lonergan and Lonergan, 2005; Taylor et al., 1995; Zhang et al., 2006). The influence of the proteolysis of these proteins will be discussed, as well as their regulation as a result of the calpain system. In addition, the influence of the calpain system as it relates to quality changes and predicting pork quality will also be reviewed further.

**Influence of proteolysis of cytoskeletal proteins on pork quality**

Proteolysis of these intermediate and costameric proteins mentioned is important for influencing water-holding capacity of pork. If intermediate filament and costameric linkages remain intact and are not degraded during the conversion of muscle to meat, myofibrillar shrinkage, as a result of the muscle entering into rigor, can be translated to the entire muscle cell and would thus reduce the volume of the muscle (Kristensen and Purslow, 2001; Melody et al., 2004). That can be result in a loss of water outside of the cell as it shrinks and the water exiting the cell is lost as drip loss, thus reducing water-holding capacity (Huff-Lonergan and Lonergan, 2005) as outlined in the following diagram from Huff-Lonergan and Lonergan (2005).
The above diagram shows that with proteolysis of the proteins linking the myofibrils to the muscle cell, the myofibrils shrink without compromising the shape or volume of the muscle cell and thus allow more water to remain in the cell. With no proteolysis, it is evident that the entire muscle cell shrinks and therefore greatly decreases cellular volume and water is mobilized out of both the myofibril and the muscle cell. Proteolysis of these proteins therefore allows for an increased water-holding capacity compared to no proteolysis.

There have been numerous investigations as to the magnitude that these proteins can influence water-holding capacity in pork (Bee et al., 2007; Gardner et al., 2005; Kristensen and Purslow, 2001; Melody et al., 2004; Zhang et al., 2006). Perhaps the protein of most interest is the intermediate filament protein desmin that can be found in tying the myofibril to the cell membrane (Huff-Lonergan and Lonergan, 2005). Desmin degradation has been observed to occur as early as 45 minutes to 6 h postmortem (Melody et al., 2004). This has led to Huff-Lonergan and Lonergan (2005) to hypothesize that degradation of desmin at such an early postmortem time would allow water that is expelled from the intramyofibrillar spaces to remain in the cell for a longer period of time. It is also hypothesized that a reduced
degradation of desmin (which ties the myofibril to the muscle cell) would result in an increased shrinkage of the cell which is ultimately translated into increased drip loss (Huff-Lonergan and Lonergan, 2005; Kristensen and Purslow, 2001; Melody et al., 2004). Several studies have presented results that are in agreement with these hypotheses (Bee et al., 2007; Kristensen and Purslow, 2001; Melody et al., 2004; Zhang et al., 2006). The intensity of intact desmin has been found to be positively correlated to drip loss during postmortem storage, meaning that an increase in the abundance of intact desmin leads to higher drip loss (Bee et al., 2007; Kristensen and Purslow, 2001; Zhang et al., 2006). The reverse is true when considering the degradation product of desmin, meaning that a higher amount of desmin degradation product was found with decrease in drip loss (Melody et al., 2004). Both results tell the same tale in that more intact desmin, and thus less degradation product, is associated with higher drip loss. Similar results were observed for the protein talin in that an abundance of intact talin is associated with higher drip loss during postmortem storage (Bee et al., 2007). The idea that a greater degree of intact cytoskeletal proteins leads to higher drip loss does not hold to be true. The proteins vinculin (Bee et al., 2007) and integrin, though not really a cytoskeletal protein, (Zhang et al., 2006) were found to be negatively correlated with drip loss during postmortem storage. Therefore, a greater degree of intact vinculin and integrin leads to a decrease in drip loss during postmortem storage of fresh pork (Bee et al., 2007; Zhang et al., 2006). This shows that not all cytoskeletal proteins can be characterized by similar degradation patterns and the increased degradation of all of these proteins may not be entirely beneficial to improving water-holding capacity.

Desmin degradation has also been positively correlated to purge loss of the sirloin (Gardner et al., 2005; Zhang et al., 2006) in addition to drip loss of the longissimus dorsi and
is essentially an indicator of water-holding capacity. As a result, desmin degradation has been shown to be a beneficial indicator into being able to predict potential variation in drip loss and water-holding capacity of fresh pork. Gardner et al. (2005) found that the addition of desmin degradation at 1 d postmortem to stepwise regression models to predict purge loss could explain 24.1% of the total variation in sirloin purge loss. In addition, 1 d desmin degradation was the first independent variable to enter the model ahead of such variables as pH decline, ultimate pH, temperature decline, and firmness (Gardner et al., 2005; Huff-Lonergan and Lonergan, 2005). The results support the hypothesis that the proteolysis of intermediate filament proteins during early postmortem periods can minimize the flow of water out of the muscle cell to drip channels which can lead to a reduction in drip loss (Huff-Lonergan and Lonergan, 2005). Thus, the degradation of cytoskeletal proteins, such as intermediate filament proteins, can influence pork quality changes through influencing drip formation and water-holding capacity and these might be independent of pH.

**The calpain system plays an important role in proteolysis and pork quality**

Intermediate filament and costameric proteins (such as desmin, vinculin, and talin) are known to be degraded by μ-calpain in postmortem muscle. Thus, factors regulating and influencing calpain activity can influence quality attributes such as water-holding capacity (Barbut et al., 2007) and tenderness (Koohmaraie, 1992; Melody et al., 2004). The calpain system consists of mainly of the calcium-dependent cysteine proteases μ- and m-calpain as well as their endogenous inhibitor calpastatin (Goll et al., 2003). Both μ- and m-calpain share similar subunit structures and require calcium for activation, yet differ in the amount of calcium necessary for activity. μ-calpain requires between 5-65 μM Ca^{2+} for half-maximal activity, while m-calpain requires 300-1000 μM Ca^{2+} for half-maximal activity (Goll et al.,
While they differ in the amount of calcium required for activation, both calpains degrade the same specific set of myofibrillar and cytoskeletal proteins that are degraded during the postmortem aging period (Geesink and Koohmaraie, 1999; Huff-Lonergan et al., 1996). Therefore, it is likely that differences in calpain, specifically µ-calpain, and calpastatin activity can influence pork quality attributes.

µ-calpain autolysis can explain variations in pork quality

Since many of the intermediate filament and costameric proteins degraded in the postmortem conversion of muscle to meat, particularly desmin, are substrates of µ-calpain (Huff-Lonergan et al., 1996), it is reasonable to hypothesize that µ-calpain autolysis and activation may explain a portion of the variation in the degradation of these proteins and could subsequently influence quality factors such as drip loss (Bee et al., 2007; Huff-Lonergan and Lonergan, 2005; Zhang et al., 2006) and tenderness (Melody et al., 2004). Autolysis of µ-calpain is considered to be the hallmark for µ-calpain activation in postmortem muscle (Barbut et al., 2007). µ-calpain autolysis is indicated by the presence and proportion of the unautolyzed 80-kDa subunit as well the intermediate 78-kDa subunit and the 76-kDa subunit autolysis product (Gardner et al., 2005; Melody et al., 2004). Barbut et al. (2007) therefore suggest that a greater proportion of the 76-kDa autolysis product subunit indicates that a greater proportion of µ-calpain has been active, while a higher proportion of unautolyzed 80-kDa subunit can be interpreted as less µ-calpain has been active.

Melody et al. (2004) found that a limited autolysis of µ-calpain during the first 24 h postmortem led to an observance of limited desmin degradation at 24 h postmortem. This led to poorer water-holding capacity and a slower rate of postmortem tenderization than when compared with a more prominent autolysis of µ-calpain and degradation of desmin. Other
studies are in agreement with the results of Melody et al. (2004) in terms of the increase in µ-calpain autolysis leading to a greater water-holding capacity and less drip loss and also demonstrate the relationship between µ-calpain activity and pH (Bee et al., 2007; Zhang et al., 2006). Zhang et al. (2006) demonstrated that a low pH early postmortem can hinder µ-calpain autolysis (determined by a decrease in the percentage of 80-kDa subunit and an increase in the percentage of the 76-kDa autolysis product subunit), thus showing that a lower pH early postmortem will delay µ-calpain activation. In addition, Bee et al. (2007) observed that a negative correlation between the 76-kDa autolysis product subunit and pH at both 45 min and 24 h postmortem which suggests that autolysis of µ-calpain occurs earlier with a faster pH decline. It is therefore evident that pH decline plays an important role in µ-calpain autolysis and their interaction can account for differences observed in pork quality.

µ-calpain autolysis can also be useful in predicting variations in water-holding capacity and tenderness. Gardner et al. (2005) used pH and temperature decline, desmin degradation, and µ-calpain autolysis to predict water-holding capacity, indicated by drip loss or purge loss, and tenderness in pork. For drip loss at day 1, they found that 6 h pH entered the regression model first and explained approximately 34% of the variation seen. When 24 h pH and percent of the 76-kDa autolysis product of the catalytic subunit of µ-calpain (expressed as %76) were included in the regression model, approximately 48% of the variation in drip loss could be predicted. The negative coefficient found for %76 means that less µ-calpain autolysis within the first 24 h postmortem predicts greater drip loss, even with the known effects of pH at 6 h and 24 h in the model. When predicting tenderness as measured by Warner-Bratzler shear force at 3 d postmortem, the percentage of 76-kDa autolysis product is the first variable to enter the equation and predicted approximately 15%
of the variation by itself. Including pH at 6 h and 4 h explains approximately 37% of the variation in WBS at 3 d postmortem. Thus, \( \mu \)-calpain autolysis is the first variable in the equation and accounts for the most variation by itself. The influence of desmin degradation on these models has already been presented in the earlier discussion on desmin degradation. Therefore, inclusion of \( \mu \)-calpain autolysis and desmin degradation in models designed to predict water-holding capacity and tenderness suggests that proteolysis is more than a response that is dependent on temperature and pH decline, but may have a direct influence on water-holding capacity and tenderness of meat by itself (Barbut et al., 2007).

*Calpastatin activity can also influence pork quality*

Calpastatin is the endogenous competitive inhibitor of both \( \mu \)- and m-calpain (Goll et al., 2003). It is competitive in that it can bind calpains, but it requires calcium to do so. The amount of calcium needed by calpastatin to allow half-maximal binding to calpains is generally lower than the calcium required for the half-maximal activity of \( \mu \)-calpain and m-calpain (Kapprell and Goll, 1989). Because calpastatin can compete with and bind calpains, it has been shown to regulate calpain activity in postmortem muscle (Koohmaraie, 1992; Koohmaraie and Geesink, 2006; Koohmaraie et al., 1995) and thus has been able to explain a high percentage of the variation in meat tenderness (Whipple et al., 1990).

Several studies have shown that high calpastatin activity has been associated with limited degradation of muscle proteins (Geesink and Koohmaraie, 1999; Koohmaraie, 1992; Lonergan et al., 2001; Melody et al., 2004). High calpastatin activity has been linked with limited postmortem proteolysis of troponin-T, evidenced by a limited appearance of the 30-kDa degradation product subunit, which resulted in high shear force and lower tenderness (Koohmaraie, 1992; Lonergan et al., 2001). Also, increasing the amount of calpastatin has
been linked with limiting the rate and extent of proteolysis of myofibrillar proteins and desmin in addition to limiting the extent of \( \mu \)-calpain autolysis (Geesink and Koohmaraie, 1999). Geesink and Koohmaraie (1999) also showed that the proteolysis of myofibrillar proteins virtually ceased after 7 d of incubation with increased amounts of calpastatin, yet there was still evidence of partially autolyzed and presumably still active \( \mu \)-calpain. This highlights the importance that calpastatin activity can have on regulating the autolysis of \( \mu \)-calpain and also influence how \( \mu \)-calpain autolysis leads to muscle protein degradation.

It has also been documented that calpastatin activity can differ between muscles when measured at 6 h and 24 h postmortem, with the differences in calpastatin activity corresponding to significant differences in desmin degradation between the muscles and ultimately in tenderness and water-holding capacity differences (Melody et al., 2004). This provides evidence that variation in calpastatin activity may provide at least a partial explanation for variation in observed proteolysis (Huff-Lonergan and Lonergan, 2005). Therefore, differences in calpastatin activity can ultimately translate to differences in pork quality and this difference can also be influenced by genetic mutations that can regulate calpain activity (Ciobanu et al., 2004), which will be further discussed later in a subsequent section that discusses genetics and pork quality.

When taking into account the information provided from the literature discussed, it is very much evident that proteolysis of muscle proteins plays a key role in influencing and determining pork quality. Proteolysis of these proteins can insure that changes in muscle structure during the conversion of muscle to meat do not translate into negative quality effects, and can be influenced by things such as temperature and pH. Differences in proteolysis can be used as a means to explain variations observed in pork quality regardless
of pH decline and can therefore be beneficial when investigating for differences in pork quality.

**Genetics and pork quality**

**Positive and negative effects on pork quality due to genes and alleles**

Pig breeding companies are now paying more attention to meat quality and are including quality traits as integral parts of selection programs (Plastow et al., 2005), thus showing an important relationship between genetics and pork quality. The role genetics plays in relation with pork quality and impacting selection decisions can be thought of as an interaction between two areas of interest. One such area is that of understanding the genetic impact from a negative pork quality standpoint such as the influence of the halothane gene (Brewer et al., 2002; Channon et al., 2000; Copenhafer et al., 2006; Fisher et al., 2000) and the Napole gene (Brewer et al., 2002; Copenhafer et al., 2006; Josell et al., 2003). A second area, one that has gained particular focus over the last decade, is trying to gain an understanding of particular genes and mutations that have a potentially positive impact on pork quality, such as the CAST gene and the PRKAG3 gene (Ciobanu et al., 2001; Ciobanu et al., 2004; Josell et al., 2003; Lindahl et al., 2004; Plastow et al., 2005). Both of these areas will be discussed further.

**Halothane and Napole genes negatively impact pork quality**

Though the halothane gene has been mentioned here as being associated with negative pork quality effects, there are some positives associated with the gene such as increased leanness, growth, and feed conversion efficiency (Channon et al., 2000), which highlights a positive impact on production aspects and perhaps explains how this mutation was propagated in the industry. However, those improvements in production are severely
offset by the drastic decrease in pork quality, such as the increased susceptibility to stress, incidences of poor water-holding capacity, and the increased likelihood of the extreme case that pork that can be considered pale, soft, and exudative (Channon et al., 2000; Cheah and Cheah, 1976; Foury et al., 2005). The Naple gene (RN-), commonly referred to as the “Hampshire effect” because of its frequency in Hampshire pigs (Josell et al., 2003), has a negative influence on pork quality again mainly due to poor water-holding capacity, even though it is positively associated with increased daily gain of the animal and decreased back fat thickness (Brewer et al., 2002), though that result has not been a consistent observation.

The poor water-holding capacity is a result of increased muscle glycogen levels that result in an increased capacity for glycolysis and pH decline. The result is an accumulation of lactic acid and an ultimate pH that is commonly below 5.4, well below the normal range of 5.5-5.7, and leads to the potential denaturation of muscle proteins and ultimately to decreased capacity to retain inherent water (Brewer et al., 2002; Copenhafer et al., 2006). The denaturation of muscle proteins is also a characteristic associated with the halothane gene, which results in sustained muscle contraction that increases ATP and glycogen utilization. Again, lactic acid builds up and the potential for low muscle pH increases that can be combined with high carcass temperatures early postmortem to cause the increased denaturation of muscle proteins and resulting decrease in water-holding capacity and paler pork color (Channon et al., 2000; Copenhafer et al., 2006). It is therefore evident that these two different genes can have similar detrimental effects on pork quality, particularly through influencing how pH decline affects water-holding capacity and drip loss in addition to other quality parameters.
The relationship between pH decline and pork quality has already been established. The rate and extent of pH decline plays an important role in muscle glycolysis and has been associated with changes in postmortem proteolysis that can impact quality traits such as drip loss and tenderness (Huff-Lonergan and Lonergan, 2005; Huff-Lonergan et al., 1996; Koohmaraie, 1992). The halothane gene and the Napole gene can influence the role of pH in such quality traits by changing both the rate and extent of pH decline. Studies have demonstrated that pigs known to be positive for the halothane gene exhibit lower pH values during the postmortem period, which are exhibited both early postmortem such as 40 and 45 minutes to 3 and 6 hours (Channon et al., 2000; Copenhafer et al., 2006) as well as later in the postmortem period such as 24 and 48 hours (Copenhafer et al., 2006; Fisher et al., 2000). The resulting lower pH values led to drip losses that were higher in the pigs possessing the halothane gene, a mutation that increases stress susceptibility, thus meaning an ultimate decrease in water-holding capacity as a result of the halothane gene (Channon et al., 2000; Copenhafer et al., 2006; Fisher et al., 2000).

