

digestibility of 65 percent or more. Thus, if this be true, bermudagrass is high in quality for only about 60 days of the year. This may explain the reason why young, growing cattle gain well during April, May and June but gain poorly during the remainder of the growing season. Furthermore, research has shown that forage intake increases as digestibility increases up to about 60 percent dry matter digestibility. Since digestibility of bermudagrass is below 60 percent except for April, May and June it is likely that cattle do not consume enough forage at other times to promote rapid gains.

Factors Influencing Muscle Fiber Variation

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Story in Brief

Skeletal muscle fibers vary greatly in size with respect to class of animal, muscle, and within muscle. These variations have been shown to be affected by specie, size, breed, sex, age, and level of nutrition. Post-mortem influences on muscle fiber size, sarcomere length, percent kinky fibers and shear force have been shown to be influenced by rigor mortis, temperature, and muscle tension.

This investigation was designed to study the effect of four levels of muscle tension on the shear force of the semitendinosus and semi-membranosus muscles. Levels of tension used were 0, 1000, 2500, 5000 gm.

Fiber size varied inversely with sarcomere length. No significant relationships were noted for fiber size and the percentage of kinky fibers.

Introduction

Skeletal muscle makes up approximately 40 percent of the live body weight of which approximately 75 percent is muscle fibers. Any variation as to quality and quantity of the muscle components can ultimately affect tenderness. The structure of muscle is a function of the relative amounts and kinds of the various component tissues. There-

fore a thorough appreciation of the important tissues comprising muscle must be realized before any consideration of fiber variation can be made.

With the advent of technological advancements in electron and light microscopy and new methods of tissue preparation the structure of the skeletal muscle fiber has drawn considerable interest. A brief review of the literature relative to striated muscle fiber will be given before considering variations.

Walls (1960) described the muscle fiber as a cylindrical, elongated, multinucleated syncytium that generally does not branch, however Bardeen (1903) has shown that variations of this description do exist. The muscle fiber is surrounded by a connective tissue sheath that is very similar to the plasma membrane and internal membranes of other cells and is referred to as the sarcolemma. The sarcolemma is not a perfectly smooth cylindrical membrane, but is marked by several small vesicles and carveolae (Porter and Palade, 1957). Beneath the sarcolemma there exists a fluid matrix referred to as the sarcoplasm, which is made of various soluble proteins such as myogen and myoglobin (color pigment). The sarcoplasm serves a function similar to that of typical cellular cytoplasm and contains the various cellular inclusions and organelles. An organelle, the myofibril, has received considerable attention due to its contractile properties. The myofibril is an elongated striated structure comprised of two different types of filaments. The coarse filament is approximately 100 angstroms in diameter and 1.5 microns in length. The fine filament is approximately 50 angstroms in diameter and 2 microns in length (Huxley and Hanson, 1957). The thick filament, comprised of the protein myosin, is called the A band. The thin filament is comprised of the protein actin and makes up what is referred to as the I band. Between adjoining I bands there is another band referred to as the Z disc. The distance from one Z disc to another comprises the contractile unit of the myofibril, the sarcomere.

Inherent Variation

Walls (1960) reported that there is considerable variation in fiber diameter, with a range of 10 to 100 microns commonly being accepted. Fiber size differs in the major animal classes with fish having the largest fibers and birds the smallest (Mayeda, 1890). The fibers of one muscle may be generally larger than those of another muscle in the same animal (Hommond and Appleton, 1932). In addition, the fiber diameters vary considerably within the same muscle. Other factors such as specie, size, age, breed, sex, and level of nutrition also have been found to influence this variation.

Joubert (1956a) reported that muscle diameter had no clear relationship to size of species, however, an increase in fiber diameter was closely associated with relative increase in body weight.

Using cattle, Joubert (1956a) studied the effect of breed on fiber diameter. He found that one breed of cattle, British Friesian, whether crossbred or purebred had significantly larger fiber diameters than another breed, Dairy Shorthorn. This breed significance was not shown to be independent of body weight. Other workers, Adametz (1888), Hammond and Appleton (1932), Strateciuc (1933), Mehner (1938) and Glebina (1952), have supported the findings that interbreed differences do exist, however, in most cases the difference is proportional to differences in body size.

