Modification of muscle inherent properties through age at slaughter, growth promotants and breed crosses

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Girard, I., Aalhus, J. L., Basarab, J. A., Larsen, I. L. and Bruce, H. L. 2011. **Modification of muscle inherent properties through age at slaughter, growth promotants and breed crosses**. Can. J. Anim. Sci. **91**: 635–648. A 2^4 factorial experiment tested the interactions of slaughter age (12–13 or 18–20 mo), growth hormone use, β-adrenergic agonist (β-AA) use and breed cross [Hereford–Aberdeen Angus (HAA) or Charolais–Red Angus (CRA)] on the composition, fibre types, and connective tissue characteristics of m. semitendinosus (ST) and m. gluteus medius (GM) from 112 crossbred steers. Muscle weights increased with slaughter age, implantation and CRA genetics ($P < 0.05$), but were not affected by ractopamine hydrochloride (RAC) ($P > 0.10$). Animal age increased fast glycolytic (FG) and decreased fast oxidative glycolytic (FOG) fibre percentages by 7.2 and 6.6%, respectively, in the ST and increased slow oxidative (SO) and FOG fibre areas in both muscles ($P < 0.05$). Cross-sectional areas of all fibre types were increased in the ST with implantation. In the GM, implantation increased SO (3.1%) and reduced FOG (3.2%) fibre percentages, while RAC reduced the SO (3.8%) and increased the FG (6.1%) fibre percentages ($P < 0.05$). Only GM total collagen content increased with slaughter age ($P < 0.05$), but collagen solubility decreased with slaughter age for both muscles ($P < 0.05$). CRA genetics increased FG percentage in the GM of yearling-fed steers and increased moisture and protein and reduced fat contents of both muscles ($P < 0.05$). In the muscles studied, IMP, slaughter age and animal genetics induced greater changes in muscle inherent properties than RAC.

Key words: Growth implants, ractopamine, beef growth rate

Girard, I., Aalhus, J. L., Basarab, J. A., Larsen, I. L. et Bruce, H. L. 2011. **Modifications des propriétés inhérentes des muscles par l'age à l'abattage, les promoteurs de croissance, et les croisements de race**. Can. J. Anim. Sci. **91**: 635–648. Un design expérimental 2^4 a été utilisé pour tester les interactions entre l'âge à l'abattage (12–13 ou 18–20 mois), les hormones de croissance, le β-adrénergique agoniste ractopaminehydrochloride (RAC), et les croisements de race (Hereford-Aberdeen Angus (HAA) ou Charolais-Angus Rouge (CRA)) sur la composition, les fibres musculaires, et le tissu conjonctif des muscles semitendinosus (ST) etgluteusmedius (GM) de 112 bouvillons. Le poids des musclesa augmenté avec l'âge à l'abattage, l'implantation et la génétique CRA ($P < 0{,}05$) mais n'ont pas été affecté par RAC ($P < 0{,}10$). Dans le ST des bouvillons plus âgés, la quantité de fibres musculaires rapides glycolytiques (FG) a augmenté de 7.2% tandis que les fibres rapides oxydatives et glycolytiques (FOG) ont diminué de 6,6%. L'aire des sections transversales des fibres lentes oxydatives (SO) et FOG ont augmenté avec l'âge dans les deux muscles et l'aire des sections transversales des trois types de fibres ont augmenté avec l'implantation dans le ST ($P < 0{,}05$). Dans le GM, le pourcentage de fibres SO a augmenté (3,1%) et celui de FOG a diminué (3,2%) avec l'implantation alors que RAC a causé une diminution de SO (3,8%) et une augmentation de FG (6,1%) ($P < 0{,}05$). Le collagène total a augmenté avec l'âge seulement dans le GM mais la solubilité du collagène a diminué avec l'âge dans les deux muscles ($P < 0{,}05$). La génétique CRA a augmenté le pourcentage de fibres FG dans le GM des bouvillons plus âgés alors que les teneurs en eau et en protéine ont augmenté et les lipides ont diminué ($P < 0{,}05$) pour les deux muscles. Les implants hormonaux, l'âge à l'abattage et la génétique ont induit des changements plus importants dans les propriétés inhérentes dans les muscles étudiés que RAC.

Mots clés: Promoteurs de croissance, implants, ractopamine, boeuf, taux de croissance

Beef producers have a myriad of production strategies to use to produce beef quickly and profitably. In Alberta, where 39% of the Canadian beef cattle and calf inventory is located (StatCan 2010), cattle are usually harvested at an average age of 18 mo (Alberta Agriculture and Rural Development 2009) and are usually British–Continental crossbreds (Canada Beef

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Abbreviations: **β-AA** β-adrenergic agonist; **CRA**, Charolais-Red Angus; **DMI**, dry matter intake; **FG**, fast glycolytic; **FOG**, fast oxidative glycolytic; **GM**, gluteus medius; **HAA**, Hereford-Aberdeen Angus; **IMP**, hormonal growth implants; **NOIMP**, no hormonal growth implants; **NORAC**, no ractopamine hydrochloride; **RAC**, ractopamine hydrochloride; **SO**, slow oxidative; **ST**, semitendinosus

Export Federation 2009). Exogenous hormone implants are widely used to improve carcass meat yield and feed efficiency, and the recent approval of the β-adrenergic agonist (β-AA) ractopamine hydrochloride (RAC) for use in Canada adds yet another growth promotant product to those available to beef producers.

Hormonal growth implants have been shown to improve final live weights and hot carcass weights of steers (Calkins et al. 1986; Perry et al. 1991; Platter et al. 2003; Roeber et al. 2000) and their mode of action is through growth hormone and insulin-like growth factor-I (Johnson et al. 1996). Hormonal growth implants induce hypertrophy of muscle fibres (Ono et al. 1996) or a shift in muscle fibre type to fast glycolytic (FG) from fast oxidative glycolytic (FOG) fibres (Fritsche et al. 2000). The β-AA RAC has been shown to increase the weight gain of steers (Avendaño-Reyes et al. 2006; Gruber et al. 2007; Winterholler et al. 2007), and this weight gain has often been accompanied by shifts in skeletal muscle fibre type (Gonzalez et al. 2009) or enlargement of FG and FOG muscle fibres (Strydom et al. 2009). Cooked beef toughness originates in part from the muscle fibre type and size (Crouse et al. 1991) and because growth promotants can cause changes in fibre type and morphology, they may also cause variation in meat tenderness. The economic return of using growth promotants to increase carcass weight is about $5 to $10 for each dollar spent on hormonal implants (Alberta Agriculture and Food 2008). This benefit may, however, be counterbalanced by an increase in beef meat toughness, which may affect the quality of the final meat product and potentially consumer satisfaction and product saleability.

