Recombinant bovine somatotropin (rbST) increases size and proportion of fast-glycolytic muscle fibers in semitendinosus muscle of creep-fed steers

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Recombinant bovine somatotropin (rbST) increases size and proportion of fast-glycolytic muscle fibers in semitendinosus muscle of creep-fed steers[1]

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ABSTRACT: The objective of this study was to determine the effect of recombinant bovine somatotropin (rbST) on muscle fiber histology and histochemistry in creep-fed beef steers. Crossbred steer calves were assigned to one of two treatment groups: control (sham-injected; n = 12) or rbST-injected (0.09 mg·kg^{-1}·d^{-1}; n = 12). Calves were injected every 14 d starting at d 28 of age until weaning at 205 d of age. Biopsies of the semitendinosus muscle were performed on d 100, and slaughter samples of semitendinosus muscle were collected for muscle fiber analyses on d 206. The rbST-treated calves had larger (P = 0.045) fast-twitch-glycolytic (FG) fibers [2,564 ± 10 vs 2,351 ± 11 μm^2 cross-sectional area, respectively] than controls. No differences (P = 0.36) between rbST-treated and control steers in cross-sectional area were detected for slow-twitch-oxidative (SO) [1,192 ± 20 vs 1,148 ± 22 μm^2, respectively] or fast-twitch-oxidative-glycolytic (FOG) fibers [1,484 ± 35 vs 1,403 ± 38 μm^2, respectively]. The percentage distribution for FOG fibers was greater for control calves than for the rbST-treated calves (38.4 vs 34.9 ± 0.1%, respectively; P = 0.014), whereas the percentage distribution for FG fibers was greater in the rbST-treated calves than for control calves (53.5 vs 48.4 ± 0.2%, respectively; P = 0.03). The percentage distribution for SO fibers tended to be greater for the control calves than for the rbST-treated calves (13.1 vs 11.7 ± 0.1%, respectively; P = 0.07). The percentage of FG fibers increased with age (45.4 vs 56.6 ± 0.8%, respectively; P = 0.001), whereas the percentage distribution of SO (14.3 vs 10.5 ± 0.5%, respectively) and FOG fibers (40.3 vs 32.9 ± 0.7%, respectively) decreased (P = 0.001) from d 100 to d 206. The increased longissimus muscle area and dissectable lean tissue in rbST-treated calves are associated with a greater percentage of FG fibers, which possess larger cross-sectional areas than the other fibers.

Key Words: Somatotropin, Beef Cattle, Muscle Fibers, Calves

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Introduction

Recombinant bovine somatotropin (**rbST**) administration is documented to increase longissimus muscle area and reduce s.c. fat thickness in finishing steers (Dalke et al., 1992). Previously reported results indicate that rbST-treated steer calves had (P < 0.03) larger longissimus muscle areas, higher carcass conformation scores, and more separable lean tissue than control calves (Vann et al., 1998). In contrast to pigs, few studies have investigated the effects of ST on muscle fiber contractile and metabolic characteristics in cattle. In Friesian bull calves, GH produced little change in fiber size in the semimembranosus muscle, although fast-twitch-oxidative-glycolytic (**FOG**) fibers in the triceps were slightly larger than controls (Maltin et al., 1990). In prepubertal Holstein-Friesian heifers, neither GH nor ovariectomy affected the proportion and relative area of the individual muscle fiber types, but GH tended to increase (P < 0.10) type I or slow-twitch-oxidative (**SO**) fiber area (Vestergaard et al., 1995). In crossbred beef steers, Ono et al. (1996) reported that the growth-promoting agents Somavubove and Synovex-S had the potential to enhance muscle hypertrophy, but that individual muscles responded differently to treatment with these compounds.

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The current study is unique in that it examines the effect of chronic administration of rbST on muscle fiber histology and histochemistry in young, growing creep-fed beef calves prior to weaning utilizing traditional cow-calf management practices. Thus, the objective of this study was to determine the effect of rbST administration on the percentage distribution of fiber types, the extent of fiber type transformation, and the individual muscle fiber cross-sectional area (**CSA**) in creep-fed beef steer calves.