A review of early reports caused Joubert (1956a) to conclude that males generally have thicker fibers than females. However, taking size into consideration he found that there was a slight tendency for females to have thicker fibers than males. Adametz (1888) reported that muscle fibers of bulls were appreciably larger than of cows, but that only slight differences existed between bulls and steers. Other workers, Hammond and Appleton (1932) using sheep, Mehner (1938) with fowl, and Ishihara *et al.* (1953) in Japanese Black cattle, confirmed these results.

Contradictory evidence has been presented by Brady (1937), and Satorius and Child (1938) that cows had significantly thicker muscle fibers than steers. The true relationship, if any, that does indeed exist is still a matter of conjecture.

The effect of age on fiber diameter has been studied extensively by many workers: McMeekan (1940-41), Thompson (1942), Meara (1947), Hiner *et al.* (1953), Joubert (1956a), Tuma *et al.* (1962), Carpenter *et al.* (1962) and Henrickson *et al.* (1963), and all are in agreement that fiber diameter increases from birth to maturity and that it increases in size rapidly while the animal is quite young and tends to level off as the animal approaches maturity.

Yeates (1964) studied starvation changes and subsequent recovery of adult beef muscle. The experiment revealed that with starvation of the adult animal the shrinkage in cross sectional areas of the muscles, after allowing for the loss of some intramuscular fat, was associated with the reduction in diameter of the individual fibers; thus, with repair of live weight, recovery both of whole muscle dimensions and muscle fiber diameter appeared to be complete.

Large fibers within a muscle are often closely associated with "growthy" or meat type animals. Unusually large muscles possess many

fibers which are intermediate to grey-white in color. This condition is first noted on the surface muscles of the thick portions of the carcass and are most extensive on the periphery of the muscle bundles. These white fibers are characterized by being low in myoglobin, but high in potassium and phosphorus. The K-40 content of total muscle may be influenced greatly by the predominance of white muscle fibers. Connective tissue surrounding the fibers are filled with fluid and the muscle is described as being soft, watery, and pale. Fibers such as these have the ability to contract at a rapid pace. Thus, leading to death of the animal often as a result of excitement. In less severe cases the animals are slaughtered and the condition is detected as light colored muscle.

The chemical composition of white muscle in the red meat animal is such that it leads to meat with undesirable quality. It would seem now that such a condition in meat should be well guarded against as we strive for improvement in the meat type animal.

Post-Mortem Variations

Another cause of structure variation of the muscle fiber is the conditions to which it is subjected after the animal is slaughtered.

Muscle contraction referred to as rigor mortis has received much attention by investigators. Rigor mortis is defined as the physical and chemical changes that take place after death of the animal. This discussion will be limited to the physical effects of rigor on the muscle fiber. The main observed physical change is from a highly extensive elastic condition of muscle or freshly killed animals to the inextensible and rigid condition of the muscle fiber in full rigor. This is a result of the actin filaments becoming bound to the myosin filaments thus greatly decreasing fiber extensibility. This actomyosin complex remains locked in a contracted state until rigor resolves (Marsh, 1954). Along with this change in extensibility, there is a gradual shortening of the sarcomere as rigor approaches, which leaves the muscle in a semi-contracted state (Locker, 1960).

Similar results with an increase in fiber diameter and a decrease in sarcomere length were obtained at the Oklahoma Station. Another well known physical effect of rigor on the muscle fiber is the presence of rigor kinks found in localized areas along some fibers. In an attempt to objectively determine the amount of kinkiness in different muscles and as a result of different treatment Gillis and Henrickson (1967) have devised a method of expressing the amount of kinkiness on a percentage basis. This method consisted of subjectively assigning a value to the condition of the muscle fiber, similar to the subjective appraisal of carcass

grade, and then relating this measurement with other known estimates of contraction.

The effect of temperature on the condition of the muscle fiber has been shown to have considerable influence. Locker and Hagyard (1963) showed that shortening of the muscle fiber occurs when exposed to very cold temperatures. This phenomenon is referred to as cold shortening. It is currently thought that cold shortening occurs simultaneously with the formation of cross-linkages in rigor; a degree of internal strain or actual disorganization occurs, and actually increases the resistance of the muscle to cleavage. Herring *et al.* (1965a) reported that slightly more shortening appeared, as indicated by sarcomere length, to take place in stretch-restrained muscle samples at 1° C. than at 5° C. It was postulated in this experiment that some cold shortening may have occurred at this temperature as well.

Cook and Wright (1966) using samples of unfrozen and pre-rigor frozen ovine semitendinosus muscle, incubated for 24 hours at six temperature levels between 0° and 40°C., found that variations in temperature caused muscle fibers to be in various states of contraction. The variations in sarcomere length of unfrozen and pre-rigor frozen muscle did not follow any specific course in relation to temperature, but a difference did exist.

