Improving the sensory and nutritional quality of fresh meat

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Fresh meat texture and tenderness

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Abstract: Strategies to consistently produce tender meat products should help maintain and build consumer confidence. Numerous antemortem and postmortem factors can impact upon tenderness, both positively and negatively. Generally, these effects are mediated through alteration of sarcomere length, postmortem proteolysis, or connective tissue integrity. The interaction of these component traits is complex and muscle dependent. Therefore, antemortem and postmortem management decisions must be made carefully, possibly on a muscle-by-muscle basis. This chapter discusses antemortem and postmortem management strategies that can be used to influence meat tenderness attributes. Additionally, tenderness assessment and prediction are addressed.

Key words: genetic markers, management, meat tenderness, prediction.

3.1 Introduction

Consumers have certain expectations regarding the quality of the meat they purchase. Eating satisfaction is determined by the perceived value delivered by three palatability traits: tenderness, juiciness, and flavor. Each of these traits is important and deficiency in any one of them could result in consumer dissatisfaction. However, the majority of meat palatability research has emphasized tenderness because of its importance in consumer perceptions of muscle foods. The importance of tenderness is evidenced by consumers' ability to discern differences in tenderness and willingness to pay premiums for guaranteed tender products (Boleman et al., 1997; Lusk et al., 2001; Shackelford et al., 2001). Additional evidence comes from consumer survey results indicating that, of the three palatability traits, tenderness is the most important contributor to their eating satisfaction (Miller et al., 1995). Certain cuts of beef have been reported to be inconsistent with regard to tenderness and need improvement relative to consumer
Fig. 3.1 Variation in tenderness, flavor, and juiciness ratings for beef longissimus steaks from young, grain-fed steers. Adapted from Wheeler et al. (2001a).

expectations (Neely et al., 1998; Savell et al., 1999; Brooks et al., 2000; Behrends et al., 2005).

Tenderness is the most variable of the three palatability traits (Fig. 3.1). In large studies comparing animals of diverse genetic backgrounds reared in a calf-fed, corn-corn silage based production system, animal-to-animal variation in tenderness traits is more than double the variation observed in flavor intensity and juiciness (Wheeler et al., 1996a, 2001a). Furthermore, tenderness differences across muscles within carcasses have been reported to be larger than differences in flavor or juiciness (Carmack et al., 1995; Shackelford et al., 1995; Rhee et al., 2004). Additionally, Rhee et al. (2004) and Searls et al. (2005) reported substantial differences in Warner-Bratzler shear force values across locations within some muscles.

3.2 Muscle constituents and structure contributing to tenderness variation

Physical and chemical properties of muscle interact to determine the tenderness of the resulting meat products. Therefore, it is important to understand the muscle constituents and structures that contribute to the variation in tenderness. For a review of the macroscopic and microscopic structure of muscle, muscle contraction, and the conversion of muscle to meat, the reader is referred to Aberle et al. (2001). Numerous sources contribute to the variation in tenderness of meat; however, these effects ultimately are asserted by altering one or more of three component traits: connective tissue amount and quality, sarcomere length, and the rate and extent of postmortem proteolysis of key structural proteins are considered to be the primary component traits contributing to explainable tenderness variation.
Fig. 3.2 Changes in Warner–Bratzler shear force and sarcomere length in lamb longissimus muscle during chilling and postmortem storage. Adapted from Wheeler and Koochmarie (1994).

The connective tissue fraction of meat, predominantly comprised of collagen, provides structural support to muscles and transfers force generated during contraction to the skeleton. The contribution of collagen to meat tenderness is determined by a number of factors, such as total collagen concentration, types of collagen present, and cross-linking of the collagen matrix. The effects of connective tissue on tenderness is often referred to as ‘background toughness’ (Marsh, 1977) and are thought to be a minor source of animal-to-animal variation in longissimus tenderness of young animals. However, as animals mature, intermolecular cross-linking stabilizes the collagen matrix (Avery et al., 1996). The stabilized collagen is more resistant to solubilization by heating, which increases meat toughness (Goll et al., 1964; Shorthose and Harris, 1990).

Total collagen content varies between muscles depending on their skeletal location and function in the live animal, and partially explains tenderness differences between muscles (McKeith et al., 1985; Wheeler et al., 2000b; Rhee et al., 2004). For example, muscles located in the limbs of the animal, which are used for locomotion, generally have greater collagen concentrations than support muscles located in the epaxial regions.

The contractile state of muscle is a key contributor to the myofibrillar tenderness of meat. The increased overlap of the thick and thin filaments associated with contracted muscle (i.e. shorter sarcomeres) is associated with greater toughness (Locke and Hagyard, 1963; Marsh and Leet, 1966). Wheeler and Koochmarie (1994) measured the effects of rigor and early postmortem storage on sarcomere length of lamb longissimus and the consequential effects on tenderness (Fig. 3.2). Sarcomere length was longest at death and was reduced to a minimum at 24 h.
Warner–Bratzler shear force increased to a maximum at 24 h and improved dramatically during 14 d of ageing. When sarcomere shortening during rigor was prevented, the increase in Warner–Bratzler shear force during the first hours post mortem was not observed (Kooihmarai et al., 1996a). However, tenderization still occurred. Collectively, these results indicate that lamb longissimus is intermediate in tenderness at death and rigor shortening causes a reduction in tenderness during the first 24 h. At some point after death, degradation of structural proteins is initiated and results in tenderization. Veiseth et al. (2004) reported that calpain degradation of key structural proteins began within a few hours post mortem. Therefore, in muscles with low to intermediate collagen concentrations, the ultimate tenderness of the muscle is dictated by the extent of sarcomere shortening that is allowed to occur and how much post mortem protein degradation occurs.