Materials and Methods

Experimental Animals

Twenty-four continental European crossbred steer calves were randomly assigned to either of two treatment groups: control (sham-injected; n = 12) or rbST-treated (n = 12) based on birth weight. All steers were 28 ± 10 d of age (age range of 18 to 38 d) at commencement of the study. The study was performed at the Brown Loam Branch Experiment Station, at Raymond, MS, and was approved by the Mississippi State University IACUC (#95-015) committee. Cows and calves grazed ryegrass pastures until late May and then grazed bermudagrass pastures until study completion. In addition, the calves were allowed ad libitum access to supplemental creep feed (38% crude protein plus Lasalocid (Bovatec); Nutrena, Inc., Memphis, TN) to compensate for any increase in protein and energy requirements due to rbST treatment. Calves were administered a single injection of rbST (0.09 $mg \cdot kg^{-1} \cdot d^{-1}$ s.c. in the neck region on alternating sides each injection period) every 14 d starting at an average age of 28 d and continuing to weaning at d 205 of age. Calves were weaned at 205 d of age (group age range of 195 to 215 d) and transported (~240 km) to the Mississippi State University Meat Laboratory (Mississippi State, MS) for slaughter the following day (206 d of age). Carcasses, injection regions (neck), and semitendinosus biopsy sites were evaluated at slaughter by the regional meat inspector and no muscle abnormalities were found due to rbST treatment or muscle biopsies.

Muscle Tissue: Collection and Preparation

The semitendinosus muscle was chosen to be evaluated in this study because of the accessibility of the muscle during the biopsy. On d 100 of age, a shot biopsy instrument developed by Schöberlein (1976), with refined sampling cannula (Lahucky et al., 1980), which does not require use of anaesthesia (Schöberlein, 1989; Cheah et al., 1997), was employed for obtaining prerigor muscle samples. This technique has been used for pigs (Schöberlein, 1989; Scholz et al., 1998) and calves (Wegner and Schöberlein, 1984) without imposing stress to the animals and with complete wound healing within 20 d. The instrument is an adaptation of a stunning gun and uses blank cartridges to drive a cannula into tissues to a gauge-selected depth. These cannulas have cutting edges and tissue extractors and are capable of removing a cylindrical plug (skin + s.c. adipose tissue + muscle) of up to 2 g wet weight in less than 1 s. The tissue samples (approximately 5.5 to 6 cm long, 1 to 1.2 cm diameter, 2 g) for evaluating muscle morphological parameters (Cheah et al., 1997; Wegner et al., 1997; Wegner and Schöberlein, 1986) were obtained from the semitendinosus muscle at midlength (about 15 cm distal to the ischiatic tuber) in the central portion of the muscle. Immediately after removal from the cannula, a sample was transferred to a flat stick, while maintaining its length to that of the depth setting, and was tied in place using a cotton cord. One end was tied across the s.c. adipose tissue so the muscle could remain attached to and restrained by the epimysium and the other end tied across the muscle fibers. The restrained samples were then frozen in liquid nitrogen and stored at –80°C until sectioned. Samples were sectioned unfixed using a cryostat microtome before the histochemical staining.

On 206 d of age, calves were weighed (shrunk weight, which includes fasted weight plus weight loss due to transportation), and, immediately following exsanguination, semitendinosus muscle samples were collected from the side opposite that on which the biopsies were performed. The muscle sample (approximately 6 cm long, 2 cm diameter) was sutured to a flat stick and excised from the carcass using a scalpel blade, thus maintaining the length of the muscle sample. The restrained samples were then frozen in liquid nitrogen and stored at –80°C. Samples were sectioned unfixed using a cryostat microtome before the histochemical staining. Previous analyses indicate that similar results are obtained whether using biopsy or postmortem muscle tissue sections for fiber type analysis (Fritsche et al., 2000). Both the muscle biopsy (d 100) and the postmortem muscle samples (d 206) were taken at corresponding regions of the semitendinosus muscle to minimize any sampling differences in fiber distribution between the superficial and deep regions of the muscle.