Examination of various beef production strategies that are not commonly practiced may reveal economic advantages to producers and improvements in beef quality. Finishing steers at about 12 to 13 mo of age could provide an economic advantage to producers by reducing production costs, which could increase profit per beef animal if meat yield and quality were unchanged. Also, reducing the age of animals at slaughter may decrease the contribution of collagen cross-linking to the toughness of cooked beef, as the complexity of collagen cross-links increases with animal age, particularly in moderate and high connective tissue content muscles (Palokangas et al. 1992). Muscle fibre cross-sectional areas (Seideman et al. 1986; Wegner et al. 2000) increase with age as well, and may contribute further to the age-related toughening of beef (Møller 1980). Connective tissue and muscle fibre properties may contribute less to meat toughness in a muscle from a steer that is 12 to 13 mo of age than in one from a steer that is 18 to 20 mo of age; therefore, increasing the tenderness of moderate connective tissue muscles could add value to the carcass through marketing these muscles as eligible for grilling rather than braising.

This study investigated the effects of production systems including age at slaughter, hormonal growth implants, ractopamine hydrochloride feed supplementation, and European and British breed crosses on the composition, muscle fibre types, and collagen characteristics of the m. gluteus medius and m. semitendinosus in order to identify meat quality advantages and disadvantages associated with various beef production practices.

MATERIALS AND METHODS

Experimental Design and Animal Management

A $2 \times 2 \times 2 \times 2$ factorial experiment was used to investigate the effect of production systems and age at slaughter, hormonal growth promotants, β-AA feed supplementation, and breed crosses, on inherent properties of beef muscles. Cattle within the study were cared for under the guidelines provided by the Canadian Council on Animal Care. One hundred and twelve crossbred Hereford-Aberdeen Angus (HAA; $n = 64$) or Charolais-Red Angus (CRA; $n = 48$) steers born in April and May at Agriculture and Agri-Food Canada, Lacombe, AB, were identified with an ear tag and weighed about 24 h after birth. Bull calves were castrated before 2 mo of age. Calves and their dams were placed on meadow brome (*Bromus biebersteinii*) and alfalfa (*Medicago sativa*) pasture at the beginning of June (northern hemisphere late spring). Calves were weaned at an average age of 182 d with barley silage supplementation for 14 d prior to weaning. At weaning, calves were stratified by weight and assigned to either the calf-fed ($n = 56$) or yearling-fed ($n = 56$) finishing groups to ensure representatives of each breed cross within each system.

Steers in the calf-fed finishing group (calf-fed) were assigned to a hormonal growth implant group (NOIMP or IMP) with each breed cross represented in each treatment and groups equalized as much as possible for body weight. The 28 steers of the IMP group were implanted with Component E-S (200 mg progesterone and 20 mg estradiol benzoate, with 29 mg of tylosin tartrate, Elanco Animal Health, a Division of Eli Lilly Canada Inc., Guelph, ON) at about 200 d of age. During a 30 d adjustment period, steers were fed a grass hay diet and an increasing quantity of high barley grain ration. Steers received a finishing diet consisting of 67.42% barley grain protein mix (88.4% rolled barley, 5% 32:14 beef supplement; 3.33% protein pellets, 1.65% vitamin E premix, 1.0% molasses, 0.5% vegetable oil, 0.1% Mold Zap™ (Alltech Inc., Nicholasville, Kentucky), 0.01% Tylan®40 (Elanco Animal Health, a Division of Eli Lilly Canada Inc., Guelph, ON) and 0.01% fortified vitamin ADE premix, as fed; 14% crude protein dry matter basis), 11.82% alfalfa-grass haylage and 20.76% barley silage. Monensin was included at 37.0 $mg kg^{-1}$ of feed. IMP steers were implanted with Component TE-S (120 mg trenbolone acetate and 24 mg

estradiol with 29 mg of tylosin tartrate, Elanco Animal Health, a Division of Eli Lilly Canada Inc., Guelph, ON) 83 d after first implantation. All steers were grown in GrowSafe Systems pens (GrowSafe Systems Ltd., Airdrie, AB) and removed from these pens about 30 d prior to slaughter and placed in feedlot pens (four NOIMP pens, four IMP pens), with seven steers per pen and at least two steers of each crossbred type per pen. Half of NOIMP steers and half of IMP steers were assigned to the RAC treatment. RAC (Optaflexx®45, Elanco Animal Health, a Division of Eli Lilly Canada Inc., Guelph, ON) was applied as a top-dress to the finishing diet and was administered as a premix consisting of 0.912% RAC, 47.96% ground barley, 20.0% ground wheat, 15% distillers grain, 15% coarse calcium, 0.63% vitamin A, D and E and 0.5% vegetable oil. Three hundred and eighteen grams of top dress were added to each 500 kg finishing diet mix so that RAC was administered at a level of 200 mg RAC $head^{-1}d^{-1}$ for 28 d assuming a dry matter intake (DMI) of 10 $kghead^{-1}d^{-1}$. Each breed cross was represented in each treatment and groups were equalized as much as possible for body weight. Steers not fed RAC (NORAC) were kept on the finishing diet and all steers were finished to a constant back fat thickness of 8 to 9 mm as predicted by ultrasound (Aloka 500V diagnostic real-time ultrasound with a 17 cm 3.5 Mhz linear array transducer, Overseas Monitor Corporation Ltd., Richmond, BC) using the procedure described by Brethour (1992).