After death, tenderization begins and will continue at varying rates and for varying periods of time post mortem. For detailed reviews of the tenderization process, the reader is referred to Kooihmarai (1992a, 1995, 1996). Postmortem changes that are observed during refrigerated storage include loss of Z-disk and sarcomere integrity resulting from proteolytic degradation of numerous cytoskeletal proteins such as troponin-T, titin, nebulin, desmin, vinculin, filamin, synemin, and dystrophin (Taylor et al., 1995; Kooihmarai, 1992a, 1996). The proteins observed to be degraded in postmortem meat function to provide muscle integrity through involvement in inter- (e.g. desmin and vinculin) and intra-myofibrillar (e.g. titin, nebulin, and possibly troponin-T) linkages and the attachment of muscle cells to the basal lamina (e.g. laminin, and fibronectin) (Price, 1991; Robson et al., 1997). Therefore, it is evident that degrading these proteins results in a weakening of the myofibril structure, resulting in tenderization. However, it is notable that the major contractile proteins, actin and myosin, are unaffected during post mortem storage.

Numerous investigations have been conducted to deduce the proteolytic system responsible for these changes. Lysosomal proteases (e.g. cathepsins; Goll et al., 1983; Ouali and Valin, 1980; Zeece et al., 1992), multicatalytic proteinase complex (Goll, 1991; Kooihmarai, 1992c, 1994) and the calpain system (Ouali and Talmant, 1990; Kooihmarai et al., 1992b, 1995, 1996) have all been examined as potentially causing the tenderization observed during post mortem storage. Of these, only the calpain system has been found to produce the changes normally seen in post mortem muscle (Kooihmarai, 1996). Calpain mediated proteolysis of cytoskeletal proteins begins soon after death (Veiseth et al., 2004) and continues for some period of time, depending on species.

Collectively, connective tissue content, sarcomere length, and the extent of post mortem proteolysis of myofibrillar proteins can explain the majority of the variations in tenderness. However, their interaction is complex and is muscle dependent. For example, psoas major is very tender due to long sarcomere lengths and low collagen content, despite a very low amount of post mortem proteolysis. Biceps femoris is relatively tough due to high collagen concentration and medium sarcomere length, despite having as much or more proteolysis as all other muscles (Rhee et al., 2004).
3.3 Antemortem factors affecting meat tenderness

3.3.1 Genetic conditions affecting tenderness

Meat tenderness is affected by complex interactions of multiple antemortem and postmortem factors. Genetics determine an animal’s potential for producing tender meat, and the interaction of genetics with ante- and postmortem environment and management will determine the ultimate tenderness of the meat from an animal. A mutation in the myostatin gene has been associated with the condition in cattle known as ‘double muscling’ (Grobet et al., 1997; Kambadur et al., 1997; McPherron and Lee, 1997; Smith et al., 1997). This syndrome is characterized by embryonic hyperplasia caused by inactive myostatin, which normally inhibits cell-proliferation. Carcasses of double-muscled cattle yield a greater percentage of retail product than carcasses of normal cattle (Arthur, 1995; Wheeler et al., 1997a). Additionally, meat from these animals is more tender, primarily due to reduced collagen concentration (Wheeler, unpublished data). Animals with one or two inactive myostatin alleles produced ribeye, top sirloin, bottom round, and top round steaks that received greater trained sensory panel tenderness ratings than animals with two normal alleles at the myostatin locus (Fig. 3.3; Wheeler et al., 2001b). In addition, bottom round steaks from animals with two inactive myostatin allele received higher tenderness ratings than steaks from animals with one inactive allele. In all muscles evaluated, increasing the number of inactive myostatin
alleles decreased collagen concentration (Wheeler, unpublished data). This trend was more pronounced in the bottom round, which had the highest collagen content of the four muscles evaluated.