Further highlighting the notion of poorer water-holding capacity being associated with the halothane gene is that pigs possessing the gene have been shown to have an increase in cook loss by as much as 3% (Channon et al., 2000; Fisher et al., 2000). The effects are not just seen in terms of negatively affecting drip loss, as pigs that are carriers for the halothane also have been found to exhibit higher Warner-Bratzler shear force values than non-carriers (Brewer et al., 2002; Fisher et al., 2000), thus suggesting a decrease in instrumental tenderness in the carriers of the halothane gene mutation.

Effects similar to those of the halothane gene are also associated with the Napole gene. Pigs possessing the RN- gene have demonstrated lower pH values than those without
the gene, but the differences are mostly associated with a lower extent of pH decline as evidenced by a lower ultimate pH measured at either 24 or 48 hours (Copenhafer et al., 2006; Josell et al., 2003) and not as closely related to a lower or more rapid rate of pH decline as has been shown for the halothane gene. Also following the lines of the halothane gene, the lower ultimate pH also leads to significantly higher drip loss (Copenhafer et al., 2006) and cook loss (Josell et al., 2003) in pigs with the presence of the RN- gene. Josell et al. (2003) also found differences in tenderness due to RN- genotype.

It was discovered that pigs with the RN- gene had a lower WBS value than pigs that did not carry the gene (65.3 vs. 75.8), thus showing a tougher resistance to force in the RN- pigs. While the instrumental difference did not translate to the sensory tenderness analysis, there was a trend for those pigs carrying the RN- gene to have higher sensory juiciness scores than those pigs that did not carry the gene, indicating the potential for an increase in eating quality, though the negative impact on water-holding capacity may offset any positive seen in sensory quality. The ultimate end use of the pork products should also be kept in mind, as a low water-holding capacity due to the RN- gene may be beneficial for things such as dry sausage production like pepperoni. So, the negative impact in water-holding capacity may be offset by things that can be done in the production of processed meats, however it still exhibits a negative influence in fresh meat. Thus, through the results of these studies as well as many others, it is apparent that both the halothane and RN- genes negatively alter fresh pork quality. However, there have been recent discoveries within the last decade that can offset these negative impacts through the use of mutations and discovery of new alleles that can have ultimately a positive influence on pork quality.
New alleles in PRKAG3 and CAST genes can potentially positively influence pork quality

The discovery of alleles on genes of interest has led to ways of understanding the principles behind how genes such as the RN- gene negatively influence pork quality. A very important discovery was that of Milan et al. (2000) in which they found a non-conserved substitution in the PRKAG3 gene (protein kinase, AMP-activated, gamma-3-subunit) that explained the dominant RN- mutation accounting for the differences in meat quality and processing yields in Hampshire pigs. The R200Q substitution in the PRKAG3 gene caused a 70% increase in glycogen content in the muscle of RN- carriers (homozygous and heterozygous animals) resulting in lower pH 24 hours postmortem, reduced water-holding capacity, and much lower cooked ham yields (Milan et al., 2000). The 200Q allele, resulting from the substitution, is associated with all RN- pigs and is present at a very high percentage in pigs from the Hampshire breed but not other breeds (Ciobanu et al., 2001; Milan et al., 2000).

However, there are also other allelic variations of the PRKAG3 gene that affect muscle glycogen content and are economically important for controlling variation in pork quality traits, such as ultimate pH, drip loss, tenderness, and cook loss (Ciobanu et al., 2001). One such example of these allelic variations is the I199V substitution (Ciobanu et al., 2001; Josell et al., 2003; Lindahl et al., 2004). When evaluated for differences based on the 199I substitution to 199V, it was found that 199I was associated with better meat quality as evidenced by lower levels of glycogen and lactate leading to higher pH in the loin and ham, in addition to better color scores (Ciobanu et al., 2001) and lower drip loss (Lindahl et al., 2004). When combined with the R200Q substitution found by Milan et al. (2000), it was proposed that the RN- genotype was thus a combination of both substitutions resulting in a
combined effect of the 199V-200Q haplotype instead of the sole R200Q substitution (Ciobanu et al., 2001). The basis for this being 199I is always found with 200R, and that the 199V-200Q effect is more prominent on increasing muscle glycogen content than 199V-200R, which means the RN- phenotype is likely a combined effect of the 199V-200Q haplotype (Ciobanu et al., 2001). Ciobanu et al. (2001) also mention the importance for geneticists to look for other additional mutations that may have an economic impact in genes similar to the PRKAG3 gene. If these mutations can be controlled, the incidence of potential pork quality problems associated with these mutations may be minimized product consistency can be increased.

Calpastatin, the competitive inhibitor of the enzyme m- and μ-calpain, has also been looked at as a way to control variations on tenderness and predict pork quality based on its activity (Gardner et al., 2005; Koohmarae, 1992; Melody et al., 2004). Based on its location and functions in tenderness, both sensory and instrumental, the CAST (calpastatin) gene was considered a good gene for Quantitative Trait Loci to explain possible variation in pork quality (Ciobanu et al., 2004; Plastow et al., 2005). Several different variants of the calpastatin gene as a result of many different substitutions were found to have significant effects on pork tenderness and other pork quality traits, and may possibly impact variations in proteolysis as well. The NKAR haplotype was found to be the most beneficial in being associated with lower Instron force for tenderness values and lower cooking loss in addition to higher juiciness scores, highlighting its association with higher eating quality (Ciobanu et al., 2004). Therefore, this beneficial haplotype can be incorporated into breeding programs to improve eating overall meat quality as it relates to tenderness and eating quality, in addition to providing more economic value to the pork industry (Ciobanu et al., 2004). With further
investigation, the role of genes such as CAST and the PRKAG3 gene could be developed so that their use can be maximized to minimize pork quality variations.

It is also important to consider that many of these newer markers have less of an impact than the major genes and mutations of interest, such as the halothane and RN- genes, which shows it is still necessary to keep the effects of the major ones in mind. As breeding programs continue to evolve and change to meet the demands of the consumer, many other markers may be discovered that can influence pork quality both positively and negatively. With the discovery of such genes and markers a better understanding of the way genetics influences pork quality will continue to occur. However, regardless of new discoveries, the way breeding programs are implemented through the use of selection practices can influence pork quality.

**Impact of selection practices on pork quality**

For a long period of time, pig breeding programs were focused mainly on reducing costs. Selection within these programs was aimed at increasing litter size, decreasing backfat thickness, and improving feed conversion. Present selection practices are directed much more toward retail carcass yield and meat quality due to the high economic value of these traits (van Wijk et al., 2005). With the change in emphasis towards meat quality, different approaches have been applied which focus on things such as breed differences both among and between lines (Latorre et al., 2003; Ramirez and Cava, 2007; Schwab et al., 2006), improvements in lean growth efficiency (Cameron and Curran, 1995; Lonergan et al., 2001), and differences in growth rate (Frederick et al., 2006; Nguyen et al., 2006; Suzuki et al., 2005; van Wijk et al., 2005).
Breed line selection and pork quality

The Duroc breed is commonly used in selection programs as a terminal sire in crossbred market hog production systems because of its advantages over other breeds in terms of growth rate and meat quality (Schwab et al., 2006). Because of these reasons, many studies have investigated the possible advantages in using the Duroc breed when compared to other breed lines on traits important for meat quality and carcass composition (Latorre et al., 2003; Ramirez and Cava, 2007; Rauw et al., 2003). A common theme between studies evaluated, however, is that there are conflicting results as to the overall benefit the use of the Duroc breed provides. Some studies have shown a decrease in carcass backfat thickness through the use of Duroc sires (Ramirez and Cava, 2007; Rauw et al., 2003) while others have shown no difference between the Duroc and other breeds such as a Pietran X Large White cross (Latorre et al., 2003), however this does not show a negative with the use of the breed it just does not show any improvement.

Mixed results in terms of pH decline are also present, as some have observed an increased rate of pH decline in accordance with a higher ultimate pH (Latorre et al., 2003), but others have observed the increased rate of pH decline and lower ultimate pH when using Duroc sires (Ramirez and Cava, 2007). There is agreement, though, in that the Duroc breed has been shown to improve instrumental tenderness measurements (Latorre et al., 2003; Schwab et al., 2006). This improvement in instrumental tenderness may be offset by a larger degree of drip loss and cook loss (Ramirez and Cava, 2007), though the effect of the Duroc breed is still debated as not all studies are in agreement as to the negative association of drip loss and cook loss with the Duroc breed (Ramirez and Cava, 2007; Rauw et al., 2003; Schwab et al., 2006). Therefore, the Duroc breed has positives in terms of production and
carcass composition improvements in addition to potential positives in terms of improving meat quality (Latorre et al., 2003; Rauw et al., 2003). However, its effectiveness is not entirely agreed upon (Ramirez and Cava, 2007) and thus the use of the Duroc breed may still account for variation in pork quality regardless of improvements in pig production.

Selection for improved lean growth and pork quality

Selection for improvements in lean growth efficiency and rate has also been investigated in terms of its effects on carcass composition and pork quality (Cameron and Curran, 1995; Lonergan et al., 2001). Selecting for improved lean growth rate has shown to be effective in increasing lean content, thus improving lean cut yield, with a subsequent decrease in the amount of backfat on the carcass (Cameron and Curran, 1995). Selection based on improved lean growth efficiency has also been shown to yield similar results. Lonergan et al. (2001) observed significant improvements in feed efficiency and carcass composition, consisting of decreased backfat thickness and increased lean cut percentage, in the selected line when compared to the control line. However, selection for improvements in lean growth efficiency has also been associated with a decrease in pork quality. Though lean growth efficiency and carcass composition improved, meat quality decreased as evidenced by higher Warner-Bratzler shear force values, lower subjective loin firmness scores, and poor water-holding capacity as seen by higher drip loss (Lonergan et al., 2001). It is possible that some the deterioration in meat quality may also be due to the influence of the selected line having significantly lower pH values early postmortem at 15, 30, and 45 minutes postmortem, although they were not due ultimate pH as no difference was detected (Lonergan et al., 2001). In addition to the decline in meat quality, Lonergan et al. (2001) also discovered less degradation of the protein troponin-T, thus showing that the role of
proteolysis in meat quality is likely altered which could lead to more variation in pork quality as a result of selection for improved lean growth efficiency. These studies highlight the notion of a deterioration of meat quality traits, likely leading to a loss of economic value, when selection practices are modified to incorporate more lean growth which is important for improving economic values in production.

Selection for improved growth rate and meat quality

Improvement in lean growth is not the sole method of selection used within the industry. Other studies have looked at selecting for increased growth rate through the use of methods such as age differences (Frederick et al., 2006) and improved daily weight gain (Nguyen et al., 2006; Suzuki et al., 2005; van Wijk et al., 2005). Frederick et al. (2006) achieved improvement based on age by using pigs reaching a market weight of 110 kg that differed in age by 27 days (153 vs. 180 d). This affected the rate of pH decline, with the older pigs exhibiting a higher pH at 45 minutes postmortem, but did not affect the extent of pH decline as both older and younger pigs exhibited similar 24 hour pH. Selecting for improved growth rate did not show an impact on drip loss due to age at time of slaughter and indicated that certain aspects of pork quality may be better in older, slow-growing pigs than younger, fast-growing pigs (Frederick et al., 2006). Thus, by using age of progeny at time of slaughter as an indicator of growth rate, it may be possible to negatively influence pork quality in younger, faster-growing pigs.

Selecting for improved average daily gain is another method of categorizing improvements in growth rate (Nguyen et al., 2006; Suzuki et al., 2005; van Wijk et al., 2005). Results of studies that have applied this method in terms of ultimate pH are contradicting, as some have observed a high 24 hour pH with a high average daily gain
(Nguyen et al., 2006) while others have seen an improved average daily gain associated with lower ultimate pH values (Suzuki et al., 2005; van Wijk et al., 2005). There is agreement from the studies in that improved average daily gain leads to pork that is lighter, paler in color (Suzuki et al., 2005; van Wijk et al., 2005) indicating a decrease in pork quality. Suzuki et al. (2005) also reported that an improved average daily gain leads to pork that is softer. Perhaps the greatest disagreement in the effect of improved growth rate through higher average daily gain is in that of its influence on drip loss as an indicator of water-holding capacity. The relationship has been shown to be positive in that water-holding capacity has improved through a decrease in drip loss (Suzuki et al., 2005), but it has also shown to be very unfavorable with an association with a remarkable increase in drip loss and subsequent decrease in water-holding capacity (van Wijk et al., 2005). So, the use of improved average daily gain as an indicator of improved growth rate leads to conflicting reports on the effect on pork quality, thus showing potential for further investigation.

With all factors taken into account, genetics play a large and increasing role in pork quality. Known genes can negatively effect pork quality, but mutations and the discovery of new alleles on these genes may actually lead to improvements in pork quality. When the use of different selection practices within the industry are accounted for in addition to the effects of genes and mutations, the entire scope of the role genetics plays in pork quality can be realized. It is a role that continues to lead to much research with the hopes of providing economic improvements to the entire industry from livestock producers through meat producers via pork quality improvements.
Conclusion

Pork quality is the end result of the interaction of many factors both pre-slaughter and postmortem. The conversion of muscle to meat initiates many structural changes of muscle cells that influence many of these factors such as pH decline and protein denaturation. Postmortem muscle protein proteolysis influences pork quality as well. Proteolysis can ensure that structural changes in the muscle cell do not influence quality attributes such as water-holding capacity and tenderness and can also be used as a means to be able to explain some of the variation in pork quality as it relates to these traits. Finally, pig genetics have influenced pork quality through the identification of genes and mutations within these genes that have led to pork quality differences when incorporated into breeding programs and selection practices. Different selection practices have also shown the potential the vary pork quality, yet questions still arise as to how these practices can be best applied to ensure that pork quality does not decline.

Literature Cited


INFLUENCE OF SELECTION FOR IMPROVED GROWTH RATE ON PORK QUALITY

A manuscript to be submitted to Meat Science

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Abstract

Variation in pork quality attributes like water-holding capacity and tenderness continues to reduce value of fresh pork. It is hypothesized that selection for improved growth rate has the potential to result in a loss of desirable fresh pork quality. The objective of this study was to investigate the contribution of selection for improved growth rate to variation in fresh pork quality. A pig population derived from the cross between a commercial line of Duroc sires and white line dams was subdivided according to the sires’ estimated breeding value (EBV) for age at 125 kg. Two slaughter groups were established. The first slaughter group included the most rapid growth High (Fast Growth) EBV pigs (n=48; 150 d at 125 kg) and a reference group that included Low (Slow Growth) EBV pigs (n=8; 160 d at 125 kg) and High EBV pigs (n=8; 160 d at 125 kg). The second slaughter group consisted of the slowest growing Low EBV pigs (n=48; 180 d at 125 kg) and a reference group that included Low EBV pigs (n=8; 174 d at 125 kg) and High EBV pigs (n=8; 169 d at 125 kg). Each group was harvested at a commercial facility. Loin pH and temperature decline was monitored on each carcass. Fresh pork quality characteristics and water-holding capacity was monitored at 2 d postmortem. Sensory characteristics (juiciness, tenderness, chewiness, flavor, and off-flavor) and star probe texture were measured 10 d postmortem. Pigs in High...
(Fast Growth) EBV for growth were younger at 125 kg (153 d vs. 177 d), which established that our criteria was successful in separation of growth rate. Growth rate group did not affect pH decline in the longissimus dorsi, however, temperature at 6 h was significantly lower in the slow growth line. Loin color and drip loss were not affected by growth rate. Loins from carcasses in the fast growth group had higher subjective marbling scores and higher lipid content than loins from carcasses in the slow growth group. Growth rate did not affect star probe or sensory quality of fresh pork loin. Selection for rapid growth by improving days of age at 125 kg did not significantly affect the quality of fresh pork loin. Therefore this method of selection can be used without compromising fresh pork quality.