Histochemical Analysis and Myofiber Classification

On d 100 and 206 of age, muscle samples were collected for muscle fiber morphology determination. Histochemical analysis was performed on biopsy and postmortem tissue samples prepared according to the procedure of Solomon and Dunn (1988), including complete succinate dehydrogenase (**SDH**) staining procedure followed by staining for acid ATPase activity using a preincubation of pH 4.15, and counterstaining the section with hematoxylin as the final step. Muscle fibers were classified into three types (slow-twitch-oxidative [SO], fast-twitch-oxidative-glycolytic [FOG], and fast-glycolytic [**FG**]) according to Peter et al. (1972). The fiber type percentages were computed manually using two to three muscle fiber bundles per photomicrograph (10.2 × 15.2 cm); thus, approximately 150 to 300 total fibers

Table 1. Least square means and pooled standard errors for the percentage distribution of fiber types and fiber cross-sectional areas as influenced by treatment

	Treatment group			
Fiber type	Control	rbST	Pooled SEM[a]	*P*-value[b]
SO, %[c]	13.1	11.7	0.11	$P = 0.07$
FOG, %[d]	38.4	34.9	0.06	$P = 0.014$
FG, %[e]	48.4	53.5	0.15	$P = 0.03$
	Fiber cross-sectional area			
SO, μm^2 [c]	1,148	1,192	21	$P = 0.37$
FOG, μm^2 [d]	1,403	1,484	36	$P = 0.36$
FG, μm^2 [e]	2,351	2,564	11	$P = 0.045$

[a]Pooled standard error means.
[b]*P*-values reflect effects due to treatment.
[c,d,e]SO = slow-twitch-oxidative, FOG = fast-twitch-oxidative-glycolytic, and FG = fast-twitch-glycolytic fibers.

were counted. For each fiber type, on average 30 fibers were measured for fiber CSA per photomicrograph, and this was performed using two photomicrographs per tissue section. A Zeiss Interactive Digital Analysis System (Carl Zeiss, New York) was used to perform the CSA measurements, which involves tracing each individual fiber into the digital computer system. Solomon and Montgomery (1988) reported that muscle fiber populations measured by template or by selecting a minimum number of fibers to be counted (e.g., based on bundle size) were statistically equivalent to those measured using the entire micrograph and counting all the fibers present. Regardless, if one chooses to use a template, different muscle bundle sizes, or the entire micrograph, the same level of precision for quantifying muscle fiber percentages is obtained (Solomon and Montgomery, 1988).

Statistical Analysis

The experimental design was a randomized complete block with two treatments, blocked by days of age. Data for muscle fiber areas and percentage distribution were analyzed as a repeated measures design using the GLM procedures of SAS (1994). Means were compared ($P < 0.05$) using Fisher's protected LSD.

Results

Muscle Fiber Distribution

The effect of treatment on the percentage distribution of fiber types was significant for FOG ($P = 0.014$) and FG ($P = 0.03$) fibers (Table 1). In addition, the percentage of SO fibers tended ($P = 0.07$) to be greater in the control calves than in the rbST-treated calves (Table 1). The treatment × age interaction was not significant for the percentage distribution for SO ($P = 0.265$), FOG ($P = 0.505$), or FG fibers ($P = 0.923$) (Table 3); however, there was a significant ($P = 0.001$) change in percentage distribution of all three muscle fiber types with age (Table 2). Values below are least-square means and pooled SE for age effects. The percentage distribution of FG fibers increased from d 100 to d 206 (45.4 vs 56.6 ± 0.8%, respectively, $P = 0.001$), whereas the percentage distribution of SO (14.3 vs 10.5 ± 0.5%, respectively, $P = 0.001$) and FOG fibers (40.3 vs 32.9 ± 0.7%, respectively, $P = 0.001$) decreased from d 100 to d 206 (Table 2). The proportional differences in distribution of fiber types were similar between d 100 and 206 of age for the rbST-treated and control calves (Table 3).