Cattle with *Bos indicus* inheritance are commonly used in tropical and subtropical environments. The heat tolerance and insect resistance possessed by these breeds, coupled with their maternal characteristics, have made them a valuable part of beef production in these regions. However, *Bos indicus* cattle, especially Brahman, have been repeatedly reported to produce tougher meat than *Bos taurus* cattle (Koch et al., 1982; Peacock et al., 1982; Crouse et al., 1989; Wheeler et al., 1990a,b, 1996a, 2001a). Increased toughness of meat produced by *Bos indicus* cattle has been demonstrated to be due to increased calpastatin levels (Wheeler et al., 1990b; Whipple et al., 1990b; Pringle et al., 1997), resulting in less proteolytic degradation (Whipple et al., 1990b) and slower improvements in tenderness with ageing (Wheeler et al., 1990a,b; O’Connor et al., 1997) in meat from *Bos indicus*-influenced carcasses. Breeding programs utilizing *Bos taurus* × *Bos indicus* matings are commonly used to capitalize on heterosis and the positive traits possessed by *Bos indicus* breeds. Crouse et al. (1989) reported that increasing the proportion of Brahman inheritance from 0 to 100% resulted in progressive decreases in trained sensory panel tenderness ratings. This effect was even more pronounced as percentage of Sahiwal inheritance increased from 0 to 100%. Additionally, the variation in tenderness within a breed group increased as the percentage of *Bos indicus* inheritance increased. In partial agreement, Johnson et al. (1990) reported that increasing Brahman influence reduced tenderness scores and inhibited improvements in Warner–Bratzler shear force after 5 or 10 d of ageing. However, Johnson et al. (1990) reported no difference in tenderness or ageing response between Angus and 1⁄4 Brahman steers. The use of composite breeds comprised of 3⁄8 *Bos indicus* inheritance and 5⁄8 *Bos taurus* inheritance is commonly used by beef producers to incorporate the positive attributes of *Bos indicus* cattle. Bidner et al. (2002) reported that calves sired by bulls of Brahman derivative breeds (3⁄8 Brahman) were less tender after 10 d of ageing than calves sired by Angus bulls. This is in agreement with the results of O’Connor et al. (1997) which found that *longissimus* steaks from 3⁄8 *Bos indicus* steers produced higher shear force values when compared to *Bos taurus* steers after ageing up to 35 d postmortem, regardless of the source of the *Bos taurus* germplasm.

A muscle hypertrophy condition in lamb that causes dramatic toughening of the resulting meat is called callipyge (Cockett et al., 1994, 2005; Koohmaraie et al., 1995; Carpenter et al., 1996; Freking et al., 1998). The hypertrophy is caused by decreased protein degradation, and is associated with increased calpastatin activity in the hypertrophied muscles (Koohmaraie et al., 1995; Lorenzen et al., 2000). The response of various muscles to the callipyge condition is proportional to the increase in calpastatin activity within the muscle (Koohmaraie et al., 1995). The meat from callipyge lamb is less tender than normal lamb because the higher calpastatin activity inhibits the rate and extent of postmortem proteolysis by μ-calpain (Koohmaraie et al., 1995).
3.3.2 Genomic approaches to meat tenderness

Measures of tenderness have been reported to be moderately heritable, with estimates ranging from 0.30 to 0.53 (Shackelford et al., 1994; Wheeler et al., 1996a, 2001a, 2004a, 2005; Dikeman et al., 2005). Smith et al. (2003) estimated that 46% of the variation in tenderness is genetic and 54% is environmental. This indicates that improving tenderness via genetic selection is possible. Palatability trait differences have been characterized among cattle breeds (Koch et al., 1982; Wheeler et al., 1996a, 2001a, 2004a, 2005) and are considered in cross-breeding programs. However, substantial variation in tenderness exists within breeds and the opportunity for improving tenderness by selecting seedstock within a breed may be as great, or greater, than by changing breeds (Fig. 3.4; Wheeler, et al., 1996a, 2001a).

Several quantitative trait loci (QTL) associated with tenderness have been identified (Smith et al., 2003). Of these, two have been found that correspond to the genes responsible for μ-calpain (CAPN1) and its inhibitor calpastatin (CAST). Two SNP markers with significant utility for marker-assisted selection have been identified for the CAPN1 gene (Page et al., 2002; White et al., 2005). The allele associated with improved tenderness in one of these markers (CAPN1 316) is present at low to intermediate frequencies in Bos taurus populations (Table 3.1; Page et al., 2004), but segregate less appreciably in Bos indicus populations (Casas et al., 2005). A second marker (CAPN1 4751) was reported by White et al. (2005) to segregate in both Bos taurus and Bos indicus populations. These authors suggested that simultaneous analysis of the CAPN1 316 and 4751 markers would provide optimal information in marker assisted selection for tenderness at the μ-calpain locus. Several markers flanking the CAST gene have been demonstrated to be associated with tenderness (Casas et al., 2006; Schenkel et al., 2006). The favorable allele of one of these markers has been reported to have a frequency of approximately 60% in commercial cattle (Table 3.1.; Schenkel et al., 2006). Casas et al. (2006) reported that the effects of the CAPN1 and CAST loci appear to be
additive and do not interact. Therefore, it appears that markers for both of these
genes can be used simultaneously in breeding programs to improve tenderness.
Markers for both genes are available in commercial tests. The effects of these
markers on tenderness are relatively small (Table 3.1), but indicate significant
opportunity to improve the tenderness of the beef population.

Continuing efforts are needed to validate the effectiveness of these markers on
independent resource populations as well as samples of commercial cattle.
Additionally, it is likely that additional markers will be identified and developed as
new populations become available. Furthermore, understanding how the genes
identified by these markers interact with one another and with environmental
factors to affect tenderness is needed. Knowledge of those interactions would
allow the development of expected progeny differences (EPDs) that are adjusted
based on genetic marker information (Smith et al., 2003). Finally, research on the
interaction between genotype and management strategies will allow a whole-
system approach to improving tenderness.