**Key words:** Pork Quality, Growth, Sensory Quality, EBV

**Introduction**

One of the main goals of the swine industry is to produce the highest quantity of meat at the least cost. However, it is becoming increasingly apparent that attention must also be paid to the production of uniform, high quality pork (Lonergan et al., 2001) as consumers are becoming more discriminating and will no longer accept pork of inferior quality (Cassens, 2000). As such, pig breeding companies are now paying more attention to meat quality and are including quality traits as integral parts of selection programs (Plastow et al., 2005) in addition to controlling the known negative effects on pork quality when incorporating the halothane gene or the Rendement Napole (RN-) gene in selection programs in light of their known associations with production benefits (Channon et al., 2000; Brewer et al., 2002; Copenhafer et al., 2006). Thus, selection practices have become increasingly important in influencing pork quality.
Lonergan et al. (2001) demonstrated that selecting for improvements in lean growth efficiency has been shown to be successful in improving carcass composition by decreasing the amount of backfat on the carcass and increasing the yield of lean cuts. However, the selected line was also observed to have a lower pH early postmortem and a decrease in the presence of degraded troponin-T when compared with the control line which led to higher Warner-Bratzler shear force values and higher drip losses in the selected line, indicating product that was tougher and had poorer water-holding capacity (Lonergan et al., 2001). Thus, selecting for improvements in lean growth has been shown to have a negative effect on pork quality. However, questions still arise as to the effect of selecting for growth rate independent of lean growth potential in terms of influencing early postmortem changes in fresh pork and ultimately in pork quality. It is therefore hypothesized that selection for improved growth rate will influence early postmortem changes in pork quality and translate to differences in the quality of fresh pork between the progeny of sires selected for two different growth rates. The objective of this study was to determine the extent to which selection for increased growth impacts fresh pork quality. Determining the extent of impact will lead to further knowledge of how selection practices can influence pork quality and consumer acceptance.

**Materials and methods**

**Animals**

A pig population was derived from a cross between a commercial line of Duroc sires and synthetic white line dams. Progeny were subdivided into two groups according to the sires’ estimated breeding value (EBV) for growth rate based on the genetic merit of the sire to improve the growth rate in the progeny, in this instance age at 125 kg. High EBV sires
were the fast growth EBV and Low EBV sires were the slow growth EBV. Progeny (n=128) consisted of 50% barrows and 50% gilts to account for any sex differences and were slaughtered on two different slaughter dates. The first slaughter group included the most rapid growing pigs sired by High EBV growth boars (n=48; 150 d at 125 kg), and a reference group that included pigs sired by Low EBV growth boars (n=8; 160 d at 125 kg) and High EBV growth boars (n=8; 160 d at 125 kg). The second slaughter group consisted of the slowest growing pigs sired by Low EBV growth boars (n=48; 180 d at 125 kg), and a reference group that included pigs sired by Low EBV growth boars (n=8; 174 d at 125 kg) and High EBV growth boars (n=8; 169 d at 125 kg). Each group was harvested at a commercial slaughter facility using conventional chilling practices. Carcass weight, composition, and meat quality data were collected. Loins were removed from the carcass, vacuum packaged and shipped to the ISU Meat Laboratory.

**Growth and carcass composition**

Age of progeny at 125 kg, calculated based on performance data, and carcass composition data were collected at the time of harvest. The growth and carcass composition traits evaluated were: off-test weight, days to 125 kg, days to produce a 90 kg hot carcass, average daily gain on test, hot carcass weight, and backfat thickness of the carcass.

**pH and Temperature measurements**

Longissimus dorsi pH was measured 2, 6, 24, 48, and 240 h postmortem. Temperature of the longissimus dorsi was measured at 2, 6, and 24 h postmortem. Temperature and pH measurements were taken by a penetration probe on right side loins using a Hanna 9025 pH/ORP meter (Hanna Instruments, Woonsocket, RI). The pH probe
was calibrated with temperature at each time period using two buffers (pH 4.2 and 7.10). Calibration was monitored after each 5 carcasses.

**Meat quality traits**

Loin quality scores were evaluated 48 h postmortem according to National Pork Board standards (2000). Loins were assigned a score for color, firmness, wetness, and marbling while a trained panel (n = 2) was used to determine a color score (1 = pale, 6 = dark) for each loin eye (National Pork Board, 2000). Firmness and wetness were evaluated on a three point scale (1 = soft and wet, 3 = firm and dry). Marbling values were based on NPB standards. Loin meat was also evaluated for lipid composition (AOAC, Hexane extraction) and moisture composition (AOAC). Hunter L*, a* and b* values were determined at 1 day postmortem on 2.54 cm thick chops. Samples were allowed to bloom for 1 hour at room temperature and were analyzed on a calibrated Hunter Labscan colorimeter (Hunter Association Laboratories, Inc.; Reston, VA.) A CIE D/65 10° standard observer and a 1.27 cm viewing port were used to obtain three color measurements on each of three chops. All nine color measurements were used to determine an average color score for each loin. Calpastatin activity was determined as described by Lonergan et al. (2001).

**Drip loss**

Loin chops were evaluated for drip loss at 48 h postmortem. Drip loss was determined using 2.54 cm-thick boneless chops (two per loin) by similar method to Lonergan et al. (2001). Drip loss was evaluated as weight lost from the entire chop, done in duplicate. Drip loss percentage was calculated by the following equation: 

\[
\frac{(\text{initial weight} - \text{final weight})}{\text{initial weight}} \times 100.
\]
**Star probe**

Star probe measurements were taken as an instrumental indication of texture of the loin, through analysis of cooked loin chops, by similar method to Lonergan et al. (2007). Star probe is a measurement of the peak load necessary to puncture and compress the product to 20% of its height. The star probe consists of a circular, five-pointed star probe measuring 9 mm in diameter with 6 mm between each point, and it punctures the product at a crosshead speed of 3.3 mm/second. Samples consisted of two chops from each loin 2.54 cm thick and aged for 7 days. Chops were then cooked to an internal temperature of 71°C in a convection oven prior to texture analysis. Each chop was compressed three times and all six measurements used to determine an average for each loin.

**Sensory Panels**

A trained sensory panel (n = 5) evaluated loin chops for sensory traits using a similar method as described by Lonergan et al. (2007). Loin chops were evaluated for sensory tenderness, chewiness, juiciness, flavor, and off-flavor. A scale of 1-10 was used (1 = not tender, chewy, juicy, flavorful, no off-flavor; 10 = very tender, chewy, juicy, flavorful, high off-flavor) to evaluate all chops. Samples consisted of loin chops 2.54 cm thick aged for 10 days. Prior to analysis, samples were cooked to an internal temperature of 71°C using an electric oven broiler.

**Statistical analysis**

Data were analyzed using the GLM procedure of SAS and Least Squares Means by growth rate, through EBV group, for all traits of interest were computed. A series of models were used to analyze the data by sire EBV group. A model consisting of EBV group and gender was used to analyze off-test weight, age at 125 kg, days to produce a 90 kg hot
carcass, calpastatin activity, lipid and moisture content, and marbling. A model including EBV group, gender, and on-test weight was used to analyze average daily gain. A model including EBV group, gender, and age at harvest was used to analyze Hot Carcass Weight. A model including EBV group, gender, and Hot Carcass Weight was used to analyze yield and backfat thickness. Finally, a model including EBV group, gender, harvest day, and EBV group x harvest day interaction was used to analyze pH, temperature, Hunter color, subjective color, drip loss, sensory traits, and star probe.

Results and Discussion

Previous studies have demonstrated the improvement in growth and carcass composition traits of pigs that have been selected for improvements in lean growth efficiency and lean growth rate (Cameron & Curran, 1995; Lonergan et al., 2001). This study investigates the influence of selecting sires with significant emphasis on improving growth rate, using progeny age at 125 kg as an indicator of growth rate, independent of lean growth efficiency or lean growth rate.

Selection differences were observed by investigating differences of progeny from two sire groups selected for growth rate. The Fast Growth EBV group was selected based on the ability of their progeny to show significant improvements in growth rate, or demonstrate their ability to reach 125 kg sooner than the status quo. The Slow Growth EBV group, on the other hand, was selected for the ability of their progeny to show no improvements for growth rate. In other words, the Slow Growth EBV group was chosen for their ability to maintain the status quo for growth rate and not show any significant improvements.

Pigs sired from Fast Growth EBV boars were significantly different than pigs sired from Slow Growth EBV boars for all growth traits evaluated, as summarized in Table 1.
Progeny of Fast Growth EBV sires were significantly heavier at the time of harvest than those pigs sired by Slow Growth EBV sires, as evidenced by a higher off-test weight (P<0.01). Fast Growth EBV pigs were also significantly younger at 125 kg than Slow Growth EBV pigs (P<0.01), thus showing success in selection for improved growth rate of the progeny. The difference between both groups is in excess of 21 days, thus the pigs from Fast Growth EBV sires have the potential to reach a market ready weight over 3 weeks sooner than pigs from Slow Growth EBV sires designed to maintain the status quo and not show any improvements for growth rate. In essence, progeny from Fast Growth EBV sires have the potential to significantly improve growth rate than those progeny with average performance.

Progeny from Fast Growth EBV sires had a higher average daily gain than progeny from Slow Growth EBV sires (P<0.01), showing a likelihood of selecting for appetite in these progeny. The difference in average daily gain was likely a result of the selected progeny consuming more feed and therefore putting on more weight sooner than the progeny designed to maintain the status quo, although feed intake was not measured in this study. Progeny from Fast Growth EBV sires also took less days to produce a 90 kg hot carcass weight (P<0.01) than progeny from Slow Growth EBV sires.

These observed growth differences are important because now the other comparisons that can be made between the two groups have merit. If there were not differences in growth traits between the two groups, comparisons based on sire EBV would not be beneficial and comparisons could only be made between all the progeny regardless of sire EBV. The differences in growth traits between both sire EBV groups are important because they show
success in selecting for improved growth rate over the status quo and they also provide merit for other comparisons made between the two groups.

No significant differences between sire EBV groups were observed for all carcass traits evaluated (Table 2). Progeny from Fast Growth EBV sires and Slow Growth EBV sires were not different in their Hot carcass weight, Yield %, or Backfat thickness (P>0.05). This differs from the results of those studies selecting for lean growth efficiency and rate in which they observed carcass composition differences between the selected and control groups (Cameron & Curran, 1995; Lonergan et al., 2001). Cameron and Curran (1995) found that selecting for improved lean growth rate was successful in improving lean content and lean yield percentage in addition to a decrease in backfat thickness of the carcass. Similar results were observed by Lonergan et al. (2001) when selecting for improved lean growth efficiency as they found a significant improvement in carcass composition as a result of decreased backfat thickness and increased lean cut percentage to coincide with the improved feed efficiency and lean growth efficiency. However, the results of this study are not surprising since it was an investigation of the effects of selecting for growth rate and was not meant to account for lean growth of the progeny.

Temperature measurements of the longissimus dorsi were taken in order to account for any differences due to slaughter day since the progeny were harvested on two slaughter dates and possible variations in carcass cooling may have resulted, as well as to be able to observe any possible variations between the two groups as a result of possible differences in terms of the rate and extent of temperature decline. Carcasses from progeny of Fast Growth EBV sires had a significantly higher temperature at 6 hr than pigs from Slow Growth EBV sires (P<0.05; Table 3). Progeny from both sire EBV groups did not differ in carcass loin
temperature at 2 hr or 24 hr (P>0.05), therefore there are essentially no differences in
temperature decline as both sire EBV groups reached similar endpoint temperatures.

Progeny from Fast Growth EBV sires did not significantly differ from the progeny of
Slow Growth EBV sires in pH measured at 2 h, 6 h, 24 h, 48 h, or 10 days (P>0.05; Table 3).
Postmortem pH decline has been identified as an important factor in determining pork quality
(van der Wal et al., 1997), especially when considering the rate and extent of pH decline. A
rapid pH decline and a low ultimate pH have been associated with the development of a low
water-holding capacity and the resulting unacceptably high drip loss (Huff-Lonergan &
Lonergan, 2005). Also, a low pH early postmortem, as early as 6 hr, has been shown to
predict poor water-holding capacity of pork (Gardner et al., 2005), thus indicating the
potential for a decrease in ultimate pork quality. Previous work has demonstrated a slower
rate of pH decline early postmortem in older, slower growing pigs as evidenced by a higher
45 minute pH, but no difference between older, slower growing pigs and younger, faster
growing pigs in terms of the extent of pH decline at 24 h postmortem (Frederick et al., 2006)
with similar results observed when selecting for improved lean growth efficiency (Lonergan
et al., 2001). In this study, no differences in the rate of pH decline or in ultimate pH were
observed between the progeny of the two sire EBV groups selected for growth rate.
Therefore, any differences in ultimate pork quality that may be due to selecting for improved
growth rate could not be attributed to differences in the rate and extent of pH decline.

Results summarized in Table 4 highlight the influence of selecting for improvement
in growth rate on meat quality traits. Progeny from Fast Growth EBV sires and Slow Growth
EBV sires did not differ according to loin color, firmness, and wetness scores (P>0.05).
However, progeny from Fast Growth EBV sires had a significantly higher Subjective loin
marbling score than progeny from Slow Growth EBV sires (P<0.01). This is expected because presumably these pigs were indirectly selected through their sires based on their appetite which would likely lead to a greater fat deposition within the muscle of the carcass. This hypothesis is supported by previous findings that have found strong correlations of feed intake with weight gain and fat deposition (Rauw, Soler, Tibau, Reixach & Raya, 2006) as well as a tendency \( P=0.07 \) for older, slower growing pigs to consume less feed than younger, faster growing pigs (Frederick et al., 2006). Rauw et al. (2006) also found a strong sire influence during the first stages of postweaning growth, lasting as long as 175 d of age, that slowly decreased with age, thus implying a greater influence of sire on feed intake of younger animals. The progeny of the Fast Growth EBV sires had a significantly higher average daily gain than the progeny from Slow Growth EBV sires and also had a higher off-test weight which would likely have resulted in the addition of more fat within the muscle as more lipid. Since no carcass composition differences were observed between the progeny of the two groups, it may be possible that the observed difference in marbling score is a result of the increased appetite of the Fast Growth EBV progeny leading to an increase in lipid deposition in the loin.

This hypothesis is contradicted with previous results that have found low correlations between marbling and average daily gain (Suzuki et al., 2005; van Wijk et al., 2005; Frederick et al., 2006). However, previous studies did not measure lipid composition nor did they discuss the possibility of lipid composition increasing as marbling increased which would provide evidence in favor of the presented hypothesis. Other studies support this idea to a certain degree in that genetic differences due to breed lead to increased feed intake and resulting increase in marbling and lipid content (Latorre et al., 2003) though age effect on
average daily gain is not accounted for. The difference in marbling score in this study is reflected in the results for lipid composition (Table 4). Progeny from Fast Growth EBV sires had a significantly higher percentage of lipid content than progeny from Slow Growth EBV sires (P<0.05). This highlights the possibility of the hypothesis that selection for improved growth rate results in a selection for appetite and subsequent increase in marbling score, since more lipid was found in the faster growing, heavier final weight progeny of Fast Growth EBV sires.

No significant differences were observed between the progeny of the Fast and Slow Growth EBV sires for Hunter color L, a, or b values (P>0.05; Table 4). Progeny from Fast Growth EBV sires were not significantly different than progeny from Slow Growth EBV sires when evaluated for drip loss, moisture content, or cook loss (P>0.05; Table 4). Thus, pork quality differences associated with water-holding capacity were not observed between the progeny of the Fast and Slow Growth EBV sires when taking all factors into account including no observed differences in pH measurements between the two groups. Other studies investigating differences in drip loss from differing genetic line backgrounds have observed differences between lines in terms of drip loss at 2 d of storage (Bee et al., 2007) so there are differences that can be present due to genetic background regardless of selection practices. Once again, this differs from the results of selecting for lean growth efficiency in which the selected line of pigs for lean growth efficiency had a poorer water-holding capacity as evidenced by a higher drip loss (Lonergan et al., 2001). Thus, there may be different factors of importance when selecting for improvements in lean growth efficiency versus strictly selecting for improvements in growth rate.
The calpain enzymes have been shown to be responsible for a great percentage of the postmortem degradation of myofibrillar and cytoskeletal proteins that are important in maintaining structural integrity of the myofibril and muscle (Koohmaraie, 1992; Koohmaraie et al., 1995; Huff-Lonergan et al., 1996). The degradation of proteins by the calpain system explains some of the variation in postmortem tenderness and water-holding capacity in fresh meat (Lonergan et al., 2001; Melody et al., 2004; Huff-Lonergan & Lonergan, 2005).