Harrison *et al.* (1949) noted that the differences between sections of raw and cooked muscle were slight, however, the cooked sections tended to have straighter fibers than the raw muscle sections.

Paul *et al.* (1944) noted that the histological appearance of the muscle fibers varied with biological aging. Harrison *et al.* (1949) noted that freshly killed beef muscle showed poorly differential straight to slightly wavy fibers. After 1 day of storage at 1.7°C. the fibers and cross striations were more distinct, and the longitudinal striations less distinct. Contracture nodes, kinks, and waves increased in the fibers with long aging, however, they did tend to disappear after 4 to 9 days of storage. Disappearance of cross striae in small, infrequent areas of the fibers was noted on the second day of storage, and this disintegration tended to increase in frequency and extent as the storage time increased.

Younger and Baigent (1965) studied the effect of precooking on freeze-dried lamb and noted that uncooked freeze-dried meat appeared to suffer much more fiber damage, in terms of fiber distortion and shrinkage, than the cooked freeze-dried samples. When rehydrated, the samples revealed a similar pattern, the uncooked freeze-dried material revealed considerable distortion of the fibers and many were smaller in

diameter than normal. The cooked, freeze-dried samples very closely resembled fresh meat. The fibers were restored almost completely in size and shape, with no abnormal spaces between them.

Carcass position has a definite effect on sarcomere length and fiber diameter, (Herring *et al.* 1965b). When the carcass is suspended vertically certain muscles are in a stretched state, as indicated by sarcomere length, while some are in a shortened state. In general, the differences in sarcomere lengths were associated with differences in diameter. When the muscles shortened, there was a corresponding decrease in sarcomere length and an increase in fiber diameter.

Recent work at the Oklahoma Station, using the semitendinosus and semimembranosus muscles from five choice grade steers of similar age, weight, and genetic background, indicated that a positive relationship existed between muscle tension and sarcomere length, fiber diameter, and percent kinkiness. Both muscle types were removed from the carcass post slaughter (45 min.), divided into four samples (6x6x21cm.) and subjected to four degrees of tension (0, 1000, 2500, and 5000 gm. pull). The samples were held in this state for 48 hr. post-mortem at 34°C. Histological and shear samples were then taken.

An analysis of variance showed that a highly significant difference ($P < .01$) existed for sarcomere length for the different degrees of tension. Further analysis, using Duncan's new Multiple Range test, clearly indicated that with succeeding increases in tension, a corresponding increase in sarcomere length occurred. All ranges were highly significant at the ($P < .01$) level except the range 2500-5000 which was significant at the ($P < .05$) level.

These findings are in general agreement with those of Herring *et al.* (1965) who noted that sarcomere length of the semitendinosus muscle shortened as a result of pre-rigor excision, but that the pre-rigor excised stretch-restrained semitendinosus muscles generally exhibited longer sarcomeres than the control samples.

A highly significant difference ($P < .01$) in fiber diameter was found for the different degrees of tension. There was also a highly significant difference ($P < .01$) between muscles, indicating that, with an increase in the amount of tension there was a corresponding decrease in fiber diameter, to a point.

Variation in percent kinkiness was found to be highly significant ($P < .01$) for the different degrees of tension, significant differences at the ($P < .05$) level were noted between muscles and for a muscle by

tension interaction. The semimembranosus muscle and an average of both muscles were found to have highly significant ($P < .01$) differences in percent kinkiness for ranges of 0-1000, 0-2500 and 0-5000 gm. pull.

Work at the Oklahoma Station by Reddy and Henrickson (1967) on the effect of pre-rigor excision of three bovine muscles on fiber diameter and percent kinkiness showed interesting relationships. Percent kinkiness was greater ($P < .10$) for the pre-rigor excised longissimus dorsi muscle than the post-rigor excised muscle. However, the opposite was true for the gluteus medius muscle thus supporting the postulation of Locker (1960) that different internal strains among muscles exist in the vertically suspended carcass. This also is in agreement with the findings of Gillis and Henrickson (1967) that the percent kinkiness is to a certain degree, a function of muscle tension.

We also found that fiber diameter of pre-rigor, exercised, semitendinosus muscle was greater than those in post-rigor, exercised muscles, apparently because of muscle shortening.