### 3.3.3 Grain feeding effects on tenderness

In the U.S. and other countries, market animals are commonly placed in feed lots
and given *ad libitum* access to concentrate-based rations to produce rapid, efficient
growth and to ensure that animals reach slaughter weights at young ages. This practice has been reported to produce heavier, fatter, and more muscular carcasses compared to forage feeding (Bowling et al., 1977; Aberle et al., 1981). Concentrate-fed animals also produced steaks that were more tender than forage-fed animals. Increased mass and fat thickness in grain-fed carcasses slows chilling and, consequently, reduces sarcomere shortening during the onset of rigor (Tatum, 1981). Bowling et al. (1977) compared the tenderness of meat from grain-fed steer carcasses and slowly or conventionally chilled forage-fed carcasses. Sarcomere lengths were longest in grain-fed carcasses, shortest in conventionally chilled, forage-fed carcasses, and intermediate in slowly chilled, forage-fed carcasses. Trained sensory panel tenderness ratings were highest for meat from grain-fed carcasses and did not differ across chilling rates.

These data suggest that increased tenderness associated with grain feeding is not solely due to reduced sarcomere shortening. The improved tenderness of grain-fed animals is likely attributable to increased growth rate, which has been associated with increased protein turnover (Koochmar et al., 2002), postmortem proteolysis (Aberle et al., 1981; Purchas et al., 2002), and collagen solubility (Aberle et al., 1981). Aberle et al. (1981) reported that increasing time on a high-energy diet to 70 d increased tenderness ratings, myofibril fragmentation index (a measure of proteolytic degradation), and collagen solubility. These authors attributed these differences to rapid growth in grain-fed animals. These findings are consistent with those of May et al. (1992), who found that sensory panel tenderness ratings were optimized at 84 d on feed. Tatum et al. (1980) found no improvements in tenderness associated with feeding steers longer than 100 d. Short et al. (1999) reported that tenderness increased with increasing time on feed, but steers placed on feed at 18 mo of age showed no further improvement after 90 d on feed while steers placed on feed at 6 mo of age displayed slight improvements through 270 d on feed. These findings suggest that grain feeding cattle for 90 to 100 d should optimize tenderness.

3.3.4 Effects of growth promotants on meat tenderness

Improving the rate and efficiency of growth in market animals is an important economic consideration to livestock producers. Therefore, the administration of agents that partition nutrients towards muscle deposition is a common practice. Though numerous metabolic modifiers have been utilized in meat production, the most commonly used include anabolic steroids and beta adrenergic agonists (BAA). Despite substantial evidence demonstrating the efficacy and safety of using growth promotants, their use is prohibited in some countries, particularly the European Union.

The vast majority of cattle fed in the U.S. receive anabolic steroid implants, which can be broadly classified according to the chemical nature of their active ingredients (estrogens, progestins, androgens, and combination) and the concentration of each (mild or strong; Montgomery et al., 2001). Of single ingredient implants, estrogenic implants are considered most effective in steers while andro-
genic implants are considered most effective in heifers (Dikeman, 2003). Combination implants containing both estrogens and androgens generally provide greater growth responses than single ingredient implants and are, therefore, considered to be most 'aggressive' (Montgomery et al., 2001; Dikeman, 2003). Animals may be implanted at multiple stages of production and may receive multiple implants during the finishing phase. Endless combinations of compounds, dosages, and timing that might be utilized in an implant strategy make discerning the effects of implants extremely complex. However, anabolic implants are generally reported to have neutral or negative effects on meat tenderness compared to non-implanted controls (Morgan, 1997; Montgomery et al., 2001; Dikeman, 2003). In a review of available literature, Morgan (1997) estimated that meat from implanted animals has a Warner–Bratzler shear force value 0.5 kg higher than meat from non-implanted animals. These effects are largely dependent on the implanting strategy used. As implanting strategies increase in aggressiveness (use of androgenic, combination and/or multiple implants), the negative effects on tenderness are amplified (Morgan, 1997; Platter et al., 2003). Schneider et al. (2007) reported that Warner–Bratzler shear force values increased linearly as the cumulative dose of estradiol 17-β plus trenbolone acetate (1:10 ratio) increased in two sequential implants. Samber et al. (1996) studied several implant protocols and reported that using a mild implanting strategy at the beginning of the feeding period was less detrimental to tenderness than strategies using aggressive implants at the beginning of the feeding period. Platter et al. (2003) studied the effects of various lifetime implanting protocols (from approximately 2 mo of age through finishing) and found that Warner–Bratzler shear force values increased as the number of lifetime implants increased from zero to two and from two to three. Steers implanted four or five times had shear force values intermediate to the shear force values of steers implanted two or three times. Dikeman (2003) concluded that cattle should not be implanted within 70 d of slaughter.