Calpastatin, the endogenous competitive inhibitor to the enzymes m- and μ-calpain, has also been shown to be involved in influencing postmortem tenderness by primarily regulating calpain activity in postmortem muscle (Koohmaraie, 1992; Koohmaraie et al., 1995), and calpastatin activity has also been shown to be correlated with drip loss when selecting for improvements in lean growth efficiency (Lonergan et al., 2001). In this study, calpastatin activity at 2 d postmortem was not affected by sire EBV group for growth rate (P>0.05; Table 4). This is in agreement with the results of selecting for improvements in lean growth efficiency (Lonergan et al., 2001) in which no difference in calpastatin activity at 24 h postmortem was observed between the selected and control groups. Therefore, selecting for improved growth rate may not be responsible for any variations in postmortem proteolysis that may be associated with variations in pork quality traits.

Star probe is an instrumental indicator of texture that provides results similar to those of instrumental cooked pork tenderness measurements by indicating the peak load necessary to compress and puncture the product to 20% of its original height (Huff-Lonergan, Baas, Malek, Dekkers, Prusa & Rothschild, 2002; Lonergan et al., 2007). Lower star probe values, indicating softer texture and increased tenderness of cooked pork, has been correlated with high pH values in addition to sensory texture traits (Huff-Lonergan et al., 2002; Lonergan et
al., 2007). EBV progeny group did not affect star probe (P>0.05; Table 4). Thus, selecting for improved growth rate did not influence instrumental texture or tenderness.

Pork sensory quality can be influenced by a number of factors including the rate and extent of pH decline (Huff-Lonergan et al., 2002; Gardner et al., 2005), extent of postmortem proteolysis (Wheeler et al., 2000), breed (Wood et al., 2004), muscle type (Melody et al., 2004), and intramuscular lipid (Huff-Lonergan et al., 2002). Of these factors, perhaps the most influential is that of ultimate pH, in which a high ultimate pH has been associated with superior pork sensory (Huff-Lonergan et al., 2002), in particular higher sensory tenderness and lower sensory chewiness scores (Lonergan et al., 2007). The effect of long term selection for improved leanness in Duroc swine on the sensory quality of pork has been investigated and no differences in sensory quality between the selected and control lines was reported (Schwab et al., 2006). Sensory traits were not affected by selection for improved growth rate (Table 5). Progeny of the two sire EBV groups did not differ according to subjective sensory juiciness, tenderness, chewiness, flavor, or off-flavor scores (P>0.05). Therefore, selection for improved growth rate did not have an effect on the sensory quality of pork.

**Conclusions**

The use of sires with different genetic merit for growth significantly changed the growth performance of progeny without affecting carcass composition when adjusted for weight. Progeny of Fast Growth EBV sires reached 125 kg in fewer days than progeny from Slow Growth sires designed to maintain the status quo for growth rate and did so without compromising carcass composition. Progeny from boars selected for improved growth rate also exhibited a higher degree of marbling in the loin which was mimicked by a higher percentage of lipid in the loin as well. The resulting increase in lipid and marbling may have
been a potential product of selecting progeny based on their appetite, such as older, slower
growing pigs consuming less feed than younger faster, growing pigs (Frederick et al., 2006),
and may not be responsible for any changes in ultimate tenderness and water-holding
capacity. Selecting sires based on their genetic merit for improving progeny growth rate
potential, in this instance progeny age at 125 kg, did not have a significant affect on the
quality of fresh pork loins. Thus, observed differences due to in growth performance were
not associated with a significant change in pork quality, since selecting for improved growth
rate did not negatively impact fresh pork quality nor was a significant positive impact
observed.

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pH decline affect proteolysis of cytoskeletal proteins and water-holding capacity in

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Augmented postmortem glycolysis does not occur early postmortem in AMPKy3-


Table 1. Growth traits means of progeny from two different sire growth rate Estimated Breeding Values (EBV).

<table>
<thead>
<tr>
<th>Item</th>
<th>Fast Growth EBV</th>
<th>Slow Growth EBV</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Off-test weight, kg</td>
<td>131.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>123.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.0</td>
</tr>
<tr>
<td>Age 125 kg, days</td>
<td>153.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>177.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.0</td>
</tr>
<tr>
<td>Average daily gain, g/day</td>
<td>1101&lt;sup&gt;a&lt;/sup&gt;</td>
<td>963&lt;sup&gt;b&lt;/sup&gt;</td>
<td>22.0</td>
</tr>
<tr>
<td>Days 90 kg hot carcass wt., days</td>
<td>159.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>179.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.8</td>
</tr>
</tbody>
</table>

<sup>a,b</sup>Within a row, means without a common superscript letter differ (P<.01).
Table 2. Carcass traits means of progeny from two different sire growth rate Estimated Breeding Values (EBV).

<table>
<thead>
<tr>
<th>Item</th>
<th>Fast Growth EBV</th>
<th>Slow Growth EBV</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hot carcass wt., kg (adj. for age)</td>
<td>89.9</td>
<td>89.6</td>
<td>1.1</td>
</tr>
<tr>
<td>Yield, %</td>
<td>76.6</td>
<td>76.7</td>
<td>0.01</td>
</tr>
<tr>
<td>Backfat thickness, mm</td>
<td>10.5</td>
<td>10.5</td>
<td>0.2</td>
</tr>
</tbody>
</table>

a,b Within a row, means without a common superscript letter differ (P<.01).
Table 3. Temperature and pH measurements means of progeny from two different sire growth rate Estimated Breeding Values (EBV).

<table>
<thead>
<tr>
<th>Item</th>
<th>Fast Growth EBV</th>
<th>Slow Growth EBV</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature, °C*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 h</td>
<td>25.6</td>
<td>25.1</td>
<td>0.4</td>
</tr>
<tr>
<td>6 h</td>
<td>14.4x</td>
<td>13.6y</td>
<td>0.2</td>
</tr>
<tr>
<td>24 h</td>
<td>2.5</td>
<td>2.3</td>
<td>0.1</td>
</tr>
<tr>
<td>pH*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 h</td>
<td>6.18</td>
<td>6.20</td>
<td>0.04</td>
</tr>
<tr>
<td>6 h</td>
<td>5.90</td>
<td>5.92</td>
<td>0.03</td>
</tr>
<tr>
<td>24 h</td>
<td>5.65</td>
<td>5.61</td>
<td>0.02</td>
</tr>
<tr>
<td>48 h</td>
<td>5.67</td>
<td>5.67</td>
<td>0.02</td>
</tr>
<tr>
<td>10 d</td>
<td>5.66</td>
<td>5.67</td>
<td>0.02</td>
</tr>
</tbody>
</table>

x,y Within a row, means without a common superscript letter differ (P<.05).

*Measured by a penetration probe on right side loins using a Hanna 9025 pH/ORP meter (Hanna Instruments, Woonsocket, RI). pH probe was calibrated with temperature at each time period using two buffers (pH 4.2 and 7.10).
Table 4. Loin meat quality traits means of progeny from two different sire growth rate Estimated Breeding Values (EBV).

<table>
<thead>
<tr>
<th>Item</th>
<th>Fast Growth EBV</th>
<th>Slow Growth EBV</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loin color score (1 to 6)*</td>
<td>2.5</td>
<td>2.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Loin marbling score (1 to 10)*</td>
<td>2.0\textsuperscript{a}</td>
<td>1.4\textsuperscript{b}</td>
<td>0.1</td>
</tr>
<tr>
<td>Loin firmness score (1 to 3)*</td>
<td>1.9</td>
<td>1.8</td>
<td>0.1</td>
</tr>
<tr>
<td>Loin wetness score (1 to 3)*</td>
<td>1.8</td>
<td>1.8</td>
<td>0.1</td>
</tr>
<tr>
<td>Hunter L color**</td>
<td>46.70</td>
<td>47.54</td>
<td>0.41</td>
</tr>
<tr>
<td>Hunter a color**</td>
<td>6.24</td>
<td>6.23</td>
<td>0.1</td>
</tr>
<tr>
<td>Hunter b color**</td>
<td>9.27</td>
<td>9.37</td>
<td>0.15</td>
</tr>
<tr>
<td>Drip loss, %</td>
<td>2.50</td>
<td>2.28</td>
<td>0.25</td>
</tr>
<tr>
<td>Lipid, %</td>
<td>1.99\textsuperscript{x}</td>
<td>1.22\textsuperscript{y}</td>
<td>0.18</td>
</tr>
<tr>
<td>Moisture, %</td>
<td>73.67</td>
<td>73.75</td>
<td>0.14</td>
</tr>
<tr>
<td>Cook loss, %</td>
<td>19.55</td>
<td>19.39</td>
<td>0.38</td>
</tr>
<tr>
<td>Star Probe, kg\textsuperscript{***}</td>
<td>5.43</td>
<td>5.54</td>
<td>0.11</td>
</tr>
<tr>
<td>Calpastatin, units of activity/g of tissue\textsuperscript{****}</td>
<td>1.03</td>
<td>0.98</td>
<td>0.03</td>
</tr>
</tbody>
</table>

\textsuperscript{a,b} Within a row, means without a common superscript letter differ (P<.01).

\textsuperscript{x,y} Within a row, means without a common superscript letter differ (P<.05).

*Evaluated 48 hr postmortem according to National Pork Board Standards (2000).

**Analyzed on a calibrated Hunter Labscan colorimeter (Hunter Association Laboratories, Inc.; Reston, VA.) A CIE D/65 10° standard observer and a 1.27 cm viewing port were used to obtain three color measurements on each of three chops. All nine used to determine average color score.

***Instrumental indication of loin texture by similar method to Lonergan et al. (2007).

****Determined 24 h postmortem as described by Lonergan et al. (2001).
Table 5. Sensory traits means of progeny from two different sire growth rate Estimated Breeding Values (EBV).

<table>
<thead>
<tr>
<th>Item</th>
<th>Fast Growth EBV</th>
<th>Slow Growth EBV</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juiciness score (1 to 10)*</td>
<td>5.3</td>
<td>5.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Tenderness score (1 to 10)*</td>
<td>5.9</td>
<td>6.4</td>
<td>0.2</td>
</tr>
<tr>
<td>Chewiness score (1 to 10)*</td>
<td>2.8</td>
<td>2.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Flavor score (1 to 10)*</td>
<td>1.9</td>
<td>2.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Off-flavor score (1 to 10)*</td>
<td>4.0</td>
<td>3.7</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*a,b Within a row, means without a common superscript letter differ (P<.01).

*Evaluated by a trained sensory panel using similar method as described by Lonergan et al. (2007). A value of 1 represents a low degree of juiciness, tenderness, chewiness, flavor, and off-flavor. A value of 10 represents a high degree of juiciness, tenderness, chewiness, flavor, and off-flavor.
INFLUENCE OF SELECTION FOR IMPROVED GROWTH RATE ON RELATIONSHIPS OF PORK QUALITY TRAITS

A manuscript to be submitted to Meat Science

C.E. Wagner, E. Huff-Lonergan, A.A. Sosnicki, S.B. Jungst, and S.M. Lonergan

Abstract

Variation in pork quality attributes like water holding capacity and tenderness continues to reduce value of fresh pork. The objective of this study was to investigate if genetic selection of sires for improved growth rate is associated with changes in the relationships of fresh pork quality traits that can account for variations in pork quality. A pig population derived from the cross between a commercial line of Duroc sires and white line dams was subdivided according to the sires’ estimated breeding value (EBV) for age at 125 kg. Differences in age at 125 kg was achieved by slaughtering pigs sired by High (Fast Growth) EBV growth boars (n=48), Low (Slow Growth) EBV growth boars (n=48) or a control group consisting of pigs from both sire EBVs (n =32). Loin pH and temperature decline curves were monitored on each carcass. Fresh pork quality characteristics and water holding capacity were monitored at 2 d postmortem. Sensory traits (juiciness, tenderness, chewiness, flavor, and off-flavor) and texture (star probe) were measured 10 d postmortem. Proteolysis was estimated by desmin degradation and µ-calpain autolysis at 2 d postmortem. Pork quality data were analyzed in a one-way analysis of variance by sire EBV group for growth. Progeny were divided into groups based on sire EBV group into a Fast Growth EBV group and Slow Growth EBV group. Correlations among quality data were evaluated for
both groups. Drip loss was negatively correlated to all measurements of pH in the Fast Growth EBV group and all except 6 h pH in the Slow Growth EBV group. Drip loss was negatively correlated to calpastatin activity in the Fast Growth EBV group only, and was not correlated to any other measurements of proteolysis. Juiciness was correlated to 2 h and 48 h pH in the Fast Growth EBV group but was not correlated to any pH measurements in the Slow Growth EBV group. Juiciness and age at 125 kg were positively correlated in the Slow Growth EBV group but were not correlated in the Fast Growth EBV group. Juiciness was not correlated to any proteolysis measurements in either group. Tenderness was similarly correlated with pH at 24- and 48 h and 10 d for both the Fast and Slow Growth EBV groups. Tenderness was correlated to indices of proteolysis (calpastatin activity and µ-calpain autolysis) in the Fast Growth EBV group but not the Slow Growth EBV group. Chewiness was not correlated to pH at any time period in the Fast Growth EBV group, but was negatively correlated to 24 h and 10 d pH in the Slow Growth EBV group. Calpastatin activity and µ-calpain autolysis were correlated with chewiness in the Fast Growth EBV group but not the Slow Growth EBV group. Star probe was negatively correlated to 48 h pH in the Fast Growth EBV group but was not correlated at any time in the Slow Growth EBV group. Star probe was also correlated to calpastatin activity in both sire EBV groups but was not correlated to any other proteolysis measurement in either group. The results demonstrate the complexity of inheritance and genetic correlations among pig growth and muscle/meat quality characteristics. It is plausible to reason that pork water-holding capacity and sensory characteristics are dependent on a combination of particular genetic background/breeding program and individual genetic predisposition of the animal for growth performance.

Key words: Growth, Pork Quality, Proteolysis, pH, EBV
Introduction

Production of pork products that possess acceptable quality is of the utmost importance, as consumers of pork are becoming more discriminating and will no longer accept products of inferior quality (Cassens, 2000). The proteolysis of muscle proteins, in addition to and independent of pH decline, has been shown as a good indicator of potential variation in pork quality (Gardner et al., 2005). Of particular importance is the degradation of proteins such as desmin, which is a known substrate of the protease μ-calpain and can be influenced by it’s activity and subsequent autolysis (Koohmaraie, 1992; Huff-Lonergan et al., 1996; Geesink & Koohmaraie, 1999). The degradation of desmin and autolysis of μ-calpain have been shown to account for differences in water-holding capacity (Melody et al., 2004; Gardner et al., 2005; Huff-Lonergan & Lonergan, 2005; Koohmaraie & Geesink, 2006) and tenderness of fresh meat (Taylor et al., 1995; Wheeler et al., 2000; Melody et al., 2004; Gardner et al., 2005). Thus, differences in proteolysis can potentially account for variation in pork quality.

In response to the need for consumer acceptance of fresh pork, pig breeding companies are now paying more attention to meat quality and are including quality traits as integral parts of selection programs (Plastow et al., 2005). As a result, it is important to understand how selection practices ultimately affect pork quality and consumer acceptance. Selecting for lean growth efficiency has been observed to lead to differences in pH decline and proteolysis and ultimately lead to products that are tougher and have higher drip losses (Lonergan et al., 2001). However, questions still arise as to whether selecting for growth potential independent of lean growth has the same negative effects on pork quality. In addition, if there are variations in pork quality as a result of selecting for growth rate, it is
important to understand the causes of the quality variations and determine how relationships between pork quality traits may have changed as a result of the selection method. It is hypothesized that selecting for improved growth rate will change the relationship between pork quality traits and alter how they can be used to explain pork quality variations. The objective of this study was to determine the extent to which selection for increased growth impacts pork quality by understanding how relationships between pork quality traits that can be used to explain variations in quality are influenced as a result of the selection practice. Understanding how these relationships are influenced will lead to a further understanding of how these multifactorial traits can be used to decrease the amount of variation in pork quality and ultimately be beneficial to the consumer acceptance of fresh pork products.