The 56 steers assigned to the yearling-fed finishing group (yearling-fed) were divided into two hormonal growth implant groups, not implanted and implanted (NOIMP vs. IMP, respectively) with each breed cross represented in each treatment and groups balanced for initial body weight. The 28 IMP steers were administered Component E-S at about 200 d of age and were kept grazing on meadow brome-alfalfa pasture for 60 d. Steers were then placed in eight feedlot pens (four NOIMP pens, four IMP pens), seven steers per pen with at least two steers of each crossbreed per pen, and fed the back-grounding diet consisting of 64% barley silage, 26.1% alfalfa and meadow brome grass hay, and 9.9% barley:oat (60:40) rolled grain on an as fed basis. IMP steers were re-implanted with Component E-S at about 280, 350, and 440 d of age. At 440 d, yearling-fed finishing steers were placed on meadow brome alfalfa pasture but were removed after 62 d instead of 90 d due to drought and poor performance on pasture. Steers were placed into pens and fed 30 d with an adjustment diet of grass hay and an increasing amount of 21.2% barley silage, 74.1% rolled barley grain, 3.1% feedlot supplement (32% CP), and 1.6% molasses (as fed basis, TDN 80.2%; CP 13.1%). After the 30 d adjustment period, steers received a finishing diet of 35.18% barley silage and 64.82% rolled barley grain protein mix (93.28% rolled barley, 4.5% 32:14 beef supplement; 1.10% vitamin E premix, 0.5% molasses, 0.5% vegetable oil, 0.1% Mold Zap™ (Alltech Inc., Nicholasville, KY) and 0.02% vitamin ADE premix as fed). The diet was formulated to 12.64% CP and contained 24.7 $mgkg^{-1}$ of monensin. Steers were implanted with Component TE-S and were removed from the pens about 30 d prior to slaughter and placed in feedlot pens. Half of NOIMP steers and half of IMP steers were assigned to the RAC treatment with each breed cross represented in each treatment and groups equalized as much as possible for body weight. RAC (Optaflexx®45, Elanco Animal Health, a Division of Eli Lilly Canada Inc., Guelph, ON) was included in the finishing diet as a top dress formulated to deliver 200 mg $RAChead^{-1}d^{-1}$ assuming a DMI of 10 $kghead^{-1}d^{-1}$. NORAC steers were kept on the control finishing diet. All steers were finished to a constant back fat thickness of 8 to 9 mm predicted by ultrasound as described for the calf-fed steers.

Slaughter

Steers in the calf-fed finishing group were sent to the Agriculture and Agri-Food Canada research abattoir in Lacombe, Alberta, at 12 to 13 mo of age and steers assigned to the yearling-fed finishing group were sent at 18 to 20 mo of age. Two pens per kill ($n = 14$ per kill) were sent to the abattoir the day before slaughter and steers were fasted overnight with free access to water. Live weight and steer identification were noted before stunning by captive bolt, and then exsanguination and carcass dressing proceeded in a simulated commercial manner. Carcasses were split and each half weighed and pasteurized with hot water pasteurization at 85°C for 10 s. Following pasteurization, carcasses were chilled overnight at 2°C with a wind speed of 5 m s^{-1}.

At 24 h post-mortem, the carcasses were fabricated and the left m. semitendinosus (ST; eye of round) and m. gluteus medius (GM; top sirloin) muscles were removed. Muscles were individually labelled and weighed. Steaks were removed from the proximal to distal end for ST and from the anterior to posterior end for GM. The first trim steak was discarded and the second was cut 2.5 cm thick and used for muscle fibre type determination. The remaining muscle portion was weighed, vacuum-packaged, and aged at 4°C for 7 d. Muscle weight was expressed as the gross muscle weight and as a percentage of the cold trimmed left carcass side.

Fibre Typing and Cross-sectional Area Measurements

A muscle sample of about 0.5 cm × 0.5 cm × 1 cm was cut along the grain of the muscle fibres at about the centre of the steak. Samples were mounted separately on cork perpendicular to the muscle fibre grain with Cryomatrix (Thermo Shandon Inc., Pittsburgh, PA), frozen in liquid nitrogen, and stored overnight at −35°C. Muscle sections, 11 μm thickwere removed at −20°C using a cryostat (Thermo Shandon Cryotome, Model 77210164 GB; Thermo Shandon Inc., Pittsburgh, PA), placed on a glass slide and frozen

overnight in a freezer set at −35°C. Staining was performed according to the simultaneous procedure of Solomon and Dunn (1988) using an acid pre-incubation (pH = 4.15) and the ATPase solution made according to Guth and Samaha (1970) and the succinate dehydrogenase (SDH) staining according to Horák (1983).

Images for fibre typing and cross-sectional area measurement were captured with an Axioscope (Zeiss, West Germany) equipped with a Sony DXC 930 Color Video Camera (Sony Corporation, Japan) at 50 × and 80 × magnification for fibre type and cross-sectional area, respectively. Measurement and typing analyses were performed on Image Pro-Plus software V4.0 (Media Cybernetics, Silver Spring, MD). Muscle fibres were classified according to their speed of contraction and their oxidative and/or glycolytic capacities as SO, FOG, or FG. Muscle fibre cross-sectional areas were averaged per type of fibre and expressed in μm^2, and muscle fibre distribution was calculated as the number of fibres of one type within a muscle bundle divided by the total number of fibres in the bundle. For each sample, to have a good representation of the muscle, fibres of four bundles were typed and fibres of three bundles were measured.

Collagen Characteristics

After 7 d of ageing muscles were removed from vacuum packaging and weighed to determine purge loss. A 2.5-cm-thick steak was then removed from each muscle. Steaks were weighed, labelled, vacuum-packaged, and frozen at −20°C until analysis. Prior to analysis, steaks were allowed to thaw at 4°C for 24 h before being cut into 1-cm^3 pieces. At least 100 g per steak were weighed and placed in an aluminum pan to be lyophilised for 100 h. After lyophilisation, samples were weighed, ground to a fine powder using a Waring blender (Model 7011C, Waring Commercial, Torrington, CT) and dry ice, and stored at −20°C until hydrolysis.

Total collagen content was quantified by determination of the hydroxyproline content with a modified version of Bergman and Loxley (1963). Two samples of approximately 0.030 ± 0.005 g of lyophilized tissue from each muscle were hydrolyzed in 6 N HCl under nitrogen for 9 h at 110°C. After hydrolysis, tube contents were filtered (Whatman filter paper #4, Fisher Scientific, Ottawa, ON), evaporated to dryness, re-suspended in deionized, distilled water, neutralized with dilute NaOH, evaporated again to dryness and then reconstituted in 5 mL of deionized, distilled water. Absorbance of final experimental samples was measured at 558 nm against a blank sample and hydroxyproline concentration derived from absorbance values of trans-4-hydroxyproline (Sigma-Aldrich Canada Ltd, Oakville, ON) standards with concentrations of 1.25 to 20 μg trans-4-hydroxyproline per mL. The factor 7.14 was used to convert the hydroxyproline content to the collagen content (Etherington and Sims 1981).