Interest in the use of BAA (e.g., Cimaterol, \(L_{64,369}, \) ractopamine, zilpaterol) in meat animals has increased because of the dramatic increases in lean growth associated with their use. Numerous reports indicate that BAA negatively affects meat tenderness (Dikeman, 2003). The toughening effect is thought to be due to reduced proteolysis resulting from increased calpastatin activity (Koohmaraie et al., 1991, 1996b). In the U.S., BAA have recently been approved for use in swine (ractopamine) and beef cattle (ractopamine and zilpaterol). The compounds also are approved for cattle in some other countries. Feeding pigs either 10 or 20 ppm ractopamine resulted in higher Warner–Bratzler shear force values, but did not affect tenderness scores compared to non-supplemented pigs (Carr et al., 2005). This is in agreement with the findings of Uttaro et al. (1993), who reported that 20 ppm ractopamine increased Warner–Bratzler shear force values and decreased myofibril fragmentation in loin chops of supplemented pigs compared with those of non-supplemented pigs. Gruber et al. (2007) reported that cattle fed 200 mg/steer/d ractopamine produced steaks that were less tender than non-supplemented control through 21 d of postmortem ageing. In their study, the effect of ractopamine on tenderness was larger in Brahman crossbred steers than in
Continental or British crossbred cattle (0.5, 0.3, 0.2 kg Warner–Bratzler shear force, respectively). Avendaño-Reyes et al. (2006) compared cattle fed ractopamine and zilpaterol to non-supplemented controls and found that both compounds increased Warner–Bratzler shear force values of longissimus steaks by 10 and 16%, respectively. Strydom and Nel (1999) fed zilpaterol (0.15 mg/kg live weight/d) to steers for the final 30 or 50 days on feed and reported that both zilpaterol treatments reduced sensory panel tenderness ratings by 0.8 units (8 point scale) compared to controls. In comparison, Casey et al. (1997) reported even greater increases in Warner–Bratzler shear force due to zilpaterol fed to steers that had been either implanted with 24 mg estradiol and 120 mg trenbolone acetate (1.5 kg) or not implanted (2 kg). Available information indicates that feeding currently available BAA would have detrimental effects on tenderness.

3.4 Postmortem technologies affecting meat tenderness

Once an animal has been harvested, postmortem management strategies can be employed to optimize the tenderness of the resulting meat. These strategies either manipulate the inherent biochemical processes that are active in postmortem muscle, or physically or chemically alter the myofibrillar or connective tissue structures of the muscle. When applied appropriately, postmortem technologies can improve the overall palatability and consistency of meat being produced.

3.4.1 Postmortem ageing

Soon after slaughter, the calpain enzyme system begins degrading cytoskeletal proteins (Koohmaraie, 1996; Veiseth et al., 2004). The rate and extent of the ageing response is influenced by numerous factors such as the calpastatin activity in the muscle, muscle pH, and storage temperature. Though tenderization with ageing is well established, identifying optimum ageing time is difficult. Koohmaraie (1996) recommended that beef, lamb, and pork longissimus be stored for 10–14 d, 7–10 d, and 5 d, respectively, to ensure adequate tenderization. It is important to note the results of muscle profiling studies (e.g. Rhee et al., 2004; Von Seggern et al., 2005) suggest that the contribution of component traits driving tenderness differences are muscle dependent. Therefore, the ageing time needed to optimize tenderness is likely to differ across muscles. Gruber et al. (2006) reported that 17 muscles differed in ageing response (2 to 28 d of storage) with the decrease in Warner–Bratzler shear force ranging from 0.5 kg in US Choice biceps femoris to 2.5 kg in US Select longissimus lumbrorum. Mies et al. (1999) reviewed literature pertaining to different subprimal cuts of beef and recommended ageing times of 12, 11, 11–15, 14, 21, 12, and 15 d for chuck roll (longissimus thoracis and complexus), shoulder clod (triceps brachii and infraspinatus), ribeye roll (longissimus thoracis), strip loin (longissimus lumbrorum), top sirloin (gluteus medius), bottom round (biceps femoris), and top round (semimembranosus and adductor)
subprimals, respectively. The identification of optimum ageing times for various muscles is further complicated by differing reports on the magnitude of tenderness improvements due to ageing. These inconsistencies in the literature may be partially due to meat that is inherently tender requiring less ageing time to reach a point where no further increases are detectable. Additionally, in some studies, ageing treatments may be confounded with intramuscular differences in tenderness (Rhee et al., 2004) which may potentially mask the effects of ageing on tenderness. King et al. (2007) attempted to mitigate the confounding effects of location within the muscle in an investigation of ageing effects on gluteus medius and triceps brachii tenderness by evaluating 50 muscles of each at six ageing times (7 to 42 d postmortem) and sampling a single location in each muscle for tenderness evaluations. In that experiment, slice shear force values decreased by 24 and 21% in gluteus medius and triceps brachii, respectively. However, most of the improvement in slice shear force values (18%) had been achieved by 28 d postmortem in both muscles.

3.4.2 Electrical stimulation
Electrical stimulation applied to pre-rigor carcasses causes muscle contraction and, consequently, rapid depletion of glycogen stores in muscle before chilling. Electrical stimulation has been reported to enhance the tenderness of beef (Cross et al., 1979, 1984; Savell et al., 1981). The improvement in tenderness is generally attributed to the prevention of cold-induced toughening (Cross et al., 1984), activation of endogenous proteases (Bowling et al., 1978; Cross, 1979), and physical disruption of muscle fibers (Savell et al., 1978). Hopkinson et al., (1985) reported that Warner–Bratzler shear force values of longissimus steaks from electrically stimulated steer carcasses at 2 d postmortem were similar to longissimus steaks from non-stimulated carcasses aged for 14 d (6.41 and 6.35, respectively). This is in agreement with the results of Savell et al. (1981), who reported that the improvement in Warner–Bratzler shear force values due to electrical stimulation at 1 d postmortem (25.8%) was similar to the improvement due to 8 d of postmortem aging (25.1%). Savell et al. (1981) also reported that the improvement in tenderness due to electrical stimulation was greater in carcasses that were initially tough than in those carcasses that were inherently tender. Electrical stimulation effects on tenderness are highly dependent on the parameters used in electrical stimulation application. Generally, high voltage is required to elicit a significant tenderization response. The extensive literature regarding electrical stimulation should be consulted for additional information.