**Materials and methods**

**Animals**

A pig population was derived from a cross between a commercial line of Duroc sires and synthetic white line dams. Progeny were subdivided into two groups according to the sires’ estimated breeding value (EBV) for growth rate based on the genetic merit of the sire to improve progeny growth rate, in this instance age at 125 kg. High EBV sires were the fast growth EBV and Low EBV sires were the slow growth EBV. Progeny (n=128) consisted of 50% barrows and 50% gilts to account for any sex differences and were slaughtered on two different slaughter dates. The first slaughter group included the most rapid growing pigs sired by High EBV growth boars (n=48; 150 d at 125 kg), and a reference group that included pigs sired by Low EBV growth boars (n=8; 160 d at 125 kg) and High EBV growth boars (n=8; 160 d at 125 kg). The second slaughter group consisted of the slowest growing pigs sired by Low EBV growth boars (n=48; 180 d at 125 kg), and a reference group that included pigs
sired by Low EBV growth boars (n=8; 174 d at 125 kg) and High EBV growth boars (n=8; 169 d at 125 kg). Each group was harvested at a commercial slaughter facility using conventional chilling practices. Carcass weight, composition, and meat quality data were collected. Loins were removed from the carcass, vacuum packaged and shipped to the ISU Meat Laboratory.

**Growth and carcass composition**

Age of progeny at 125 kg, calculated based on performance data, and carcass composition data were collected at the time of harvest. The growth and carcass composition traits evaluated were: off-test weight, days to 125 kg, days to produce a 90 kg hot carcass, average daily gain on test, hot carcass weight, and backfat thickness of the carcass.

**pH and Temperature measurements**

Longissimus dorsi pH was measured 2, 6, 24, 48, and 240 h postmortem. Temperature of the longissimus dorsi was measured at 2, 6, and 24 h postmortem. Temperature and pH measurements were taken by a penetration probe on right side loins using a Hanna 9025 pH/ORP meter (Hanna Instruments, Woonsocket, RI). The pH probe was calibrated with temperature at each time period using two buffers (pH 4.2 and 7.10). Calibration was monitored after each 5 carcasses.

**Meat quality traits**

Loin quality scores were evaluated 48 h postmortem according to National Pork Board standards (2000). Loins were assigned a score for color, firmness, wetness, and marbling while a trained panel (n = 2) was used to determine a color score (1 = pale, 6 = dark) for each loin eye (National Pork Board, 2000). Firmness and wetness were evaluated on a three point scale (1 = soft and wet, 3 = firm and dry). Marbling values were based on
NPB standards. Loin meat was also evaluated for lipid composition (AOAC, Hexane extraction) and moisture composition (AOAC). Hunter L*, a* and b* values were determined at 1 day postmortem on 2.54 cm thick chops. Samples were allowed to bloom for 1 hour at room temperature and were analyzed on a calibrated Hunter Labscan colorimeter (Hunter Association Laboratories, Inc.; Reston, VA.) A CIE D/65 10° standard observer and a 1.27 cm viewing port were used to obtain three color measurements on each of three chops. All nine color measurements were used to determine an average color score for each loin. Calpastatin activity was determined as described by Lonergan et al. (2001).

Drip loss

Loin chops were evaluated for drip loss at 48 h postmortem. Drip loss was determined using 2.54 cm-thick boneless chops (two per loin) by similar method to Lonergan et al. (2001). Drip loss was evaluated as weight lost from the entire chop, done in duplicate. Drip loss percentage was calculated by the following equation: \[
\left(\frac{\text{initial weight} - \text{final weight}}{\text{initial weight}}\right) \times 100.
\]

Star probe

Star probe measurements were taken as an instrumental indication of texture of the loin, through analysis of cooked loin chops, by similar method to Lonergan et al. (2007). Star probe is a measurement of the peak load necessary to puncture and compress the product to 20% of its height. The star probe consists of a circular, five-pointed star probe measuring 9 mm in diameter with 6 mm between each point, and it punctures the product at a crosshead speed of 3.3 mm/second. Samples consisted of two chops from each loin 2.54 cm thick and aged for 7 days. Chops were then cooked to an internal temperature of 71°C in a convection...
oven prior to texture analysis. Each chop was compressed three times and all six measurements used to determine an average for each loin.

**Sensory Panels**

A trained sensory panel (n = 5) evaluated loin chops for sensory traits using a similar method as described by Lonergan et al. (2007). Loin chops were evaluated for sensory tenderness, chewiness, juiciness, flavor, and off-flavor. A scale of 1-10 was used (1 = not tender, chewy, juicy, flavorful, no off-flavor; 10 = very tender, chewy, juicy, flavorful, high off-flavor) to evaluate all chops. Samples consisted of loin chops 2.54 cm thick aged for 10 days. Prior to analysis, samples were cooked to an internal temperature of 71°C using an electric oven broiler.

**Whole-muscle sample preparation for gel electrophoresis**

Samples were prepared from muscle (.2 g) taken at 2 d postmortem from the longissimus dorsi for SDS-PAGE analysis and Western blotting of desmin degradation and μ-calpain autolysis. Whole-muscle protein extraction (extraction buffer consisted of 10 mM sodium phosphate and 2% [vol/vol] SDS; pH 7.0) and gel electrophoresis sample preparation was conducted according to Lonergan et al. (2001). Protein concentration was determined using the method described by Lonergan et al. (2001) using premixed reagents (Bio-Rad Laboratories, Hercules, CA). Gel samples, containing 4 mg/mL of protein, were frozen and stored at -80°C until subsequent analysis.

**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, and 0.5 M Tris-HCl, pH 8.8) were used for determination of desmin degradation at 2 d of storage. Nine
percent polyacrylamide separating gels were used for determination of $\mu$-calpain autolysis at 2 d of storage. Both gels were used with 5% 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) to fractionate muscle proteins.

Gels (10 cm wide x 8 cm tall x 1.5 mm thick) for analysis of desmin degradation were run on Hoefer Mighty Small II SE 250/SE 260 electrophoresis units (Hoefer Scientific Instruments, San Francisco, CA). Gels (10 cm wide x 12 cm tall x 1.5 mm thick) for analysis of $\mu$-calpain autolysis were run on Hoefer Tall Mighty Small SE 280 electrophoresis units. The running buffer used for electrophoresis contained 25 mM Tris, 192 mM glycine, 2 mM EDTA, and 0.1% [wt/vol] SDS. Gels were loaded with 40 $\mu$g per lane of total protein for desmin or 80 $\mu$g per lane of total protein for $\mu$-calpain. Gels were run at a constant voltage of 120V for approximately 2.5-2.75 h.

Gels for both desmin and $\mu$-calpain were transferred to polyvinylidene (PVDF) membranes (Millipore Corporation, Bedford, MA) using a Hoefer TE22 Mighty Small transfer tank electrophoresis unit (Hoefer Scientific Instruments) at 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. The temperature of the transfer buffer was maintained between 4°C and 8°C using a refrigerated circulating water bath (Ecoline RE106; Lauda Brinkmann, Wesbury, NY).

**Western blots.** Western blotting and chemiluminescent detection were done as described by Lonergan et al. (2001) and Melody et al. (2004). Posttransfer membranes were incubated for 1 h at room temperature in a blocking solution consisting of PBS-Tween (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. Desmin blots were incubated with primary polyclonal rabbit anti-desmin (No. V2022; Biomeda, Foster City, CA) diluted 1:10,000 in PBS-Tween overnight at 4°C. µ-calpain blots were incubated with primary monoclonal mouse anti-µ-calpain (No. MA3940; Sigma, St. Louis, MO) diluted 1:10,000 using the same protocol as the desmin blots. The following day, blots were removed from cold room and equilibrated to room temperature for 30 min. Blots were rinsed three times (10 min per rinse) in PBS-Tween. Blots were then incubated in secondary antibody for 1 h at room temperature. Desmin blots were incubated in goat anti-rabbit-HRP IgG (81-6120; Zymeda Laboratories, San Francisco, CA) diluted 1:5,000 in PBS-Tween. µ-calpain blots were incubated in goat anti-mouse IgG (5120611; Sigma) diluted 1:5,000 in PBS-Tween. Blots were rinsed in PBS-Tween three times (10 min per rinse) to remove any unbound secondary antibody. A chemiluminescent detection system was used to detect labeled protein bands for both desmin degradation and µ-calpain autolysis as described by the supplier (ECL, Amersham Pharmacia Biotech). Densities of immunoreactive protein bands were quantified by densitometry using ChemiImager 5500 (Alpha Innotech, San Leandro, CA) and Alpha Ease FC (v. 2.03; Alpha Innotech). Desmin degradation was indicated by a decrease in intensity of an approximately 55-kDa intact band and the presence of an increasing intensity desmin degradation product band of approximately 38-kDa (Melody et al., 2004). Intact desmin degradation ratio was calculated as the intensity of each immunoreactive desmin band over the intensity of the immunoreactive desmin band in a determined reference sample for consistency of intact desmin that was loaded on each gel. µ-calpain autolysis was indicated by the presence of a non-autolysed 80-kDa band in addition to the presence of an intermediate 78-kDa autolysis
product and the presence of a 76-kDa autolysis product. Autolysis of μ-calpain was calculated as the percentage of non-autolysed 80-kDa subunit as well as the percentage of the 78-kDa and 76-kDa subunit autolysis products.

**Statistical analyses**

Data were analyzed in a one-way analysis of variance by sire EBV group for growth rate using JMP 6.0 (SAS Institute, South Cary, NC). Progeny were divided into groups based on sire EBV group for growth rate into a High EBV group and a Low EBV group. Least Squares Means were calculated for all traits of interests and then compared for both groups using a Tukey-Kramer HSD test. Pearson correlations were also calculated and evaluated for both groups. Correlations were defined as significant if pairwise correlations $P<.05$.

**Results and Discussion**

Previous studies have demonstrated the improvement in growth and carcass composition traits of pigs that have been selected for improvements in lean growth efficiency and lean growth rate (Cameron & Curran, 1995; Lonergan et al., 2001). This study investigates the influence of selecting sires with a significant emphasis on improving growth rate independent of lean growth efficiency or lean growth rate. Selection differences were observed by investigating differences of progeny from two sire groups selected for growth rate. The Fast Growth EBV boars were selected based on the ability of their progeny to show significant improvements in growth rate, or demonstrate their ability to reach 125 kg sooner than the status quo. The Slow Growth EBV group, on the other hand, was selected for the ability of their progeny to show no improvements for growth rate. In other words, the Slow Growth EBV group was chosen for their ability to maintain the status quo for growth rate and not show any significant improvements.
Table 1 presents means, maximums, minimums, and standard deviations for traits measured in this study for all progeny evaluated separated by sire EBV for growth rate. This makes it easier to show variation of traits across groups.

The influence of selecting for improved growth rate on proteolysis traits is highlighted in Table 2. Proteolysis is thought to play a role in pork quality mainly through the influence of the calpain system of enzymes. The calpain enzymes have been shown to be responsible for a great percentage of the postmortem degradation of myofibrillar and cytoskeletal proteins that are important in maintaining structural integrity of the myofibril and muscle (Koohmaraie, 1992; Koohmaraie et al., 1995; Huff-Lonergan et al., 1996). Included among these proteins that have been shown to be of importance is the intermediate filament protein desmin (Melody et al., 2004). The degradation of proteins by the calpain system has been shown to be able to explain some of the variation in postmortem tenderness and water-holding capacity in fresh meat (Lonergan et al., 2001; Melody et al., 2004; Huff-Lonergan & Lonergan, 2005).

In the present study, significant differences were observed for the degradation of desmin between the progeny of Fast Growth EBV sires and Slow Growth EBV sires (Table 2). Progeny of Fast Growth EBV sires had a greater degree of intact desmin than progeny from Slow Growth EBV sires (P<0.01) in addition to a greater degree of desmin degradation product (P<0.05). The greater degree of intact desmin would suggest less proteolysis in the progeny of Fast Growth EBV sires, however that would also be associated with a decrease in the amount of desmin degradation product which is not the case here. It does show, though, that there are proteolysis differences when selecting for growth rate.
The proteolysis of key myofibrillar proteins that are known influence pork quality characteristics is most frequently associated with the autolysis of μ-calpain (Gardner et al., 2005). Therefore, it is important to investigate any potential differences in μ-calpain autolysis to truly understand the role of proteolysis in contributing to the variation in fresh pork quality as autolysis is the hallmark of calpain activation in postmortem muscle. The percentage of 76-kDa subunit autolysis product has been shown to be very beneficial in understanding the variation in fresh pork quality. The 76-kDa subunit has been positively correlated to pH early postmortem, meaning a low early pH will hinder μ-calpain autolysis (Gardner et al., 2005). Appearance of 76-kDa autolysis product has also been useful in being able to explain variations in drip loss and Warner-Bratzler shear force in fresh pork (Gardner et al., 2005). In the present study, progeny from Fast Growth EBV sires had a larger percentage of catalytic subunit present as the 76-kDa autolysis product than progeny from Slow Growth EBV sires (P<0.05). Therefore, any differences in ultimate pork quality could possibly be due to the differences in proteolysis as evidenced by differences in desmin degradation and μ-calpain autolysis.

Calpastatin, the competitive inhibitor to m- and μ-calpain, has also been shown to be involved in influencing postmortem tenderness by primarily regulating calpain activity in postmortem muscle (Koohmararie, 1992; Koohmararie et al., 1995), and calpastatin activity was also shown to be correlated with drip loss when selecting for improvements in lean growth efficiency (Lonergan et al., 2001). In this study, no significant differences were observed between the progeny of the Fast Growth EBV group and the Slow Growth EBV group for calpastatin activity (P>0.05; Table 2). This is in agreement with the results of selecting for improvements in lean growth efficiency (Lonergan et al., 2001) in which no
difference in calpastatin activity was observed between the selected and control groups. Therefore, even though no differences were observed in terms of calpastatin activity, selecting for improved growth rate may be responsible for any variations in postmortem proteolysis that may be associated with variations in pork quality traits.

It is recognized that traits may be significantly correlated in the Fast Growth EBV group but not in the Slow Growth EBV group, meaning that selection for an improvement in growth rate changed the relationship between the traits in question. One reason for this may be that a trait exhibited too much variation in response to selection, but given the statistics presented in Table 1 that is probably not the case. The more likely reason, which presents a stronger, interesting possibility, is that selection for growth rate might make a third trait different thus changing the relationship between the first two or making one of the two traits not be as significant in explaining variation. For example, a trait may correlate differently with pH between the two groups, but there also may be a change in how significantly proteolysis is correlated with the trait between groups and therefore could change the relationship between the trait of interest and pH. Such will be the basis behind much of the presented discussion.

Correlations among important loin meat quality scores and pork quality traits

Correlations for loin color, firmness, and marbling scores were grouped together because they are subjective measurements of loin quality and may potentially exhibit similar relationships between traits. There were significant correlations among the pork quality scores for many traits among the progeny of the Fast and Slow Growth EBV sires, though in some instances the groups differed on which correlations were significant (Table 3). Loin color score was positively correlated to the ultimate pH values at 48 h and 10 d in the Fast
Growth EBV group, but no correlation was observed in the Slow Growth EBV group. However, the Slow Growth EBV group was correlated with 24 h pH and the Fast Growth EBV group was not. For both groups at the different pH time periods, the correlations were positive, indicating a higher pH at the time periods led to darker loin color. Both groups show similar results from previous studies that have shown positive correlations between color score and pH at both 24 and 48 h (Huff-Lonergan et al., 2002).

Loin color score was correlated with the three Hunter color scores for both the Fast and Slow Growth EBV groups, with the only exception being no correlation to Hunter a score in the Fast Growth EBV group. Thus, in essence, selecting for growth rate did not change the relationship between subjective and instrumental color score correlations. The correlations for both groups are consistent with previous results, particularly the negatively correlated relationship between color score and Hunter L value (Huff-Lonergan et al., 2002) which is not surprising considering a lower Hunter L value would mean a darker loin color.

In the Fast Growth EBV group, loin color score was negatively correlated to lipid percentage, thus indicating a lighter loin color with an increasing amount of lipid content, and is in agreement with previous studies that also found a negative correlation between color score and lipid percentage (Huff-Lonergan et al., 2002; Schwab et al., 2006). Color score was not correlated to lipid percentage in the Slow Growth EBV group. This may be due to the progeny of the Fast Growth EBV group having a significantly greater percentage of lipid content than the progeny of the Slow Growth EBV group. It is possible in this instance that variation in correlations with lipid may be due the Fast Growth EBV group having a greater range of lipid values (Table 1; Wagner et al. 2007). In this case, the idea of lipid overriding a factor such as pH with respect to loin color may be as big of an influence as the
observed variation in lipid between the progeny of both groups, meaning it likely is more important than the effects of the known variation in lipid content. Therefore, the increased lipid content for the Fast Growth EBV group may have the potential to more significantly influence pork quality traits such as loin color.