In a study to determine the relationship of fiber diameter to tenderness Hiner *et al.* (1953) showed that a curvilinear relationship exists between fiber diameter and tenderness. He found that, up to a point, an increase in fiber diameter results in an increase in shear force. Tenderness in this report is considered to be the resistance to shear. A position correlation does exist between the taste panel score for tenderness and a mechanical shear force. Tuma *et al.* (1962) also reported that with an increase in fiber diameter there was a corresponding increase in shear force among different age groups of cattle. However, when the effect of age was removed little relationship existed. Carpenter *et al.* (1962) on the other hand found that with an increase in maximum fiber diameter there was a decrease in shear force of raw longissimus dorsi muscle. Opposite results were found for cooked longissimus dorsi muscles. They postulated that for a given size core there may be more small than large fibers per unit area, therefore more of the sarcolemma and endomyial connective tissue was present, resulting in a less tender product.

Herring *et al.* (1965b) noted that as fiber diameter increased tenderness decreased whereas the opposite was true when fiber diameter decreased. It was also shown that a change in fiber diameter was related to a change in sarcomere length. In a previous experiment Herring *et al.* (1965a) found that stretching a muscle rather than not stretching it increased tenderness and resulted in smaller fiber diameters. It was assumed that a greater number of fibers per unit area, were being severed in the stretched sample. This assumption is in agreement with that of Carpenter *et al.* (1962) in that the greater number of smaller fibers

should theoretically make the muscle less tender. However, the stretched muscle was more tender, indicating that the thickness of the sarcolemma and endomysial connective tissue was reduced in thickness when the fibers were stretched (Cassella, 1950).

This fact is applicable to our work with muscles subjected to four degrees of tension. An analysis of variance indicated a significant difference ($P < .05$) in shear force. Further analysis indicated that shear force decreased up to 1000 and 2500 gm. pull for the semimembranosus and semitendinosus muscles, respectively.

Fiber diameter and shear force decreased as tension increased indicating that the stretched samples with the smallest average diameters were the most tender.

The relation of fiber size, amount of fat, and amount of connective tissue per unit area undoubtedly all effect tenderness.

The degree of muscular contraction as it effects tenderness has received considerable interest in recent years. Locker (1960) first postulated that different muscles in the carcass go into different states of contraction in rigor as a result of different internal strains imposed on the muscles of the vertically suspended carcass. In an experimental study of the effects of pre-rigor excision of several muscles he concluded that muscles in a relaxed state, as indicated by fibrillar pattern, are more tender than those partly contracted. To this effect Marsh and Leet (1966) studied the effects of cold shortening on tenderness. They noted that with a decrease in length of up to about 20 percent caused little or no toughening, but with 20 to 40 percent shortening the toughness increased several fold. Beyond 40 percent shortening the meat became increasingly more tender, and at 60 percent shortening it was cleaved almost as easily as meat in which almost no shortening had occurred. They postulated that the 40-60 percent range may be a zone of progressive rupturing thus causing a rapid decrease in internal strain in this phase, with consequent realignment of previously distorted cleavage planes.

Our work agrees with that of Herring *et al.* 1965 and indicates that, with increasing amounts of strain on a muscle, sarcomere length increases to a point of physical limitation, and there is a subsequent increase in tenderness.

The percent kinkiness decreased with the application of tension to the muscle samples. The semimembranosus muscle tended to increase in percent kinkiness greater than the 100 gm. pull treatment. A gradual increase in shear force was also noted, after the 2500 gm. pull treatment.

for this muscle, indicating that some fiber breakage may have occurred when the amount of tension overcame the physical limits of the fiber. This may have resulted in partial contraction of some of the broken fibers which would account for the increase in shear. Theoretically this also would allow these broken fibers to be distorted to a greater degree. A similar response was noted by Herring *et al.* (1965) when they tried to stretch the psoas major muscle; tearing and failure of the muscle to regain its initial length resulted.

In summary, the condition in which the muscle fiber is found is highly variable. Inherent differences of diameter and sarcomere length as a result of species, breed, sex, age and level of nutrition exist. Differences occur after the slaughter of the animal as a result of contraction and distortion in rigor, due to temperature change, and as a result of different amounts of tension on the muscle.

These structural variations affect the ultimate tenderness of the muscle. It stands to reason then that some of the commonly associated differences in tenderness with age, sex etc. may be due to the structural condition of the muscle fiber.

Further work appears necessary to clarify the relationship of sex to muscle fiber size and fiber size to muscle degeneration.

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