Muscle Fiber Areas

Values reported below are least-square means and pooled SE for treatment and(or) age effects. The rbST-treated calves had larger FG fiber CSA ($P = 0.045$) than control calves (2,564 vs 2,351 ± 11 μm^2, respectively) (Table 1). No differences ($P = 0.36$) between the rbST-treated calves and control calves in fiber CSA were detected for the SO (1,192 and 1,148 ± 21 μm^2, respectively) or FOG (1,484 and 1,403 ± 36 μm^2, respectively) fiber areas due to effects of treatment. The CSA of all fiber types (SO, FOG, and FG) increased ($P = 0.001$) from d 100 to d 206 (Table 2). However, for the SO and FOG fibers there was a significant treatment × days of age interaction ($P = 0.034$ and $P = 0.047$, respectively), indicating that the rbST-treated calves had a greater increase in fiber CSA for SO and FOG fibers from d 100 to d 206 than control calves (Table 3). On a percentage basis, the rbST-treated calves had a greater percentage increase in fiber CSA from d 100 to d 206 than control calves for SO (40 vs 19%, respectively) and FOG fibers (47 vs 29%, respectively) (Table 3). The percentage increase for FG fibers (26 vs 19%, respectively) was similar between the rbST-treated and control calves (Table 3). The proportional differences in fiber CSA between the control and rbST-treated calves increased from 100 to 206 d of age, such that the CSA of all myofiber types were approximately 12% greater in the rbST-treated calves.

Table 2. Least square means and pooled standard errors for the percentage distribution of fiber types and fiber cross-sectional areas as influenced by days of age

	Days of age			
Fiber type	100	206	Pooled SEM[a]	*P*-value[b]
SO, %[c]	14.3	10.5	0.50	$P = 0.0001$
FOG, %[d]	40.3	32.9	0.70	$P = 0.0001$
FG, %[e]	45.4	56.6	0.83	$P = 0.0001$
	Fiber cross-sectional area			
SO, μm^{2} [c]	1,021	1,319	34	$P = 0.0001$
FOG, μm^{2} [d]	1,215	1,672	38	$P = 0.0001$
FG, μm^{2} [e]	2,212	2,704	57	$P = 0.0001$

[a]Pooled standard error mean.
[b]*P*-values reflect effects due to days of age.
[c,d,e]SO = slow-twitch-oxidative, FOG = fast-twitch-oxidative-glycolytic, and FG = fast-twitch-glycolytic fibers.

Discussion

Skeletal muscle growth is characterized by the increase in the cross-sectional area of muscle fibers and by the increase in the length of muscle fibers, due either to addition of new sarcomeres or lengthening of existing sarcomeres (Bendall and Voyle, 1967; Swatland, 1978). Administration of growth promotants such as rbST is documented to increase longissimus muscle area, reduce s.c. fat thickness (Dalke et al., 1992), and increase plasma IGF-I concentrations in finishing steers (Elsasser et al., 1989). However, some studies show very little benefit of bST administration on growth performance and carcass traits in finishing steers (Early et al., 1990; Preston et al., 1995). In addition, Elsasser et al. (1998) reported that administration of growth promotants such as somatotropin or Synovex to cattle differentially affected growth characteristics in certain muscles and, when used in combination, had additive effects on protein gain. Recombinant ST and(or) Somavubove administered to steers increased the efficiency of energy deposited as protein in both empty body and carcass (Rumsey et al., 1996). Recombinant ST also increased both the minimum and maximum fractional rate of protein synthesis in muscle, but not in liver or intestinal tissues (Eisemann et al., 1989). Daily administration of ST to female Fleckvieh veal calves increased ADG and improved feed conversion rate; however, the semitendinosus muscle protein and water content were unchanged and fat content was slightly reduced after ST treatment (Kirchgessner et al., 1987). Administration of rbST to the steers in this study increased longissimus muscle areas, carcass weights, and carcass conformation scores, and it increased the mass of separated muscle in weaned steers (Vann et al., 1998).

Muscle Fiber Distribution

The results from our study agree with those reported by Jurie et al. (1995), which stated that postnatally the semitendinosus muscle contained a low overall proportion of SO fibers compared with FOG and FG fibers.