The progeny of the Fast and Slow Growth sire EBV groups showed differing significant correlations in terms of loin firmness scores (Table 3). Firmness score was positively correlated to pH at 24- and 48 h in the Slow Growth EBV group but did not show a correlation in the Fast Growth EBV group. The results for the Slow Growth EBV group are similar to previous studies that also found positive correlations for firmness score and pH at 24- and 48 h (Huff-Lonergan et al., 2002). Combined with the results of the loin color scores, it is apparent that the progeny of each group shows a different response to the rate and extent of pH decline in terms of explaining the variation in pork quality.

The Slow Growth EBV group also showed a positive correlation between firmness and color scores, indicating a firmer loin as with darker color. No correlation between firmness and color score was observed for the Fast Growth EBV group. Both sire EBV groups had significant negative correlations between firmness score and Hunter L color score which were in agreement with the positive correlation to subjective color score in this study and also agree with correlations found in previous studies (Huff-Lonergan et al., 2002). Firmness score increased as Hunter L score decreased, meaning the loin got firmer as the lightness score decreased indicating a darker product. Firmness score as also negatively correlated to Hunter b value, showing similar results to subjective color scores in this study. In the Slow Growth EBV group, firmness score was positively correlated to calpastatin
activity meaning loins were firmer as calpastatin activity increased. No correlation between firmness score and calpastatin activity was observed in the Fast Growth EBV group.

Progeny from the Fast and Slow Growth EBV groups also showed differing significant correlations among marbling scores (Table 3). The first thing to note is that neither group showed any significant correlations between marbling score and any pH measurement. This differs from previous studies that have shown positive correlations between marbling and pH at 24- and 48 h (Huff-Lonergan et al., 2002), though this paper did not investigate the influence of selection practices. Therefore, it appears as though selecting for improvements in growth rate potentially alters the interactions between pork quality traits that can be used to account for quality variations.

Significant positive correlations were observed in the Slow Growth EBV group for marbling score and temperature at 6- and 24 h, but the correlations were not present in the Fast Growth EBV group. Marbling was negatively correlated to color score in the Fast Growth EBV group but did not show a correlation in the Slow Growth EBV group. Previous studies did not show a correlation between marbling score and color score (Huff-Lonergan et al., 2002). Thus, a paler colored loin was associated with a higher marbling score which means more lipid may make the loin look lighter in color but that has not been shown to be a true relationship in other studies. This result in interesting because loin color was also negatively correlated with lipid content in the Fast Growth EBV group only, but one would not expect a paler colored loin to have a greater degree of marbling and lipid. However, it could be that lipid content plays a larger role in meat color when selecting for improved growth rate.
The results were once again mimicked in the positive correlation between marbling score and Hunter L value in the Fast Growth EBV group, meaning more marbling as a result of lighter colored loins. A positive correlation was also observed for Hunter b score in the Fast Growth EBV group. No correlations were found between marbling score and Hunter color scores in the Slow Growth EBV group.

Marbling score and lipid percentage were very strongly positively correlated in both the Fast and Slow Growth EBV groups. This is not surprising, since marbling score has been found to be closely associated with an increase in lipid percentage in other studies (Huff-Lonergan et al., 2002). Conventional thinking is that an increase in lipid content can be closely associated with a decrease in moisture content, since the lipid would take up space that moisture cannot reside in. Thus, it is not surprising that both the Fast and Slow Growth EBV groups show negative correlations between marbling score and moisture content, indicating an increase in marbling score as moisture content decreases and lipid content subsequently increases even though the two sire EBV groups differed in their marbling scores.

Marbling score was also positively correlated to the 78-kDa subunit autolysis product of μ-calpain for the Slow Growth EBV group. In this instance, a greater degree of proteolysis as evidenced by the positive correlation to the 78-kDa subunit is associated with more marbling, though few studies have investigated similar findings, but it also may mean that there is less proteolysis since at 2 d postmortem a higher degree of 78-kDa autolysis product means there is less of the 76-kDa subunit. This highlights the further potential for proteolysis to impact the variation in fresh pork quality. No correlation was observed between marbling score and the 78-kDa subunit in the Fast Growth EBV group, further highlighting potentially
different sources of variation for subjective pork quality traits when selecting for improvements in growth rate. The relationship between marbling score and proteolysis is thus complicated and is not usually thought of as being a significant one in terms of account for variation in pork quality. It may be that selecting for improved growth rate puts more emphasis on proteolysis accounting for more variations in pork quality, especially in traits that are not typically thought of as being influenced by proteolysis.

**Correlations among traits associated with variations in water-holding capacity**

Correlations are presented as a group for wetness score, drip loss, and cook loss because those are the traits that are commonly associated with variations in water-holding capacity. There were significant correlations between traits of importance in determining water-holding capacity of fresh pork among the progeny of Fast Growth EBV and Slow Growth EBV sires (Table 4). Much like the loin meat quality scores, differences between traits were observed between both sire EBV groups.

Wetness scores were evaluated as a subjective indicator of water-holding capacity of fresh pork loins. Wetness score was positively correlated to 6 h pH for the Fast Growth EBV group but was not correlated in the Slow Growth EBV group although it was close to being a significant correlation. However, both sire EBV groups showed positive correlations between wetness score with 24- and 48 h and 10 d pH. Within both groups, as pH increased wetness score increased meaning a drier product, indicating the potential for a better water-holding capacity at a higher pH throughout both the rate and extent of pH decline. Thus, it is likely that ultimate pH plays a significant role in determining wetness score regardless of sire EBV and that selection for improved growth rate did not have a large impact on pH in this instance.
Progeny from the Slow Growth EBV group had a positive correlation between wetness score and 6 h temperature but no correlation was observed in the progeny of Fast Growth EBV sires. Similar positive correlations were observed between wetness scores and both color and firmness scores in the Fast and Slow Growth sire EBV groups, indicating drier loins being associated with darker, firmer loins. In general, negative correlations were observed for both EBV groups between wetness score and Hunter color values, exception being a negative correlation with Hunter a value in the Fast Growth EBV group but no correlation in the Slow Growth EBV group.

So, when considering the results of the correlations between wetness score and other traits, both groups exhibited similar relationships with a few exceptions. This means water-holding capacity may potentially be influenced by similar traits in both groups, which is different from the results of the subjective quality scores. In this instance most of the variation that would arise in these pigs would likely be due to things such as pH differences, since no indicator of proteolysis was found to be significant in explaining variations with wetness scores, and it shows the potential for pH to be an overriding factor in traits associated with water-holding capacity.

Drip loss showed similar correlation results as the wetness score in that there were few differences between the Fast Growth and Slow Growth EBV groups for many of the traits (Table 4). In the progeny of the Fast Growth EBV group, drip loss was negatively correlated to pH at all time points: 2, 6, 24, 48 h and 10 d. Similar results were seen in the Slow Growth EBV group in which drip loss was negatively correlated to pH at all time periods evaluated with the only exception being no correlation to 2 h pH. These results are in agreement with previous studies that observed a negative correlation between drip loss and
pH at 24 and 48 h (Huff-Lonergan et al., 2002) as well as 24 h pH (Lonergan et al., 2001). In both groups, drip loss was found to increase at lower ultimate pH values throughout the rate of pH decline and also at a lower ultimate pH. pH appears to be beneficial in explaining potential variations in drip loss and it does not appear to be affected by selecting for improved growth rate. Thus, the relationship between pH and drip loss does not seem to be changed with genetic selection.

Drip loss was negatively correlated to 6 h temperature in the Slow Growth EBV group, showing a higher drip loss at lower temperatures, but no correlation was found in the Fast Growth EBV group. Negative correlations between drip loss and both color and firmness scores were found in the Slow Growth EBV group. Drip loss and firmness score were also negatively correlated in the Fast Growth EBV group but no correlation was found for color score. However, it does indicate that an increase in drip loss was associated with paler, softer loins, which would be in agreement with what one would expect in the extreme case of pale, soft, and exudative (PSE) pork. The results are also comparable with the results of previous studies that found negative relationships between drip loss and color and firmness scores (Huff-Lonergan et al., 2002).

It was originally thought that wetness score would be used as a good subjective indicator of drip loss in this study. The results for both the Fast and Slow Growth EBV groups showed a very strong negative correlation between drip loss and wetness score. Thus, drip loss increases as wetness score decreases, meaning a higher instance of drip loss in loins that show more exudate (a wetness score of 1 = exudative). So, the thinking in this instance was accurate in assuming that wetness score would be a good subjective indicator of drip loss.
and water-holding capacity. Thus, such a high correlation with visual observation of water-holding capacity means visual grading works as a successful tool in evaluating loins.

Positive correlations were observed between drip loss and all three Hunter color scores in the progeny of the Fast Growth EBV group and similar results were found in the progeny of the Slow Growth EBV group with the exception being no correlation between drip loss and Hunter $a$ value. This is in agreement with the results of other studies that observed a positive correlation between drip loss and Hunter $L$ value specifically (Huff-Lonergan et al., 2002), indicating more drip loss as the product is lighter or paler in color.

The progeny of the Fast Growth EBV group showed a negative correlation between drip loss and calpastatin activity, meaning potentially more drip loss with less calpastatin activity indicating more proteolysis. The result for the Fast Growth EBV group is different than the results seen when investigating for the influence of selecting for improvements in lean growth efficiency. Selecting for improvement in lean growth efficiency found a positive correlation between calpastatin activity and drip loss, meaning more drip loss with more calpastatin activity or less proteolysis (Lonergan et al., 2001). This shows that comparisons between progeny of selecting for improvement in growth rate and progeny of selecting for improvement in lean growth efficiency may not be practical when trying to determine what can be used to explain the variation in pork quality. It also emphasizes that these are two very different selection methods.

Though it was correlated with calpastatin activity, drip loss in the Fast Growth EBV group was not correlated with any other measurement of postmortem proteolysis, such as desmin degradation and $\mu$-calpain autolysis, nor were there any correlations between indices or measurements of proteolysis in the progeny of the Slow Growth EBV group. So, in this
study, it appears that proteolysis at the times measured is not beneficial in explaining variations in drip loss due to selecting for improved growth rate. This further highlights the influence of the relationship between pH and drip loss, since selection did not have an influence on pH or other traits such as proteolysis that may override any effects of pH on water-holding capacity. Therefore, it is unlikely that a third trait may change the relationship of two other traits with respect to drip loss and water-holding capacity, though it still may be possible even though drip loss was not affected by selection in this study.

Significant correlations were observed between cook loss and other traits as indices of water-holding capacity in the progeny of the Fast and Slow Growth sire EBV groups (Table 4). It has previously been stated that the basis on selecting for improved growth rate was progeny age at 125 kg. In the results of this study previous to this point, age at 125 kg has not been correlated with any traits of importance in either sire EBV group for growth rate. However, the Slow Growth EBV group showed a negative correlation between cook loss and age at 125 kg. That means that within the Slow Growth EBV group, a higher cook loss was associated with younger animals. That does not apply to all progeny since no correlation was found between cook loss and age at 125 kg in the progeny of the Fast Growth EBV group.

Cook loss showed different correlations to pH in both groups. Cook loss was negatively correlated to 2 h pH in the Fast Growth EBV group but was not correlated to 2 h pH in the Slow Growth EBV group. Cook loss was, however, negatively correlated to both 24 h and 48 h pH and 10 d pH in the Slow Growth EBV group but was not correlated to any of the three measurements in the Fast Growth EBV group, again showing results comparable to those of other studies that also showed negative correlations between cook loss and pH at 24- and 48 h (Huff-Lonergan et al., 2002). So, this shows that pH decline affects both groups
differently in terms of cook loss, with initial pH being associated with cook loss variations in the Fast Growth EBV group and the extent of pH decline being associated with cook loss variations in the Slow Growth EBV group. It may be possible that there is another factor, such as proteolysis, responsible for this change in relationship between cook loss and pH between the two groups.

Negative correlations between cook loss and temperature at 2 h and 6 h postmortem were found in the Fast Growth EBV group, but only a negative correlation to 6 h temperature was significant in the Slow Growth EBV group. In the progeny of the Slow Growth EBV group, cook loss was negatively correlated to color score and positively correlated to Hunter L and b values, which were also found to be correlated similarly in previous studies (Huff-Lonergan et al., 2002). No correlations were observed between cook loss and color score or any Hunter L value in the Fast Growth EBV group meaning color is useful in explaining variation in the Slow Growth but not the Fast Growth EBV group.

Cook loss and drip loss were positively correlated in the Slow Growth EBV group, which is in agreement with the results of previous studies (Huff-Lonergan et al., 2002), but were not correlated in the Fast Growth EBV group. No indicator of proteolysis showed a correlation, either positive or negative, to cook loss in either of the sire EBV groups. Therefore, differences in proteolysis was not a factor that would be responsible for the change in relationship between pH and cook loss like was previously thought to be the case. Thus, any variations in correlations with cook loss and pH would be as a result of a different factor that does not include proteolysis. This study shows that the possible variations in cook loss as a result of selecting for improvement in growth rate can be due to number of different
traits depending on the genetic makeup of the animals of interest and it may be possible that these traits are very dependent on genetic background or selection practice.

**Correlations among traits for sensory and instrumental indices of tenderness**

Sensory juiciness, tenderness, chewiness, and star probe were grouped together because they are the traits commonly associated with pork tenderness and thus have the potential to exhibit similar correlations with other traits. Significant correlations were observed for traits associated with sensory and instrumental measures of tenderness in the progeny of Fast Growth and Slow Growth EBV sires (Table 5). Sensory juiciness was positively correlated with age at 125 kg in the progeny of the Slow Growth EBV group, but it was not correlated in the Fast Growth EBV group. Hence, juiciness score increased with pig age in the Slow Growth group only and not in all progeny because the correlation was not significant in the Fast Growth EBV group.

Juiciness was positively correlated with 2 h and 48 h pH in the Fast Growth EBV group but was not correlated with either pH measurement in the Slow Growth EBV group. Higher initial and ultimate pH were associated with higher juiciness in the Fast Growth group only. This compares with other studies that also found a positive correlation between juiciness score and 48 h pH (Huff-Lonergan et al., 2002). It is likely that there is another factor that may be more important than pH that is responsible for controlling variations in juiciness, possibly proteolysis or even lipid content.

Juiciness scores of progeny from the Fast Growth EBV group were positively correlated to 2 h temperature but were not correlated to either 6 h or 24 h temperature. The opposite was true in the progeny of the Slow Growth EBV group, as juiciness was positively correlated to 6 h and 24 h temperature but was not correlated to 2 h temperature and thus
selection for improved growth rate changed the relationship between juiciness and 
temperature decline. Juiciness was positively correlated to color score and negatively 
correlated to Hunter L and b values in the Slow Growth EBV group. Thus, loins that were 
darker in color were associated with an increase in sensory juiciness. No correlations were 
oberved between juiciness and color score or either Hunter color value in the Fast Growth 
EBV group.

A negative correlation was observed between drip loss and juiciness in the Slow 
Growth EBV group, indicating higher juiciness scores as drip loss decreased, but drip loss 
and juiciness were not correlated in the Fast Growth EBV group, which is in agreement with 
previous results that did not show a correlation, either (Huff-Lonergan et al., 2002). The 
change in this relationship may be due to differences in ultimate pH between the two groups, 
but it may also be that another factor may influence this change more so than pH. Juiciness 
was positively correlated with moisture content in Slow Growth EBV progeny but was not 
correlated in Fast Growth EBV progeny.

Both Fast and Slow Growth EBV progeny exhibited a negative correlation between 
juiciness and cook loss, meaning lower juiciness scores as cook loss increased. Previous 
studies also showed similar correlations between juiciness and cook loss (Huff-Lonergan et 
al., 2002; Lonergan et al., 2007), thus this relationship is likely a strong one for the industry 
as selecting for improved growth rate did not seem to have a significant effect from what has 
been seen before. No measurements of proteolysis were correlated with juiciness in either of 
the EBV groups, so it is not likely that proteolysis is more beneficial in explaining variations 
in juiciness than pH regardless of the impact of selection for growth rate. However, the same 
may not be true for other sensory traits. It may be possible that lipid content differences
between the two groups may have an important influence on juiciness score variations which would override any effects on pH measurements.