Soluble collagen content was determined following a modified procedure for Hill (1966), in which 1.00 ± 0.01 g of lyophilized ground muscle was incubated with 12 mL of one-quarter strength Ringer's solution. Following incubation, each tube was centrifuged, washed and centrifuged again. A 1.8 mL aliquot of the supernatants was clarified using centrifugation (ManSci Mini Centrifuge, Mandel Scientific, Guelph, ON) for 25 s at 2000 × *g* and 1 mL hydrolyzed in 4 mL of 7 N HCl. Samples were hydrolysed for 9 h at 110°C (Accu-BlockTM Digital Dry bath, Labnet International, Inc., Edison, NJ). Hydroxyproline was determined as described for total collagen.

Proximate Analyses

After 7 d of ageing, 100 g of ground fresh muscle were oven dried at 102°C in a stainless steel beaker for 24 h in a gravity convection-drying oven (VWR Scientific Model 1370FM; Mississauga, ON). The following day, beakers were removed from the oven and allowed to equilibrate at room temperature for 10 min before final weights were recorded. Dried samples were crushed (Grindomix Model GM200, Retsch Inc., Newton, PA) and analyzed for fat content by petroleum ether extraction (Foss Soxtec System Model 2050; Foss Analytical AB, Hoganas, Sweden) (Association of Official Analytical Chemists 1995, Method 960.39). Crude protein content determination was performed on fat-free samples (AOAC 1997, Method 992.15) with a Nitrogen/Protein Determinator CNS2000 (Leco Corp., St. Joseph, MI).

Statistical Analysis

Data were analyzed as a 2 × 2 × 2 × 2 factorial design using the MIXED procedure of SAS (SAS Institute, Inc. 2003) with sources of variation including age at slaughter, hormonal growth promotants, β-AA feed supplementation, and breed crosses, and their two-, three-, and four-way interactions. Pen nested within slaughter age × implant × β-agonist was included as a random effect. The initial model included day of kill as a source of variation, but it was removed when it was found not to be significant ($P > 0.05$) in an analysis of covariance. Denominator degrees of freedom were calculated using the Kenward-Roger approximation. Differences between treatment or interaction means were separated using the F-test protected LSD procedure ($P \leq 0.05$).

RESULTS

Muscle Weights

Muscles were significantly heavier ($P < 0.05$) in yearling-fed than in calf-fed steers for both ST (Table 1) and GM (Table 2) muscles. IMP steers had significantly heavier mean muscle weight in the GM ($P < 0.05$) and the ST ($P < 0.05$), a mass increase of about 8.5 and 16%, respectively. Also, the ST muscle represented a greater percentage of the carcass side weight when steers were

Table 1. Effect of production systems (P), implantation strategy (I), ractopamine hydrochloride feed supplementation (R), and breed cross (B) on inherent composition of the m. semitendinosus

	Production system		Implantation		Ractopamine feeding			Breed cross			Interaction
Variable	Calf-fed	Yearling-fed	NOIMP[z]	IMP[z]	NORAC[z]	RAC[wz]	SEM[y]	HAA[z]	CRA[z]	SEM[x]	P × R × B
$n =$	56	56	56	56	56	56	–	64	48	–	–
Muscle weight (g)	2192.53*b*	2745.88*a*	2282.00*b*	2656.41*a*	2414.26	2524.15	46.64	2357.95*b*	2580.45*a*	44.13	NS
Muscle weight (%)	1.31	1.26	1.23*b*	1.34*a*	1.27	1.30	0.02	1.24*b*	1.33*a*	0.02	NS
Moisture content (%)[v]	74.54	74.16	74.19	74.52	74.37	74.33	0.16	74.17*b*	74.53*a*	0.13	NS
Fat content (%)	2.97	3.02	3.22*y*	2.77*x*	2.98	3.01	0.15	3.36*a*	2.63*b*	0.14	NS
Total collagen (mgg^{-1})	15.44	16.81	15.88	16.37	16.17	16.08	0.55	16.43	15.82	0.54	*
Soluble collagen (%)[u]	23.34*y*	20.04*x*	22.78	20.6	22.19	21.19	1.05	22.27	21.11	0.95	NS

[z]CRA, Charolais-Red Angus; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; RAC, ractopamine hydrochloride.
[y]Pooled standard error of the mean (SEM) for production systems, implantation, and ractopamine feeding.
[x]Pooled standard error of the mean (SEM) for breed cross.
[w]200 mg RAChead^{-1}d^{-1} for 28 d.
[v]Summation of moisture and fat contents within a treatment effect may not equal 100.00 due to number rounding.
[u]Expressed as a percentage of total collagen content.
a, *b* Means within the same row within a main effect with different letters are significantly different ($P < 0.05$).
x, *y* Means within the same row within a main effect with different letters tend to be significantly different ($P < 0.10$).
*, **, *** $P < 0.10$, $P < 0.05$, and $P < 0.01$, respectively; NS, not significant.

implanted ($P < 0.05$). RAC affected neither the GM nor the ST mean muscle weights. The CRA crossbred steers had heavier GM ($P < 0.0001$) and ST ($P < 0.05$) muscles and the muscles represented a greater percentage of the left side weight (GM, $P < 0.0001$; ST, $P < 0.05$) than those of the HAA crossbred steers.

Proximate Analyses

There was a four-way interaction for protein content of the ST. This four-way interaction appeared to be dominated by breed, RAC and implant differences, with IMP RAC CRA steers having greater mean muscle protein content than NOIMP NORAC HAA steers when yearling-finished (Table 3). ST moisture and fat contents were not affected by production systems, IMP, and RAC, but mean fat content tended to be higher ($P = 0.07$) in the muscles of NOIMP steers than in those of IMP steers (Table 1). ST muscles from CRA steers had greater mean moisture ($P < 0.05$) and protein ($P < 0.05$) contents and lower fat ($P < 0.05$) content than those of HAA steers (Table 1).