Table 3. Least square means and pooled SEM for percentage distribution of fiber types and cross-sectional areas of fiber types for control and rbST-treated calves as influenced by the treatment × days of age interaction

	Treatment group							
	Control			rbST				
Fiber type	Day 100	Day 206	Percentage change	Day 100	Day 206	Percentage change	Pooled SEM[a]	*P*-value[b]
SO, %[c]	15.5	10.8	–30	13.2	10.1	–23	0.7	$P = 0.265$
FOG, %[d]	41.8	35.1	–16	38.9	30.8	–21	0.9	$P = 0.505$
FG, %[e]	42.7	54.1	+27	47.9	59.1	+23	1.2	$P = 0.923$
	Fiber cross-sectional area							
SO, μm^{2} [c]	1,050	1,245	+19	992	1,392	+40	48	$P = 0.034$
FOG, μm^{2} [d]	1,227	1,580	+29	1,203	1,765	+47	53	$P = 0.047$
FG, μm^{2} [e]	2,152	2,550	+19	2,273	2,857	+26	80	$P = 0.242$

[a]Pooled standard error of the mean.
[b]*P*-values reflect the treatment × days of age interaction.
[c,d,e]SO = slow-twitch-oxidative, FOG = fast-twitch-oxidative-glycolytic, and FG = fast-glycolytic fibers.

The percentage of FOG fibers decreased, whereas that of FG fibers increased in muscle between 1 and 12 mo of age, but thereafter the composition was stable (Jurie et al., 1995). The period of growth between 1 and 12 mo of age was characterized by increased glycolytic metabolism, as evidenced by the conversion of FOG fibers into FG fibers, and the period between 12 and 16 mo was characterized by a reduction in the conversion of FOG fibers into FG fibers (Jurie et al., 1995). An increase in the conversion of FOG to FG fibers was reported by Solomon et al. (1986) in bulls, as evidenced by the decreased percentage of FOG fibers and the increased percentage of FG fibers with increasing live weight. Ono et al. (1996) reported that Somavubove (a bST preparation administered every 14 d) in steers increased FG fibers and decreased the distribution of FOG fibers in the rectus femoris muscle. The results from our study support the transformation of fiber types because the percentage distribution of FG fibers increased whereas the percentage distribution of FOG and SO fibers decreased from d 100 to d 206. In contrast to the results in our study, Maltin et al. (1990) reported that bovine pituitary ST-treated British Friesian bull calves had no significant change in fiber percentage frequency or fiber size in semimembranosus muscle, although FOG fibers in the triceps muscle were slightly larger than those in the control bull calves. In addition, Vestergaard et al. (1995) reported that neither ST (15-wk treatment) nor ovariectomy affected the proportion and relative area of the individual longissimus muscle fiber types, but ST tended to increase type I (SO) fiber area ($P < 0.10$) in prepubertal Friesian heifers (from 143 to 231 kg). The inconsistency in the results of Maltin et al. (1990) and Vestergaard et al. (1995) and the results in our study can be attributed to differences in age and weight at initiation of treatment, differences in rbST dosage in each study, as well as different muscles being tested in each study. The calves in our study were started on rbST treatment at 64 kg, which is considerably smaller in size and weight than the calves in the Vestergaard et al. (1995) study. The calves in the Maltin et al. (1990) study began treatment at 7 d of age; however, the 35 μg/kg BW dose of bST was less compared with the dose of 90 $\mu g \cdot kg^{-1} \cdot d^{-1}$ of bST used in the current study. The calves in the Maltin et al. (1990) study were slaughtered between 112 to 116 d of age, which is similar to the age of the calves at the time of the muscle biopsy in the current study. The lower dosage of bST could have contributed to the lack of response to bST treatment in the Maltin et al. (1990) study.

Investigators have evaluated porcine, ovine, and bovine muscles histochemically to determine growth patterns and concluded that FOG fibers have the capacity to transform into FG fibers (Ashmore et al., 1972). Muscle size is directly proportional to the degree to which FOG fibers transform into FG fibers, and the FG fibers may conceivably achieve their full growth potential later in life or at heavier body weights than either FOG or SO fibers and thereby delay the onset of the "fattening phase" of growth (Ashmore et al., 1972; Solomon et al., 1986). The increased muscle size due to rbST-treatment in the current study was directly proportional to the increased glycolytic metabolism, as evidenced by the transformation of FOG to FG fibers in the rbST-treated calves compared to the control calves.