Differences among significantly correlated traits with sensory tenderness scores were also found between the progeny of the Fast Growth and Slow Growth EBV groups (Table 5). Both the Fast Growth and Slow Growth EBV progeny showed positive correlations between sensory tenderness and pH measurements at 24 h, 48 h and 10 d, which is in agreement with the correlations found in previous studies (Huff-Lonergan et al., 2002). Thus, for all progeny, a higher ultimate pH led to higher sensory tenderness scores, and selecting for improvement in growth rate did not affect the relationship between pH and tenderness score and shows pH is important regardless of sire EBV.

Sensory tenderness was positively correlated to color score in the Slow Growth EBV group but was not correlated in the Fast Growth EBV group. As one would expect, sensory tenderness was negatively correlated to cook loss for the progeny of both the Fast and Slow Growth EBV groups, meaning loins were more tender as cook loss decreased. The negative correlation is consistent with previous studies that showed the same result (Huff-Lonergan et al., 2002; Lonergan et al., 2007). Sensory tenderness and juiciness were positively correlated for both EBV groups, a result that is also evident in previous studies (Huff-Lonergan et al., 2002; Lonergan et al., 2007).

Progeny of the Fast and Slow Growth EBV groups exhibited different correlations in terms of proteolysis measurements. Sensory tenderness in the Fast Growth EBV group was negatively correlated to calpastatin activity and positively correlated to the 76-kDa subunit µ-calpain autolysis product. Less calpastatin activity led to more autolysis of µ-calpain and thus a product that was associated with higher tenderness values. Therefore, µ-calpain was
activated in Fast Growth EBV progeny and thus proteolysis was important in accounting for variations in tenderness in these pigs. Progeny of the Slow Growth EBV group did not show any correlations between sensory tenderness score and any measurement of proteolysis. This may be an instance where pH may change the relationship between tenderness and proteolysis when selecting for improved growth rate. Though there were no differences in pH between sire EBV groups, the relationship between pH and proteolysis may be stronger and more beneficial in progeny from Fast Growth EBV sires in relation to explaining variations in tenderness. The relationship between pH and proteolysis likely did not change as a result of selecting for improved growth rate and likely is responsible for a lot of the variation in tenderness between the sire EBV groups.

Differences in correlations with sensory chewiness scores were also found between the progeny of the Fast and Slow Growth sire EBV groups (Table 5). Sensory chewiness was negatively correlated to 24 h and 10 d pH in the Slow Growth EBV group but was not correlated in the Fast Growth EBV group. Once again, this highlights the idea that pH can influence quality traits and account for pork quality variations differently depending on genetic makeup.

Chewiness was positively correlated to cook loss in the Slow Growth EBV group, a result similar to previous studies (Lonergan et al., 2007), but was not correlated in the Fast Growth EBV group. This differs from the results of sensory tenderness that was correlated for both groups and is interesting when considering that tenderness and chewiness are often thought of as occurring hand in hand. As can be expected, chewiness was negatively correlated to both juiciness and tenderness for both Fast and Slow Growth EBV progeny. The
correlation for both traits with sensory chewiness were also found in previous studies (Lonergan et al., 2007).

There was also a lack of a relationship between lipid and sensory traits for tenderness in this study. This is interesting because the relationship between lipid and sensory traits has been well documented (Lonergan et al., 2007), but it is apparently not an important factor when selecting for improved growth rate or it may be that selecting for improved growth rate changed the relationship so that it no longer had a significant influence on sensory tenderness traits.

Much like the correlation results for sensory tenderness, correlations between sensory chewiness and measurements of proteolysis differed between the progeny of the Fast Growth and Slow Growth EBV groups. Results of correlations for sensory chewiness in the Fast Growth EBV group were opposite of those for tenderness, as chewiness was positively correlated to calpastatin activity and negatively correlated to the 76-kDa µ-calpain autolysis product. Therefore, an increase in calpastatin activity resulted in less autolysis of µ-calpain and an increase in sensory chewiness. There were no correlations between sensory chewiness and any of the measurements of proteolysis in the progeny of Slow Growth EBV sires which is consistent with results observed for tenderness. pH may also be responsible for the different relationship between chewiness and proteolysis between the two groups. The Fast Growth EBV group did not show correlations with pH but did show correlations with proteolysis. The opposite was true for the Slow Growth EBV group so one of these two traits is likely responsible for the change in relationships with chewiness between the sire EBV groups. When combined with the results of tenderness, this study demonstrates that selecting
for improvements in growth rate may influence how proteolysis can be used to explain variations in pork quality as they relate to product tenderness.

Star probe measurements are instrumental indices of product texture that are beneficial in being able to understand instrumental tenderness, with high star probe values being linked with lower tenderness values (Lonergan et al., 2007). Differences in traits correlated with star probe were found between progeny from the Fast Growth EBV group and Slow Growth EBV group (Table 5). Star probe was negatively correlated to 48 h pH in the Fast Growth EBV group, which was similar to previous studies (Huff-Lonergan et al., 2002) but was not correlated in the Slow Growth EBV group. That was the only correlation observed for either group in terms of star probe and pH, thus showing that pH cannot be thought of as a single source of variation in pork quality in relation to star probe and it is likely a result of many interacting factors.

Star probe was negatively correlated with both 2 h and 6 h temperature in the Slow Growth EBV group but was not correlated with either in the Fast Growth EBV group. So, in the Slow Growth EBV group star probe increased at lower initial temperatures. This might be due to something such as cold shortening in the muscles of the Slow Growth EBV pigs, and it may potentially show a relationship between genetic background and cold shortening that is more prominent in slower growing pigs, though no studies have confirmed this hypothesis.

A negative correlation between star probe and color score was also observed in the Slow Growth EBV group but again no correlation was found in the Fast Growth EBV group. Star probe was positively correlated with both drip loss and cook loss in the Slow Growth EBV group, again similar to the results of previous studies (Huff-Lonergan et al., 2002; Lonergan et al., 2007), but was not correlated with the Fast Growth EBV group. Therefore,
product that exhibited more drip loss and lost more weight as a result of cooking exhibited higher star probe measurements and thus lower instrumental tenderness values and was tougher. This compares similarly to the sensory tenderness results in that more cook loss led to lower tenderness values.

Similar results were observed between star probe measurements and sensory indices of tenderness, i.e. juiciness, tenderness, and chewiness, for both sire EBV groups. Both the Fast and Slow Growth EBV groups showed negative correlations between star probe and sensory juiciness and tenderness as well as a positive correlation between star probe and chewiness. The correlations between star probe and sensory indices of tenderness were all similar to what has been shown in previous studies (Huff-Lonergan et al., 2002; Lonergan et al., 2007). Thus, as star probe increased instrumental tenderness decreased which was also associated with a decrease in sensory tenderness properties. In the Fast Growth EBV group, high star probe measurements were correlated with a decrease in sensory pork flavor, which has also been found in previous studies (Huff-Lonergan et al., 2002), but no correlation to pork flavor was observed in the Slow Growth EBV group. The decrease in pork flavor may possibly be due to the decrease in sensory tenderness properties.

Both sire EBV groups showed a positive correlation of star probe to calpastatin activity but did not show any other correlations to other proteolytic measurements. Thus, this selection practice may be responsible for changing the relationship between proteolysis and star probe measurements, even though it was a similar result for both groups.

Selecting for improvements in growth rate potentially alters how the variation in sensory and instrumental tenderness can be explained based on genetic merit, especially in terms of the influence of proteolysis on trait variations. It may be that selection for improved growth rate...
growth rate alters things such as fiber types in the faster growing pigs that may account for the increase in growth. As a result, this would change the conversion of muscle to meat and influence things like muscle protein proteolysis which would be of greater significance in faster growing pigs and not in slower growing pigs. It would then be possible for proteolysis to influence more pork quality traits and account for more variations in the faster growing pigs. This is a very plausible explanation as to the differences in proteolysis accounting for more variations in pork quality and is one that could be very beneficial for future research.

**Correlations among sensory flavor traits based on sire EBV group for growth rate**

Correlations for sensory flavor and off-flavor are grouped together because there are likely similar correlations between both traits. Sensory flavor and off-flavor are important traits used to determine consumer acceptance of fresh pork based on pork flavor with flavor being a positive perception of flavor and off-flavor being a negative perception of flavor (Lonergan et al., 2007). Traits correlated with sensory flavor were found to differ between the progeny of Fast Growth and Slow Growth EBV groups (Table 6). Progeny of the Fast Growth EBV group showed positive correlations between sensory flavor and pH at 24 h, 48 h and 10 d. Higher pH values were thus associated with more acceptable pork flavor, which has been found in prior studies (Huff-Lonergan et al., 2002). No correlations were observed between sensory flavor and any of the three pH measurements in the Slow Growth EBV group.

The Slow Growth EBV group did show a negative correlation between color score and flavor, though the Fast Growth group did not exhibit the same correlation. Flavor showed a negative correlation to Hunter L and b values in the Fast Growth group. A negative correlation between flavor and drip loss was found in the progeny of Fast Growth EBV sires,
showing a more acceptable flavor as drip loss decreased, a result that has also been shown in previous studies (Huff-Lonergan et al., 2002).

Flavor also exhibited correlations to sensory indices of tenderness in the Fast Growth EBV group as well. Flavor was positively correlated to sensory juiciness and tenderness and negatively correlated to chewiness. Thus, a more acceptable flavor was linked to product that was more desirable in sensory tenderness, which has been found in previous studies (Huff-Lonergan et al., 2002) and is probably related to varying correlations with pH. The correlation between color score and flavor was the only significant correlation found in the progeny of Slow Growth EBV sires as no correlations within the group were found between flavor and Hunter color value, drip loss, juiciness, tenderness, or chewiness.

As has been previously stated, sensory off-flavor is an indicator of unacceptable consumer acceptance, with a higher off-flavor score linked with an unacceptable product (Lonergan et al., 2007). Similar to the results of previous traits, differences were observed in traits correlated with sensory off-flavor for both sire EBV groups (Table 6). Both the Fast and Slow Growth EBV group showed negative correlations between off-flavor and pH at 6, 24, 48 h and 10 d. This shows that pH can be used to explain the variations in off-flavor irregardless of genetic makeup, which is also evident in that the results compare with the negative correlations between off-flavor and pH in previous studies (Huff-Lonergan et al., 2002).

The Fast Growth EBV group showed a negative correlation between off-flavor and both wetness and marbling scores, again likely related to pH, but no correlation was observed in the Slow Growth EBV group. This is important because product with a lower marbling score was linked with higher off-flavor, which was also found in previous studies (Huff-
Lonergan et al., 2002). This highlights how marbling may be important in ultimate consumer
acceptance of pork. Off-flavor was positively correlated with drip loss and moisture content
in the Fast Growth EBV group, again shown to be correlated similarly in prior studies (Huff-
Lonergan et al., 2002), indicating product with more moisture and higher drip loss being
associated with a potentially more unacceptable product. No correlation was found between
off-flavor and drip loss or moisture content in the Slow Growth EBV group.

Off-flavor was negatively correlated with sensory tenderness in the Fast Growth EBV
group, meaning product that was less tender was linked to having higher off-flavor scores.
There was no correlation between off-flavor and sensory tenderness in the Slow Growth
EBV group. As expected, there was a negative correlation between flavor and off-flavor
scores for both sire EBV groups. In terms of indices of proteolysis, off-flavor was negatively
correlated with desmin degradation product in the Fast Growth EBV group, indicating higher
off-flavor score for product that had less degradation of desmin. That was the only
measurement of proteolysis correlated with off-flavor in either sire EBV group. This all
highlights that selecting for improved growth rate may not ultimately play a role in
determining the sources for variation in pork quality when it comes to measurements of
proteolysis.

In conclusion, when considering all correlation data presented in this study, it is
evident that pork quality traits are correlated differently based on genetic merit of the animal,
especially when progeny are selected based on improved growth rate potential of the sire. In
general, sensory parameters tended to show similar correlations and thus potentially may be
able to be explained by similar sources of variation. It is also evident that measurements of
proteolysis may be very dependent on genetic background of progeny and that selecting for
improved growth rate may substantially influence the role proteolysis plays in the variation of pork quality. Overall, the results of this study demonstrate the complexity of inheritance and interactions among pig growth and muscle/meat quality characteristics. Therefore, it is plausible to reason the water-holding capacity and sensory characteristics of pork are dependent on a combination of particular genetic background breeding program and individual genetic predisposition of the animal for growth performance.

**Implications**

Pork quality is influenced by a number of interacting factors. Changing one or more factors has the potential to alter the relationship of pork quality traits. Proteolysis has been identified as one factor that can be used to account for variation in pork quality. In the present study, measurements of proteolysis were not important factors for sensory traits such as tenderness and chewiness in the Slow Growth EBV sired pigs but were very important in the Fast Growth EBV sired pigs. Therefore, we may conclude that selection for some economically important trait, such as improved growth rate, changes the relationships of traits known to be useful in controlling pork quality variations. Combining selection practices with the genetic background of the animal potentially changes how many factors interact with each other and can account for subsequent differences in pork quality traits such as water-holding capacity and sensory attributes. Future work addressing the causative agents controlling the variation in quality will be beneficial when selecting progeny for improved growth rate performance.
Literature Cited


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<td>Loin firmness score (1 to 3)</td>
<td>1.80</td>
<td>1.80</td>
</tr>
<tr>
<td>Loin wetness score (1 to 3)</td>
<td>1.80</td>
<td>1.80</td>
</tr>
<tr>
<td>Hunter L color2</td>
<td>46.31</td>
<td>46.83</td>
</tr>
<tr>
<td>Hunter a color2</td>
<td>6.02</td>
<td>7.79</td>
</tr>
<tr>
<td>Hunter b color2</td>
<td>9.28</td>
<td>10.81</td>
</tr>
<tr>
<td>Drip loss, %</td>
<td>2.52</td>
<td>2.25</td>
</tr>
<tr>
<td>Lipid, %</td>
<td>1.99</td>
<td>1.99</td>
</tr>
<tr>
<td>Moisture, %</td>
<td>73.45</td>
<td>73.99</td>
</tr>
<tr>
<td>Cook loss, %</td>
<td>20.99</td>
<td>23.25</td>
</tr>
<tr>
<td>Star probe, kg4</td>
<td>5.57</td>
<td>5.51</td>
</tr>
<tr>
<td>Juiciness score (1 to 10)</td>
<td>4.68</td>
<td>4.82</td>
</tr>
<tr>
<td>Tenderness score (1 to 10)</td>
<td>5.88</td>
<td>6.49</td>
</tr>
<tr>
<td>Chewiness score (1 to 10)</td>
<td>5.64</td>
<td>6.49</td>
</tr>
<tr>
<td>Flavor score (1 to 10)</td>
<td>2.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Off-flavor score (1 to 10)</td>
<td>3.7</td>
<td>3.7</td>
</tr>
</tbody>
</table>

1Measured by a penetration probe on right side loins using a Hanna 9025 pH/ORP meter (Hanna Instruments, Woonsocket, RI). pH probe was calibrated with temperature at each period using two buffers (pH 4.2 and 7.10). 
2Evaluated 48 hr postmortem according to National Pork Board Standards (2000).
3Evaluated by a trained sensory panel using similar method as described by Lonergan et al. (2007).
**Table 2.** Proteolysis measurements of progeny from two different sire growth rate Estimated Breeding Values (EBV).

<table>
<thead>
<tr>
<th>Item</th>
<th>Fast Growth EBV</th>
<th>Slow Growth EBV</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Desmin Day 2 Intact, ratio(^1)</td>
<td>1.55(^a)</td>
<td>1.10(^b)</td>
<td>0.10</td>
</tr>
<tr>
<td>Desmin Day 2 Degraded, ratio(^1)</td>
<td>1.91(^x)</td>
<td>1.46(^y)</td>
<td>0.13</td>
</tr>
<tr>
<td>(\mu)-Calpain 78 kDa subunit, %(^2)</td>
<td>5.37(^x)</td>
<td>9.81(^y)</td>
<td>1.29</td>
</tr>
<tr>
<td>(\mu)-Calpain 76 kDa subunit, %(^2)</td>
<td>94.63(^x)</td>
<td>88.73(^y)</td>
<td>1.60</td>
</tr>
<tr>
<td>Calpastatin, units of activity/g of tissue(^3)</td>
<td>1.03</td>
<td>0.97</td>
<td>0.03</td>
</tr>
</tbody>
</table>

\(^a,b\) Within a row, means without a common superscript letter differ (P<.01).