Four-way interactions were also significant in the GM for moisture ($P < 0.05$) and fat ($P < 0.05$) content (Table 3). The mean GM moisture level was highest in

Table 2. Effect of production systems (P), implantation strategy (I), ractopamine hydrochloride feed supplementation (R), and breed cross (B) on inherent composition of the m. gluteus medius

	Production systems		Implantation		Ractopamine feeding			Breed cross			Interaction	
Variable	Calf-fed	Yearling-fed	NOIMP[z]	IMP[z]	NORAC[z]	RAC[zy]	SEM[x]	HAA[z]	CRA[z]	SEM[w]	I × R	P × R × B
$n =$	56	56	56	56	56	56	–	64	48	–	–	–
Muscle weight (g)	3179.14*b*	4138.78*a*	3509.86*b*	3808.06*a*	3633.43	3684.49	73.24	3449.78*b*	3868.14*a*	64.13	NS	NS
Muscle weight (%)	1.91	1.90	1.89	1.92	1.9	1.91	0.03	1.82*b*	1.99*a*	0.03	*	NS
Protein content (%)[v]	22.03*y*	21.73*x*	21.77	21.99	21.92	21.84	0.10	21.65*b*	22.11*a*	0.09	NS	NS
Total collagen (mgg^{-1})	11.98*b*	14.32*a*	13.02	13.28	12.95	13.36	0.56	13.56	12.74	0.50	NS	*
Soluble collagen (%)[u]	52.31*a*	34.02*b*	43.01	43.32	43.33	43.00	2.13	42.62	43.71	2.13	NS	*

[z]CRA, Charolais-Red Angus; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; RAC,ractopamine hydrochloride.
[y]200 mg RAC head^{-1} d^{-1} for 28 d.
[x]Pooled standard error of the mean (SEM) for production systems, implantation strategy, and ractopamine feed supplementation.
[w]Pooled standard error of the mean (SEM) for breed crosses.
[v]Summation of protein contents within a treatment effect may not equal 100.00 due to number rounding.
[u]Expressed as a percentage of total collagen content.
a, *b* Means within the same row within a main effect with different letters are significantly different ($P < 0.05$).
x, *y* Means within the same row within a main effect with different letters tend to be significantly different ($P < 0.10$).
*, **, *** $P < 0.10$, $P < 0.05$, and $P < 0.01$, respectively; NS, not significant.

Table 3. Means of proximate analyses of the m. gluteus medius (GM) and m. semitendinosus (ST) with significant four-way interactions involving age at slaughter, implantation strategy, ractopamine hydrochloride feed supplementation, and breed cross

			NOIMP[z]				IMP				
			NORAC[z]		RAC[zy]		NORAC		RAC		SEM[x]
Muscle	Variable	Age atslaughter	HAA[z]	CRA[z]	HAA[z]	CRA[z]	HAA	CRA	HAA	CRA	
GM	Moisture content (%)	Calf-fed	73.05*def*	73.42*cdef*	72.74*f*	73.77*abcd*	73.58*bcde*	74.34*abc*	73.52*bcdef*	73.58*bcdef*	0.31
		Yearling-fed	72.87*ef*	73.46*bcdef*	73.71*bcd*	73.70*abcde*	74.32*ab*	73.90*abcd*	74.06*abc*	74.59*a*	
GM	Fat content (%)	Calf-fed	3.96*abc*	3.26*bcd*	4.52*a*	3.12*cde*	3.33*bcd*	2.09*f*	3.46*bcd*	3.03*cdef*	0.34
		Yearling-fed	4.34*a*	3.24*bcd*	4.11*ab*	3.16*bcd*	2.71*def*	3.02*cdef*	3.06*cdef*	2.17*ef*	
ST	Protein content (%)	Calf-fed	21.52*bcd*	21.83*abcd*	21.44*d*	21.94*abce*	21.35*de*	22.06*abc*	21.65*bcd*	21.95*abcd*	0.20
		Yearling-fed	21.61*cd*	22.13*ab*	21.79*abcd*	21.92*abcd*	21.88*abcd*	22.08*abc*	21.75*bcd*	22.29*a*	

[z]CRA, Charolais-Red Angus; GM, gluteus medius; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; NS, nonsignificant; RAC, ractopamine hydrochloride; ST, semitendinosus.
[y]200 mg RAChead^{-1}d^{-1} for 28 d.
[x]Pooled standard error of the mean (SEM).
a–f Means within each variable with different letters are significantly different ($P < 0.05$).

Table 4. Effect of production systems (P), implantation strategy (I), ractopamine hydrochloride feed supplementation (R), and breed cross (B) on fibre cross-sectional areas (μm^2) of the m. semitendinosus and m. gluteus medius, including significant interactions

	Production systems		Implantation		Ractopamine feeding			Breed cross			Interaction		
Variable	Calf-fed	Yearling-fed	NOIMP[z]	IMP[z]	NORAC[z]	RAC[zy]	SEM[x]	HAA[z]	CRA[z]	SEM[w]	I × R × B	P × R × B	I × P × B
n =	56	56	56	56	56	56	–	64	48	–	–	–	–
M. *semitendinosus*													
SO[z]	2519.62*b*	3111.59*a*	2537.78*b*	3093.43*a*	2772.55	2858.66	107.47	2929.32*y*	2701.88*x*	100.06	NS	NS	*
FOG[z]	3238.19*b*	3691.98*a*	3211.16*b*	3719.02*a*	3496.75	3433.43	83.30	3425.45	3504.73	81.73	NS	**	NS
FG[z]	4354.51	4784.63	4094.88*b*	5044.26*a*	4474.51	4664.62	194.71	4457.38	4681.75	156.06	**	**	*
M. *gluteus medius*													
SO	2471.93*b*	3119.56*a*	2632.63*y*	2958.87*x*	2794.00	2797.50	101.46	2830.05	2761.45	85.71	NS	NS	NS
FOG	3016.99*b*	3558.14*a*	3167.59	3407.53	3312.17	3262.95	138.05	3299.29	3275.83	108.58	NS	NS	NS
FG	4467.29	4889.84	4481.85	4875.29	4638.20	4718.94	201.71	4529.81*b*	4827.33*a*	160.64	NS	NS	NS

[z]CRA, Charolais-Red Angus; FG, fast glycolytic; FOG, fast oxidativeglycolytic; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; RAC, ractopamine hydrochloride; SO, slow oxidative.
[y]200 mg RAChead^{-1}d^{-1} for 28 d.
[x]Pooled standard error of the mean (SEM) for production systems, implantation strategy, and ractopamine feed supplementation.
[w]Pooled standard error of the mean (SEM) for breed crosses.
a, *b* Means within the same row within a main effect with different letters are significantly different ($P < 0.05$).
x, *y* Means within the same row within a main effect with different letters tend to be significantly different ($P < 0.10$).
*, **, *** $P < 0.10$, $P < 0.05$, and $P < 0.01$, respectively; NS, not significant.