3.4.3 Chilling effects on tenderness
During the first 24 h postmortem, anaerobic glycolysis depletes muscle glycogen causing the accumulation of lactate. As a result, muscle pH declines from 7.4 to approximately 5.5. As ATP stores are depleted, actomyosin bonds are fixed. During this process, sarcomere shortening occurs, causing toughening (Wheeler
and Koohmaraie, 1994). At lower temperatures, the sarcoplasmic reticulum’s ability to sequester calcium is reduced (Whiting, 1980). As a result, low temperatures (below 10 °C) in early postmortem muscle possessing adequate ATP stores to cause contraction result in sarcomere shortening (Locker and Hagyard, 1963), which causes toughening (Marsh and Leet, 1966; Marsh et al., 1968). This condition is termed ‘cold shortening’. Marsh and Leet (1966) suggested that cold shortening could be minimized by not allowing muscle temperatures to fall below 10 °C until muscle pH had declined below 6.2.

Additionally, the rate of temperature decline can have profound effects on proteolytic degradation of muscle proteins. Extremely rapid chilling of longissimus and triceps brachii muscles resulted in less desmin degradation (10 percentage points) during the first 24 h postmortem (King et al., 2003). Rates of desmin degradation were similar in rapidly chilled and conventionally chilled muscles during the next 13 d of ageing. In contrast, Whipple et al. (1990a) compared conventional chilling to holding carcasses at ambient temperatures for 6 h before chilling. Delayed chilling provided a more favorable environment for proteolysis, resulting in higher myofibril fragmentation index values at 3, 7, and 14 d postmortem and lower shear force values at 1 d postmortem in carcasses subjected to delayed chilling. However, Warner–Bratzler shear force values were not affected by delayed chilling at 14 d postmortem. Though high-temperature conditioning is effective in improving tenderness, this practice is not recommended due to food safety concerns.

### 3.4.4 Pre-rigor alterations in carcass position

The extent of sarcomere shortening during the onset of rigor mortis in an intact carcass is limited by skeletal restraint. Herring et al. (1965a,b) and Hostetler et al. (1970) found that hanging carcasses by the Achilles tendon stretches some muscles while allowing others to contract, which impacted tenderness. Several investigators have examined the use of alternative methods of hanging or altering carcasses to increase the tension on valuable muscles. In a method called ‘tenderstretch’, Hostetler et al. (1970 and 1972) hung carcasses by the obturator foramen to stretch the longissimus and other valuable muscles. This method is used by some processors in Europe. Carcasses in Australia can be tenderstretched to qualify for a higher quality grade. This strategy is not currently used in the U.S., primarily because tenderstretched carcasses require more space in the chilling cooler, and the shape of muscles from tenderstretched carcasses are not conducive to traditional fabrication methods. However, with the advent of marketing individual muscles, this strategy might merit reconsideration by U.S. processors. Another procedure termed ‘tender cut’ involves severing the bones and connective tissue at the 12th thoracic vertebrae and in the pelvic girdle to stretch the longissimus and round muscles (Wang et al., 1994, 1996; Ludwig et al., 1997). This process places the weight of the carcass on the muscle rather than the skeleton, thereby lengthening sarcomeres and improving tenderness in economically important muscles.
3.4.5 Enhancement strategies to improve tenderness
Processing strategies can be applied to post-rigor muscle to improve palatability. Blade tenderization is commonly applied to cuts destined for food service establishments. In this process, thin, needle-like blades are used to disrupt muscle fibers and connective tissue. George-Evins et al. (2004) reported that blade tenderization improved the tenderness of gluteus medius steaks without negative effects on other palatability traits. Savell et al. (1977) evaluated the use of blade tenderization on four beef muscles and noted that a single pass through a blade tenderizer decreased shear force values of gluteus medius, semimembranosus, and longissimus steaks, but did not affect biceps femoris steaks relative to non-tenderized controls. A second application of blade tenderization further reduced Warner-Bratzler shear force values of semimembranosus and also improved biceps femoris steaks. Additionally, after a single application of blade tenderization, longissimus steaks received higher sensory panel ratings for overall and myofibrillar tenderness, and perceivable connective tissue (less connective tissue), but were also rated as less juicy. Another approach to muscle enhancement is to use injection of marinades containing non-meat ingredients to increase palatability traits (Miller, 1998). Marinades commonly contain salts (e.g. sodium chloride), water-binders (e.g. sodium phosphates), exogenous enzymes (e.g. papain, bromelain, and ficin), and/or antioxidants (e.g. rosemary). The effects of these solutions on tenderness are mediated through the dilution of myofibrillar proteins, the degradation of myofibrillar or connective tissue proteins by exogenous enzymes or the activation of endogenous enzymes by calcium chloride (Koohmaraie et al., 1989; Wheeler et al., 1992, 1993). Vote et al. (2000) found that injecting beef strip loins with distilled water or 0.25% sodium tripolyphosphate solution decreased tenderness relative to untreated controls, but injecting with 0.25% sodium tripolyphosphate, 2.5% sodium lactate, 0.5% sodium chloride solution improved tenderness. Additionally, Vote et al. (2000) reported that increasing the level of injection from 7.5 to 15% of green weight provided incremental increases in tenderness. Mueller et al. (2006) reported that beef round muscles injected (12% pickup) with a 5% sodium chloride and 2.95% sodium tripolyphosphate solution received higher consumer ratings for tenderness, juiciness, and flavor than blade tenderized or non-injected muscles. Calcium chloride has been used to activate the calpain system and increase tenderization in beef longissimus, semimembranosus, and triceps brachii compared to non-injected or water-injected controls, regardless of injection level, calcium chloride concentration, or time of injection (Wheeler et al., 1993; 1997b); however, no commercial implementation of calcium chloride marinades has occurred to our knowledge.