\(^x,y\) Within a row, means without a common superscript letter differ (P<.05).

\(^1\) Evaluated by similar method to Melody et al. (2004). Ratio expressed as intensity of intact and degradation product bands over intensity of bands in a reference sample.

\(^2\) Evaluated by similar method to Gardner et al. (2005). Expressed as percentage of autolysis products present at 78- and 76-kDa subunits.

\(^3\) Determined 24 h postmortem as described by Lonergan et al. (2001).
Table 3. Pearson correlations for color, firmness, and marbling scores from progeny of two different sire Estimated Breeding Values (EBV) for growth rate.\(^1\)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Fast Growth EBV Correlations</th>
<th>Slow Growth EBV Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>by Variable</td>
<td>Correlation</td>
</tr>
<tr>
<td>Color Score(^2)</td>
<td>24hr pH</td>
<td>0.195</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>0.335</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>0.255</td>
</tr>
<tr>
<td></td>
<td>Hunter L(^3)</td>
<td>-0.398</td>
</tr>
<tr>
<td></td>
<td>Hunter a(^3)</td>
<td>-0.131</td>
</tr>
<tr>
<td></td>
<td>Hunter b(^3)</td>
<td>-0.536</td>
</tr>
<tr>
<td></td>
<td>Lipid, %</td>
<td>-0.248</td>
</tr>
<tr>
<td>Firmness Score(^2)</td>
<td>24hr pH</td>
<td>0.181</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>0.180</td>
</tr>
<tr>
<td></td>
<td>Color(^2)</td>
<td>0.178</td>
</tr>
<tr>
<td></td>
<td>Hunter L(^3)</td>
<td>-0.291</td>
</tr>
<tr>
<td></td>
<td>Hunter b(^3)</td>
<td>-0.262</td>
</tr>
<tr>
<td>Calpastatin(^4)</td>
<td>0.159</td>
<td>0.211</td>
</tr>
<tr>
<td>Marbling Score(^2)</td>
<td>6hr temp</td>
<td>0.042</td>
</tr>
<tr>
<td></td>
<td>24hr temp</td>
<td>-0.011</td>
</tr>
<tr>
<td></td>
<td>Color(^2)</td>
<td>-0.280</td>
</tr>
<tr>
<td></td>
<td>Hunter L(^3)</td>
<td>0.427</td>
</tr>
<tr>
<td></td>
<td>Hunter b(^3)</td>
<td>0.260</td>
</tr>
<tr>
<td></td>
<td>Lipid, %</td>
<td>0.731</td>
</tr>
<tr>
<td></td>
<td>Moisture, %</td>
<td>-0.702</td>
</tr>
<tr>
<td>Mu-Calp % 78</td>
<td>-0.136</td>
<td>0.284</td>
</tr>
</tbody>
</table>

\(^1\)Significant correlations are shown in bold \((P<.05)\).
\(^2\)Evaluated 48 hr postmortem according to National Pork Board Standards (2000).
\(^3\)Hunter color score. Evaluated on a calibrated Hunter Labscan colorimeter.
\(^4\)Units of activity/g of tissue. Determined 24 h postmortem as described by Lonergan et al. (2001).
Table 4. Pearson correlations for water-holding capacity traits of progeny from two different sire Estimated Breeding Values (EBV) for growth rate. 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>Fast Growth EBV Correlations</th>
<th>Slow Growth EBV Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>by Variable</td>
<td>Correlation</td>
</tr>
<tr>
<td>Wetness Score1</td>
<td>6hr pH</td>
<td>0.264</td>
</tr>
<tr>
<td></td>
<td>24hr pH</td>
<td>0.285</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>0.473</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>0.441</td>
</tr>
<tr>
<td></td>
<td>6hr temp</td>
<td>-0.138</td>
</tr>
<tr>
<td></td>
<td>Color22</td>
<td>0.254</td>
</tr>
<tr>
<td></td>
<td>Firmness2</td>
<td>0.503</td>
</tr>
<tr>
<td></td>
<td>Hunter L3</td>
<td>-0.440</td>
</tr>
<tr>
<td></td>
<td>Hunter a3</td>
<td>-0.331</td>
</tr>
<tr>
<td></td>
<td>Hunter b3</td>
<td>-0.471</td>
</tr>
<tr>
<td>Drip Loss</td>
<td>2hr pH</td>
<td>-0.265</td>
</tr>
<tr>
<td></td>
<td>6hr pH</td>
<td>-0.525</td>
</tr>
<tr>
<td></td>
<td>24hr pH</td>
<td>-0.552</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>-0.671</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>-0.673</td>
</tr>
<tr>
<td></td>
<td>6hr temp</td>
<td>0.161</td>
</tr>
<tr>
<td></td>
<td>Color22</td>
<td>-0.131</td>
</tr>
<tr>
<td></td>
<td>Firmness2</td>
<td>-0.252</td>
</tr>
<tr>
<td></td>
<td>Wetness2</td>
<td>-0.641</td>
</tr>
<tr>
<td></td>
<td>Hunter L3</td>
<td>0.290</td>
</tr>
<tr>
<td></td>
<td>Hunter a3</td>
<td>0.394</td>
</tr>
<tr>
<td></td>
<td>Hunter b3</td>
<td>0.533</td>
</tr>
<tr>
<td>Cook Loss</td>
<td>Age 125</td>
<td>-0.120</td>
</tr>
<tr>
<td></td>
<td>2hr pH</td>
<td>-0.256</td>
</tr>
<tr>
<td></td>
<td>24hr pH</td>
<td>-0.116</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>-0.098</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>-0.060</td>
</tr>
<tr>
<td></td>
<td>2hr temp</td>
<td>-0.387</td>
</tr>
<tr>
<td></td>
<td>6hr temp</td>
<td>-0.275</td>
</tr>
<tr>
<td></td>
<td>Color22</td>
<td>0.140</td>
</tr>
<tr>
<td></td>
<td>Hunter L3</td>
<td>-0.104</td>
</tr>
<tr>
<td></td>
<td>Hunter b3</td>
<td>0.064</td>
</tr>
<tr>
<td></td>
<td>Drip Loss</td>
<td>0.188</td>
</tr>
</tbody>
</table>

1Significant correlations are shown in bold (P<.05).
2Evaluated 48 hr postmortem according to National Pork Board Standards (2000).
3Hunter color score. Evaluated on a calibrated Hunter Labscan colorimeter.
4Units of activity/g of tissue. Determined 24 h postmortem as described by Lonergan et al. (2001).
Table 5. Pearson correlations for sensory and instrumental tenderness traits from progeny of two different sire Estimated Breeding Values (EBV) for growth rate.  

<table>
<thead>
<tr>
<th>Variable</th>
<th>Fast Growth EBV Correlations</th>
<th>Slow Growth EBV Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>by Variable</td>
<td>Correlation</td>
</tr>
<tr>
<td>Juiciness</td>
<td>Age 125</td>
<td>0.192</td>
</tr>
<tr>
<td></td>
<td>2hr pH</td>
<td>0.304</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>0.266</td>
</tr>
<tr>
<td></td>
<td>2hr temp</td>
<td>0.266</td>
</tr>
<tr>
<td></td>
<td>6hr temp</td>
<td>0.186</td>
</tr>
<tr>
<td></td>
<td>24hr temp</td>
<td>-0.008</td>
</tr>
<tr>
<td>Color</td>
<td>-0.081</td>
<td>0.525</td>
</tr>
<tr>
<td>Hunter L</td>
<td>-0.116</td>
<td>0.361</td>
</tr>
<tr>
<td>Hunter b</td>
<td>-0.149</td>
<td>0.241</td>
</tr>
<tr>
<td>Drip Loss</td>
<td>-0.181</td>
<td>0.153</td>
</tr>
<tr>
<td>Moisture, %</td>
<td>0.053</td>
<td>0.676</td>
</tr>
<tr>
<td>Cook Loss</td>
<td>-0.432</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Tenderness</td>
<td>24hr pH</td>
<td>0.334</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>0.334</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>0.287</td>
</tr>
<tr>
<td>Color</td>
<td>0.045</td>
<td>0.724</td>
</tr>
<tr>
<td>Cook Loss</td>
<td>-0.375</td>
<td>0.002</td>
</tr>
<tr>
<td>Juiciness</td>
<td>0.415</td>
<td>0.001</td>
</tr>
<tr>
<td>Calpastatin</td>
<td>-0.396</td>
<td>0.001</td>
</tr>
<tr>
<td>Mu-Calp % 78</td>
<td>-0.376</td>
<td>0.002</td>
</tr>
<tr>
<td>Mu-Calp % 76</td>
<td>0.376</td>
<td>0.002</td>
</tr>
<tr>
<td>Chewiness</td>
<td>24hr pH</td>
<td>-0.229</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>-0.186</td>
</tr>
<tr>
<td>Cook Loss</td>
<td>0.178</td>
<td>0.159</td>
</tr>
<tr>
<td>Juiciness</td>
<td>-0.287</td>
<td>0.022</td>
</tr>
<tr>
<td>Tenderness</td>
<td>-0.802</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Calpastatin</td>
<td>0.433</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Mu-Calp % 78</td>
<td>0.469</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Mu-Calp % 76</td>
<td>-0.469</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Star Probe</td>
<td>48hr pH</td>
<td>-0.294</td>
</tr>
<tr>
<td></td>
<td>2hr temp</td>
<td>0.104</td>
</tr>
<tr>
<td></td>
<td>6hr temp</td>
<td>0.070</td>
</tr>
<tr>
<td>Color</td>
<td>0.019</td>
<td>0.896</td>
</tr>
<tr>
<td>Hunter a</td>
<td>0.117</td>
<td>0.416</td>
</tr>
<tr>
<td>Drip Loss</td>
<td>0.109</td>
<td>0.445</td>
</tr>
<tr>
<td>Cook Loss</td>
<td>0.028</td>
<td>0.847</td>
</tr>
<tr>
<td>Juiciness</td>
<td>-0.312</td>
<td>0.026</td>
</tr>
<tr>
<td>Tenderness</td>
<td>-0.655</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Chewiness</td>
<td>0.502</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Flavor</td>
<td>-0.343</td>
<td>0.014</td>
</tr>
<tr>
<td>Calpastatin</td>
<td>0.320</td>
<td>0.022</td>
</tr>
</tbody>
</table>

1Significant correlations are shown in bold (P<.05).
2Evaluated 48 hr postmortem according to National Pork Board Standards (2000).
3Hunter color score. Evaluated on a calibrated Hunter Labscan colorimeter.
4Units of activity/g of tissue. Determined 24 h postmortem as described by Lonergan et al. (2001)
Evaluated by a trained sensory panel using similar method as described by Lonergan et al. (2007). A higher value represents a greater degree of juiciness, tenderness, or chewiness.

Instrumental indication of loin texture by similar method to Lonergan et al. (2007).

Evaluated by similar method to Gardner et al. (2005). Expressed as percentage of autolysis products present at 78- and 76-kDa subunits.
Table 6. Pearson correlations for sensory flavor traits from progeny of two different sire Estimated Breeding Values (EBV) for growth rate. 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>Fast Growth EBV Correlations</th>
<th>Slow Growth EBV Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>by Variable</td>
<td>Correlation</td>
</tr>
<tr>
<td>Flavor 4</td>
<td>24hr pH</td>
<td>0.430</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>0.618</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>0.600</td>
</tr>
<tr>
<td>Color 2</td>
<td>Hunter L 3</td>
<td>-0.357</td>
</tr>
<tr>
<td></td>
<td>Hunter b 3</td>
<td>-0.253</td>
</tr>
<tr>
<td>Drip Loss</td>
<td>-0.260</td>
<td>0.038</td>
</tr>
<tr>
<td>Juiciness 5</td>
<td>0.352</td>
<td>0.004</td>
</tr>
<tr>
<td>Tenderness 5</td>
<td>0.461</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Chewiness 3</td>
<td>-0.404</td>
<td>0.001</td>
</tr>
<tr>
<td>Off-flavor 6</td>
<td>6hr pH</td>
<td>-0.268</td>
</tr>
<tr>
<td></td>
<td>24hr pH</td>
<td>-0.465</td>
</tr>
<tr>
<td></td>
<td>48hr pH</td>
<td>-0.600</td>
</tr>
<tr>
<td></td>
<td>10 d pH</td>
<td>-0.585</td>
</tr>
<tr>
<td>Wetness 2</td>
<td>-0.286</td>
<td>0.022</td>
</tr>
<tr>
<td>Marbling 2</td>
<td>-0.289</td>
<td>0.021</td>
</tr>
<tr>
<td>Hunter b 3</td>
<td>0.283</td>
<td>0.024</td>
</tr>
<tr>
<td>Drip Loss</td>
<td>0.438</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Moisture, %</td>
<td>0.265</td>
<td>0.034</td>
</tr>
<tr>
<td>Tenderness 4</td>
<td>-0.365</td>
<td>0.003</td>
</tr>
<tr>
<td>Flavor 4</td>
<td>-0.551</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Day 2 Degraded 6</td>
<td>-0.337</td>
<td>0.007</td>
</tr>
</tbody>
</table>

1Significant correlations are shown in bold (P<.05).
2Evaluated 48 hr postmortem according to National Pork Board Standards (2000).
3Hunter color score. Evaluated on a calibrated Hunter Labscan colorimeter.
4Evaluated by a trained sensory panel using similar method as described by Lonergan et al. (2007). A higher value represents a greater degree of flavor or off-flavor.
5Evaluated by a trained sensory panel using similar method as described by Lonergan et al. (2007). A higher value represents a greater degree of juiciness, tenderness, or chewiness.
6Evaluated by similar method to Melody et al. (2004). Ratio expressed as intensity of intact and degradation product bands over intensity of bands in a reference sample.
Figure 1. Western blots of proteolysis indices. A) Sample desmin degradation blot highlighting intact desmin band. B) Sample μ-calpain autolysis blot highlighting 78-kDa and 76-kDa autolysis product bands.
GENERAL SUMMARY

Pork quality is a multifactorial phenomenon that is influenced by many factors both pre-slaughter and postmortem. These factors include such things as genetics, the rate and extent of pH decline, and the postmortem proteolysis of muscle proteins. The present study investigated the relationships between all three of these factors in terms of determining and accounting for variations in ultimate pork quality. Previous studies have shown genetic background combined with selection practices for improved lean growth have negative influences on pork quality. In the present study, however, selection practices based on sire Estimated Breeding Value (EBV) for improved growth rate did not show a negative impact on pork quality. Improvements in growth traits did not translate to differences in carcass composition, pH decline, or sensory quality of fresh pork. Therefore, selecting for improved growth using age at 125 kg as a basis can be implemented as an effective selection strategy without being detrimental to pork quality.

The relationships between postmortem events in the conversion of muscle to meat and pork quality traits can be used to predict variations in pork quality. It is also likely that implementing selection practices can change the relationships between the postmortem events and traits and thus influence how pork quality variations are accounted for. One possible reason for the change in relationship between two traits or events of interest is that by selecting for improved growth rate a third trait or event was changed that led to a change in the relationship between the other two traits. As a result, this would have more of an impact than overall trait variation and could be the reason for observed differences in pork quality.
Drip loss is known to be a good indicator of fresh pork water-holding capacity, and it is also known to greatly be influenced by pH decline and the proteolysis of proteins such as desmin. In the present study, selecting for improved growth rate did not result in any changes in the relationship between drip loss and pH decline, and thus this relationship is one that seems to be very strong and important regardless of this selection practice. Proteolysis was not correlated with drip loss in this study, and so it is likely that any differences in proteolysis would not be significant enough to override the relationship between drip loss and pH.

The most interesting result of this study, however, is that more measurements and indices of proteolysis were correlated to meat quality traits in the progeny from the faster growing boars and not the progeny from the slower growing boars. A number of different factors may play into this phenomenon, such as possible fiber type differences between the two growth rate groups and differences in pH decline. However, pH decline did not differ between the two groups so that highlights the importance of some other undetermined factor. As such, the relationship between postmortem proteolysis and meat sensory quality continues to be one that is complex in nature and warrants the use of further studies to enhance this understanding.

The results from this study demonstrate the complexity in the relationship between genetic selection and pork quality. Pork quality is very dependent on genetic predisposition of the animal as well as how selection practices of these animals are applied that may potentially influence how variations in pork quality can be explained. Further work addressing the causative agents of these variations will be beneficial when selecting for improvements in growth rate.
ACKNOWLEDGMENTS

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