RAC CRA yearling fed steers and lowest in RAC HAA calf-fed steers. RAC CRA yearling-fed steers had greater mean muscle moisture content than all calf-fed HAA steers and all non-implanted HAA yearling-fed steers. GM protein content tended to be lower ($P = 0.07$) in yearling-fed steers compared with calf-fed steers without modification to the fat content (Table 2). CRA crossbred steers had a higher mean protein ($P < 0.05$) content in the GM than did HAA crossbred steers (Table 2).

Muscle Fibre Characteristics

Mean SO fibre cross-sectional areas in the ST were larger ($P < 0.05$) in muscles from carcasses of the yearling-fed than of the calf-fed steers and larger ($P < 0.05$) when steers were implanted than when not implanted (Table 4). Mean SO fibre cross-sectional areas in the ST were not affected by RAC, but there was a trend for mean SO fibre cross-sectional areas to be largest ($P = 0.08$) in HAA steers. IMP resulted in larger ($P < 0.05$) mean FOG fibre cross-sectional areas in the ST than the NOIMP FOG fibres. FOG fibre cross-sectional areas were involved in a three-way interaction where ST muscles from the carcasses of yearling-fed HAA steers had significantly greater ($P < 0.05$) mean FOG fibre cross-sectional areas than calf-fed HAA steers when not fed RAC. Conversely, CRA yearling-fed steers had greater mean FOG cross-sectional areas than CRA calf-fed steers when fed RAC (Fig. 1a). FG fibres in the ST were also involved in a three-way interaction where calf-fed CRA steers not fed with RAC had significantly larger ($P < 0.05$) mean FG cross-sectional areas than HAA calf-fed steers not supplemented with RAC (Fig. 1b). When they were fed with RAC, the ST muscles of yearling-fed CRA steers had larger mean FG cross-sectional areas than those of yearling-fed HAA steers supplemented with RAC. FG fibres of the ST were involved in a three-way interaction (Fig. 1c) in which muscles of carcasses from NORAC HAA steers of the IMP treatment had larger ($P < 0.05$) mean cross-sectional areas compared with those of the NORAC NOIMP HAA treatment. This difference was no longer significant when steers were fed RAC. On the other hand, ST muscles from carcasses of IMP and NOIMP NORAC CRA steers did not have significantly different mean FG cross-sectional areas, but when they were supplemented with RAC, ST muscles from carcasses of IMP CRA steers had greater mean FG cross-sectional areas than those of the NOIMP CRA steers, the NORAC NOIMP steers, and the NORAC IMP steers.

In the GM muscle, IMP and RAC did not affect fibre cross-sectional areas. Production systems affected cross-sectional areas of SO and FOG fibres with yearling-fed steers having the largest mean cross-sectional areas of both fibre types ($P < 0.05$). Mean FG cross-sectional areas were not affected by production systems but the CRA breed cross had larger ($P = 0.05$) cross-sectional areas. Crossbreed type did not affect the mean SO and FOG cross-sectional areas of the GM.

RAC did not affect the fibre distribution of the ST and, moreover, SO fibre distribution of this muscle was not affected by any of the experimental treatments (Table 5). The proportion of FG fibres was higher in yearling-fed steers compared with calf-fed steers ($P < 0.05$), while the proportion of FOG fibres was lower ($P < 0.05$). Also, NOIMP HAA and CRA steers were similar for both FG and FOG fibre distribution in the ST; however, with IMP, HAA steer had lower ($P < 0.05$) proportions of FG fibres and higher ($P < 0.05$) proportions of FOG fibres than CRA steer (Fig. 2a and 2b).

In the GM, the proportions of FG fibres in HAA and CRA steers were similar when calf-fed whereas the proportion of FG fibres in the carcasses of HAA steers was lower ($P < 0.05$) than that of CRA steers when yearling-fed (Fig. 2c). In this same muscle, RAC supplementation resulted in increased proportions of FG fibres ($P < 0.05$) and reduced proportions of SO fibres without changing the proportion of FOG fibres. The proportion of SO fibres was increased ($P < 0.05$) in IMP steers, while the proportion of FOG fibres was decreased and the proportion of FG fibres did not change ($P < 0.05$). The proportion of SO fibres tended to be greater ($P = 0.08$) in yearling-fed steers than in calf-fed steers and the CRA crossbred had reduced proportions of ($P < 0.05$) SO fibres. Production systems and breed cross did not affect the proportion of FOG fibres in the GM.

Collagen Characteristics

IMP, RAC, and breed cross had no effect on the collagen content in either the ST or GM (Tables 1 and 2). Total and soluble collagen contents of the ST were not affected by age at slaughter, although soluble collagen content tended to be reduced ($P = 0.06$) in yearling-fed steers (Table 1). For the GM, total collagen content was significantly higher ($P < 0.05$) in yearling-fed steers than in calf-fed steers, while the soluble collagen content was decreased in the same population ($P < 0.05$) (Table 2).