3.5 Laboratory tenderness assessment
The evaluation of strategies intended to improve tenderness requires that tenderness assessments be accurate and repeatable. AMSA (1995) provides a set of guidelines for tenderness assessment by trained sensory panels and shear force
measurements. Regardless of the method used, care must be exercised to collect accurate and repeatable tenderness data.

3.5.1 Trained sensory panel
The gold standard for tenderness assessment is a trained sensory panel comprised of highly trained individuals. There are numerous ways to use a trained sensory panel, depending on the question to be addressed. One of the most common is a trained descriptive attribute panel for detecting differences in traits such as tenderness, juiciness, and flavor intensity. Some considerations for the selection and training of panel members include availability, motivation, skill, and consistency (Wheeler et al., 1997d). Panelists should be identified, screened to assure their ability to discern differences, and trained as described by Cross et al. (1978) and AMSA (1995). Samples presented to the panel must be of sufficient quantity to allow all panel members to evaluate the sample adequately and representative of the inferences to be made. Constant evaluation of the panel and periodic refresher training of the panelists is necessary to prevent drift and to maintain accuracy and precision. In addition, a well trained sensory panel is expensive for a laboratory to maintain.

3.5.2 Untrained/consumer panel
Consumer evaluations of meat products provide excellent information regarding acceptability of products. In-home tests provide important information about consumer acceptance and preferences when actually using the product (e.g. Neely et al., 1998; Savell et al., 1999). However, these studies are complicated by lack of control over sample preparation, consumers failing to complete the study, and the potential for incomplete or incorrect recording of data. Central location consumer panels provide the opportunity to collect consumer impressions while controlling sample presentation and provide a data collection environment that may improve accuracy (e.g. Hoover et al., 1995; Carr et al., 2004). Wheeler et al. (2004b) evaluated untrained laboratory consumer panels in relation to slice shear force and noted that consumer panels were able to detect differences in tenderness categories with as few as four panelists, although the correlation of mean panel ratings to slice shear force values increased as the number of panelists increased to 16 ($r = -0.68$ and $-0.92$ for panels consisting of 4 and 16 panelists, respectively). The repeatability of mean panel scores of duplicate samples was 0.80, although accuracy and repeatability varied widely among individual panelists. These data suggest that, depending on the samples of interest, untrained laboratory consumer panels may be a valuable tool in evaluating meat tenderness.

3.5.3 Warner-Bratzler shear force
Sensory panel data collection is a slow, cumbersome process. The need to collect data on a large number of samples in a narrow time frame has led to the widespread
use of instrumental measures of tenderness. The most common instrumental objective tenderness measurement is Warner–Bratzler shear force. Warner–Bratzler shear force involves shearing 1.27 cm-diameter cores (removed from cooked steaks parallel to the muscle fiber orientation) with a V-notch blade (1.016 mm-thick with a half-round bevel) attached to a load cell on a Warner–Bratzler shear machine or a universal testing machine. Though collection of shear force data is viewed as routine, differences in accuracy and repeatability exist between individual laboratories conducting tests (Wheeler et al., 1997c). Obtaining accurate and repeatable Warner–Bratzler shear force data requires investigators to be vigilant with regard to numerous factors such as cooking methodology, core removal, and shearing of cores (Wheeler et al., 1996b, 1998). For detailed discussions of standardizing protocols, the reader is referred to Savell et al. (1994) and Wheeler et al. (1997d).

3.5.4 Slice shear force
Efforts to develop a rapid tenderness measurement to be used in on-line tenderness classification programs resulted in the advent of slice shear force (Shackelford et al., 1999). Slice shear force involves the shearing of a 1 cm thick x 5 cm long slice removed parallel to the muscle fiber orientation with a flat, blunt-ended blade. The thickness and bevel of the slice shear force blade is the same as those used for the Warner–Bratzler V-notch blade. Slice shear force values are highly repeatable ($r = 0.91$) and more strongly related to trained sensory panel ratings than Warner–Bratzler shear force values ($r = -0.82$ and -0.77, respectively; Shackelford et al., 1999). Additionally, removing ‘good’ slices for slice shear force is easier than acquiring ‘good’ cores for Warner–Bratzler shear force. Finally, since slice shear force can be measured on hot steaks and is measured on one slice rather than 6 or more cores, lab throughput is increased relative to Warner–Bratzler shear force.