Muscle Fiber Areas

Several investigators have established that throughout normal growth, mean muscle fiber area of all fiber types increase with age or weight in cattle (Bendall and Voyle, 1967; Jurie et al. 1995; Solomon et al. 1986). Some studies indicate that mean fiber area increases more rapidly in FG fibers than either SO or FOG fibers (Cooper et al., 1970; Swatland and Cassens, 1972). However, Miller et al. (1975) reported that an increase in area of any one of the three fiber types was accompanied by an increase in area of the other two fiber types. In agreement with Miller et al. (1975), the results from our study revealed an increased myofiber CSA in the semitendinosus muscle of all three fiber types from d 100 to 206 in beef steer calves. Johnston et al. (1975) reported that steers at 233 d of age had significantly larger SO fiber diameters and larger SO fiber areas for all fiber types than 153-d-old steers. In our study, in an effort to minimize the effects of age and(or) breed type on muscle fiber CSA, all steers were slaughtered at a similar age and were of similar breed type (continental European crossbred).

Several investigators have suggested that ST does not have a uniform effect on percentage distribution of muscle fiber types and that each muscle seems to react differently in response to ST treatment in steers (Ono et al., 1996; Rumsey et al., 1996; Elsasser et al., 1998). Steers treated with a combination of Synovex-S and Somavubove had increased fiber areas (18.5 to 54.8%) in five out of six muscles studied (Ono et al., 1996). However, administration of Somavubove independent of Synovex-S resulted in increased fiber areas for all three fiber types in the psoas major and increased SO fibers in the supraspinatus and semitendinosus muscles (Ono et al., 1996). The discrepancy in muscle response to ST treatment has been discussed previously.

Earlier, Pell and Bates (1987) indicated that it is possible for a muscle to seem less responsive to partitioning agents than to another if the muscle was already at its maximum rate of growth or protein accretion. Pell and Bates (1987) also suggested that red-type muscles were more responsive to enhanced accretion rates by exogenous repartitioning agents. Muscles such as the psoas major and semitendinosus may be near maximum capacity for growth and cannot be made to increase their growth further with the use of the exogenous hormone treatments (Elsasser et al., 1998). Administration of rbST to calves in our study appears to have affected the fibers with aerobic metabolism as evidenced by the time × treatment interaction for the SO and FOG fibers.

In summary, the results from our study indicate that rbST-treated calves had a higher percentage distribution and larger FG fibers than control calves. The percentage distribution of FG fibers increased, whereas the percentage distribution of FOG and SO fibers decreased from d 100 to 206. The semitendinosus muscle of the rbST-treated calves appeared to have increased glycolytic metabolism as evidenced by the greater conversion of FOG into FG fibers compared with control calves. The muscle fiber CSA increased for all three fiber types from d 100 to d 206. However, the FG fiber CSA were larger in the rbST-treated calves than in control calves. Thus, the larger longissimus muscle areas and higher carcass conformations scores and increased separable lean tissue previously reported by Vann et al. (1998) were the result of a greater distribution of FG fibers, which possess larger cross-sectional areas than FOG or SO fibers. Thus, to our knowledge this is the only study examining the effects of chronic rbST administration on muscle fiber distribution and size prior to weaning in creep-fed crossbred beef steer calves under traditional cow and calf management practices.

Implications

The rbST-treated calves had increased muscle mass as a result of the increased rate of transformation from the fast-twitch-oxidative-glycolytic to larger fast-twitch-glycolytic myofibers. Based on relative changes in differences of myofiber distribution between rbST-treated and control calves from 100 to 205 d of age, withdrawal of rbST at weaning would eventually result in a moderation of the differences in myofiber distribution between rbST-treated and control calves and thus muscling differences at market weights would be less obvious. These results should be considered in management strategies used in vertical intergration in the beef industry (i.e., retained feedlot ownership).

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