DISCUSSION

Muscle yield is of primary importance for beef producers because it contributes to their income from each carcass; thus, it is an economic concern that affects the viability of their enterprise. In North America, cattle are grown for 16 to 20 mo in order to fit agronomic conditions and achieve adequate carcass size without compromising meat tenderness. To enhance muscle yield further, Continental breed genetics, hormonal growth implants, and now β-AA are used to increase feed efficiency and weight gain of cattle as well as carcass yield grade. The effect of these production practices may be additive, and understanding how these strategies interact on muscles is necessary in order to interpret their effect on beef quality. Consumers may not directly

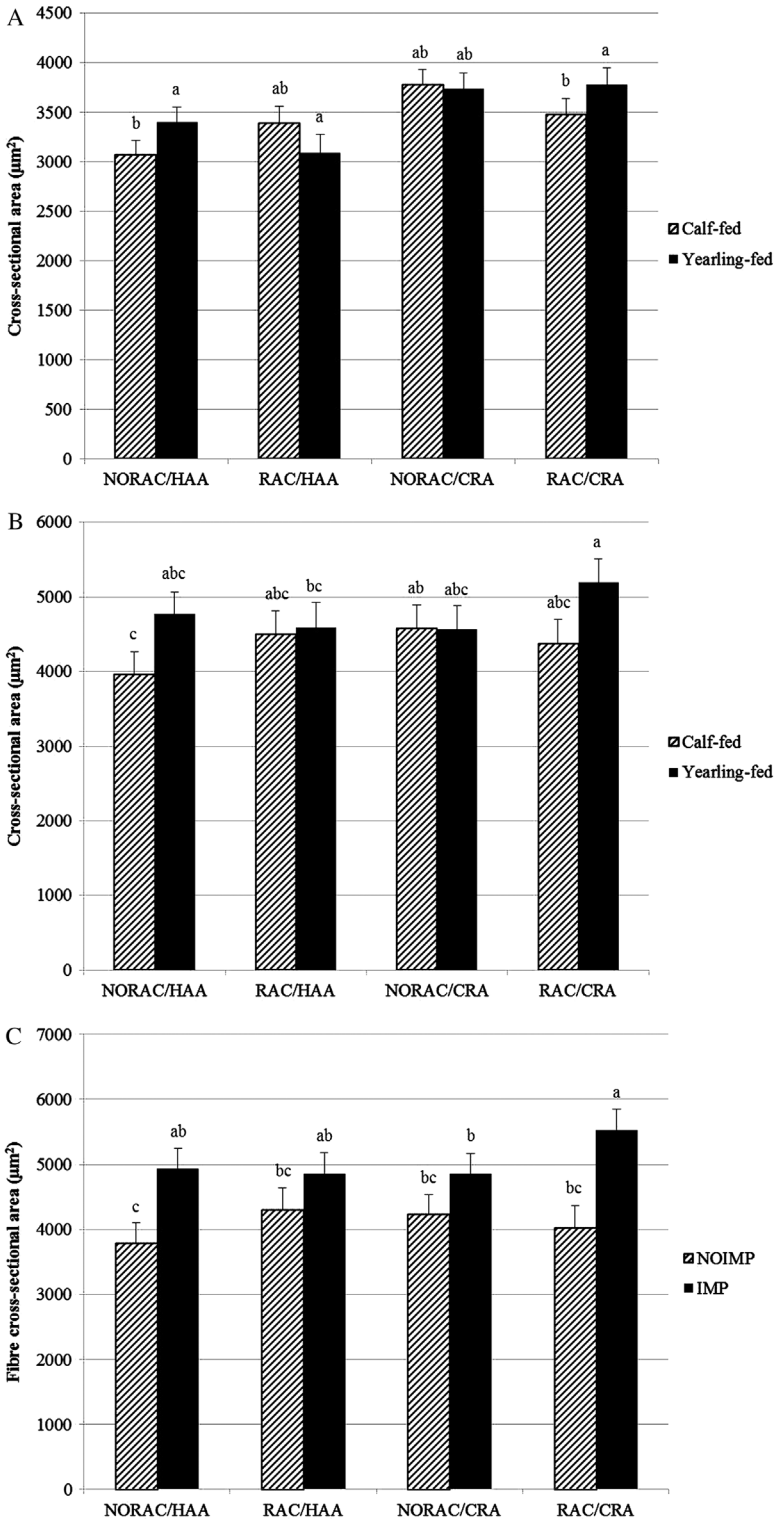

Fig. 1. Fibre cross-sectional areas of the m. semitendinosus. A. FOG fibre as affected by RAC, production systems, and breed crosses. B. FG fibre as affected by RAC, production systems, and breed crosses. C. FG fibre as affected by RAC, implantation strategy, and breed crosses. Columns with different letters are significantly different ($P < 0.05$). Error bars are pooled standard error of the mean (SEM). Abbreviations: CRA, Charolais-Red Angus; FG, fast glycolytic; FOG, fast oxidative glycolytic; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; NS, not significant; RAC, ractopamine hydrochloride; SO, slow oxidative.

Table 5. Effect of production systems (P), implantation strategy (I), ractopamine hydrochloride feed supplementation (R), and breed cross (B) on fibre distribution[z] (%) of the m. semitendinosus and m. gluteus medius, including significant interactions

	Production systems		Implantation		Ractopamine feeding		Breed cross			Interaction				
Variable	Calf-fed	Yearling-fed	NOIMP[y]	IMP[y]	NORAC[y]	RAC[yx]	SEM[w]	HAA[y]	CRA[y]	SEM[v]	P × B	I × B	R × B	I × R
$n =$	56	56	56	56	56	56	–	64	48	–	–	–	–	–
M.semitendinosus														
SO[y]	13.13	12.49	12.25	13.37	13.34	12.28	0.59	12.87	12.75	0.56	NS	NS	NS	*
FOG[y]	30.35*a*	23.72*b*	26.47	27.60	25.71	28.36	1.04	27.34	26.73	0.86	NS	***	*	NS
FG[y]	56.54*b*	63.78*a*	61.28	59.03	60.94	59.38	0.96	59.77	60.55	0.87	NS	**	*	NS
M. gluteus medius														
SO	20.74*y*	23.36*x*	20.52*b*	23.58*a*	23.95*a*	20.15*b*	0.90	22.93*a*	21.18*b*	0.77	NS	*	NS	NS
FOG	38.34	38.34	39.93*a*	36.74*b*	39.51	37.16	0.91	38.12	38.55	0.79	NS	NS	*	NS
FG	40.89	38.32	39.54	39.67	36.55*b*	42.66*a*	1.69	39.04	40.16	1.31	**	NS	NS	NS

[z]Summation of SO, FOG, and FG% within a treatment effect may not equal 100.00 due to number rounding.
[y]CRA, Charolais-Red Angus; FG, fast glycolytic; FOG, fast oxidativeglycolytic; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; RAC, ractopamine hydrochloride; SO, slow oxidative.
[x]200 mg RAChead^{-1}d^{-1} for 28 d.
[w]Pooled standard error of the mean (SEM) for production systems, implantation strategy, and ractopamine feed supplementation.
[v]Pooled standard error of the mean (SEM) for breed crosses.
a, *b* Means within the same row within a main effect with different letters are significantly different ($P < 0.05$).
x, *y* Means within the same row within a main effect with different letters tend to be significantly different ($P < 0.10$).
*, **, *** $P < 0.10$, $P < 0.05$, and $P < 0.01$, respectively; NS, nonsignificant.