Other instrumental measures of tenderness have been used, depending on the type of information desired by the investigator. These include compression tests, Allo–Kramer shear, the MIRINZ tenderometer, as well as various modifications of shear tests. Regardless of the type of shear force measured, investigators should be cognizant of the limitations of shear force data. It is common to attempt to identify thresholds for consumer acceptance. However, the inherent differences between labs and varying consumer acuity and perceptions for tenderness make these attempts dubious (Wheeler et al., 1997c,d). A level of tenderness that is perfectly acceptable to one consumer may be completely unacceptable to another. In general, inferences made using shear force data should be limited to relative treatment differences within an experiment. Finally, Warner–Bratzler and slice shear force values do not accurately reflect differences in tenderness between muscles (Harris and Shorthose, 1988). Shackelford et al. (1995) reported that Warner–Bratzler shear force values identified few differences among 10 beef muscles, but trained sensory panel ratings stratified these muscles into four tenderness groups. This is likely because shear force measures do not accurately represent the contribution of connective tissue to tenderness differences between
Fig. 3.5 Consumer ratings of sensory traits of steaks certified tender or not-certified by a slice shear force tenderness classification system. Adapted from Shackelford et al. (2001).

muscles (Bouton et al., 1978). Those conclusions were confirmed by the results of Rhee et al. (2004).

### 3.6 On-line tenderness prediction

Many investigators have attempted to apply technologies such as Tendertec (George et al., 1997; Belk et al., 2001), connective tissue probe (Swatland, 1995; Swatland and Findlay, 1997; Swatland et al., 1998), elastography (Berg et al., 1999), near-infrared spectroscopy (Hildrum et al., 1994; Park et al., 1998), ultrasound (Park and Whittaker, 1991; Park et al., 1994), image analysis (Li et al., 1999, 2001), lean color attributes (Wulf et al., 1997), image analysis traits using prototype Beef Cam modules (Belk et al., 2000), and a combination of colorimetric, marbling, and hump height traits (Wulf and Page, 2000), for the purpose of tenderness classification of meat, with little success. In the early 1990s, scientists at USMARC concluded that a direct measure of tenderness was required to obtain an accurate enough measurement to create a useful tenderness classification system, if the tenderness assessment could be made at normal processing speeds. To this end, slice shear force was developed and incorporated into a rapid process for cooking and obtaining a slice shear force value of the longissimus muscle as carcasses were presented for grading (Shackelford et al. 1998, 1999). Consumers gave higher ratings for all sensory traits to U.S. Select beef classified as tender by slice shear force compared to beef not classified as tender (Fig. 3.5; Shackelford et al., 2001).
Fig. 3.6 Distribution of slice shear force values of *longissimus* steaks predicted as tough or tender by VISNIR spectroscopy. Adapted from Shackelford *et al.* (2005).

To date, one large beef processor is using the slice shear force technology in cooperation with a large retailer to produce a guaranteed-tender product line. Anticipating that the majority of the industry would deem it to be too invasive and costly for implementation, simultaneous efforts were focused on developing a non-invasive approach. Visible and near-infrared-reflectance (VISNIR) spectroscopy technology appeared to have the most potential to classify beef carcasses according to tenderness (Shackelford *et al.*, 2005). Early application of VISNIR tenderness classification was focused on US Select carcasses because these carcasses are discounted relative to US Choice carcasses, even though the vast majority of US Select carcasses are acceptably tender. Shackelford *et al.*, (2005) reported that VISNIR spectroscopy was effective in identifying carcasses that produced tender meat after ageing. In the validation data set reported in that study, carcasses predicted to be tender had higher sensory panel tenderness ratings compared to those not predicted to be tender (5.6 versus 5.1, respectively). Furthermore, only 5.5 percent of carcasses predicted to be tender had slice shear force values greater than 25 kg compared to 30.1% of those not predicted to be tender (Fig. 3.6). Future research objectives related to tenderness prediction include the application of this technology to carcasses of all quality grades, muscles other than the *longissimus*, and other species.

### 3.7 Conclusions

Tenderness is critical to the consumer acceptance of meat products. Numerous
antemortem and postmortem factors can impact tenderness, both positively and negatively. Therefore, antemortem and postmortem management decisions must be made carefully. Recent advances in the development of genetic markers for use in selection decisions are encouraging. Meanwhile, antemortem management should strive to optimize efficiency and palatability traits. Tenderness prediction technology can be used to segregate carcasses into product lines. Additionally, postmortem strategies can be used singularly or in concert to further ensure the eating quality of muscle foods.

3.8 Sources of further information and advice

Muscle structure, contraction, and conversion of muscle to meat

Postmortem tenderization

Growth promotants

Tenderness measurement

3.9 References


of mutations disrupting the myostatin function and causing double-muscling in cattle. 

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Improving the sensory and nutritional quality of fresh meat


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