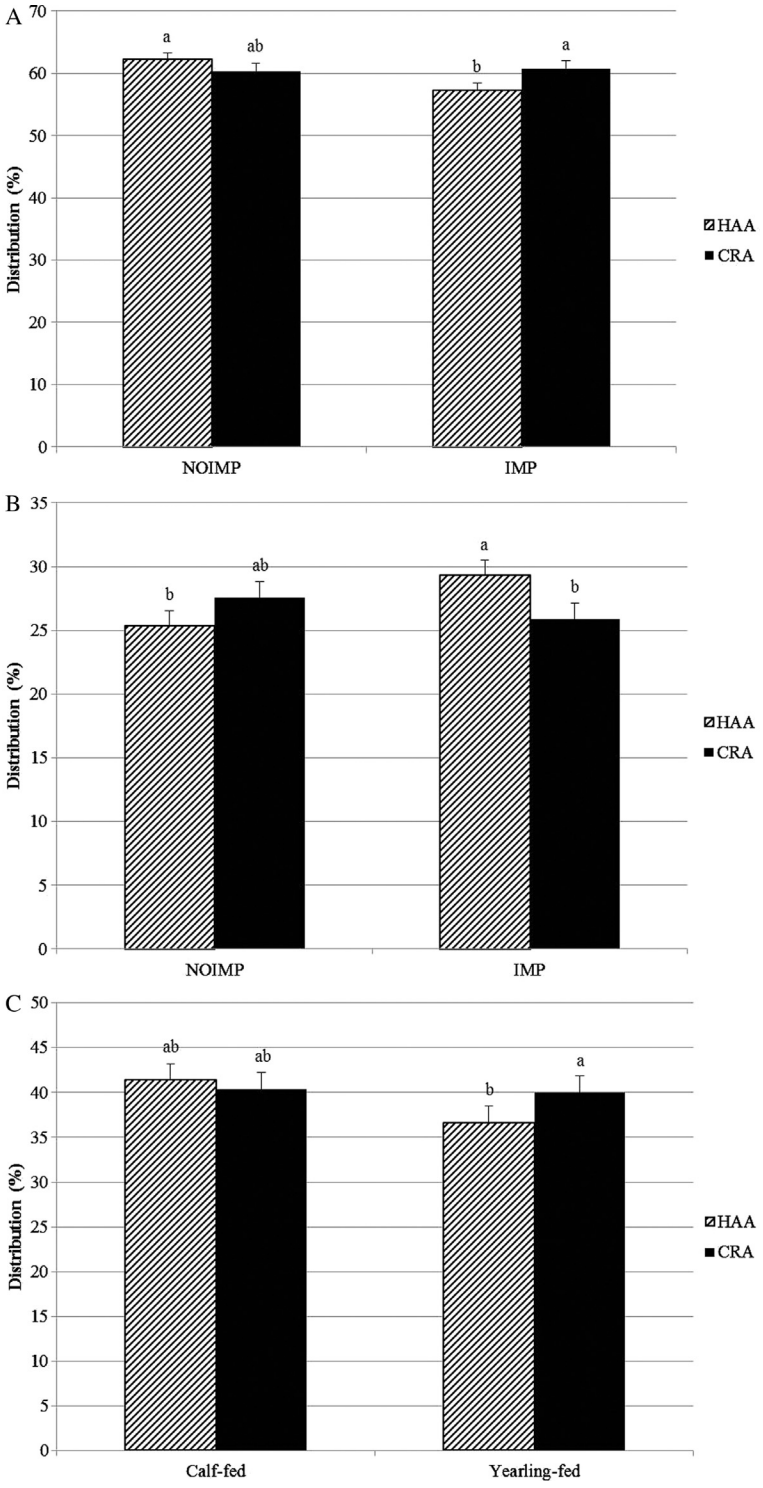

Fig. 2. Interactions of breed cross, implantation and age on muscle fibre distributions. A. FG fibre distribution of the ST as affected by implantation strategy and breed crosses. B. FOG fibre distribution of the ST as affected by implantation strategy and breed crosses. C. FG fibre distribution of the GM as affected by production systems and breed crosses. Columns with different letters are significantly different ($P < 0.05$). Error bars are pooled standard error of the mean (SEM). Abbreviations: CRA, Charolais-Red Angus; FG, fast glycolytic; FOG, fast oxidative glycolytic; GM, gluteus medius; HAA, Hereford-Aberdeen Angus; IMP, hormonal growth implants; NOIMP, no hormonal growth implants; NORAC, no ractopamine hydrochloride; NS, nonsignificant; RAC, ractopamine hydrochloride; SO, slow oxidative; ST, semitendinosus.

benefit from β-AA supplementation or implantation of steers, but because the cost of production is reduced with these strategies, consumers may have the same quality of meat for a reasonable price.

Expected results of the study included a decrease in muscle fat content and a concomitant increase in muscle protein content with Continental genetics (Buchanan and Dolezal 1999) and steroidal implant use (Bruns et al. 2005). An increase in mean ST and GM muscle weights was also expected with increased age at slaughter, Continental breed genetics (Buchanan and Dolezal 1999), and implantation (Perry et al. 1991). Implantation also increased the ST and GM proportional to the carcass weight, a result only observed in the top butt wholesale cut by Perry et al. (1991), of which the GM is a major muscle, although these researchers did not examine cuts containing the ST. The increase in muscle weight with animal age was due to an increase in muscle fibre cross-sectional area that accompanies myofibrillar protein accretion (Jurie et al. 1995; Wegner et al. 2000), while the increase in muscle weight and proportion with Continental genetics was augmented by an increase in the number of large FG fibres in the ST and GM muscles, particularly in GM muscles harvested from yearling-fed CRA steers. Muscle weight increase with age and breed was also most likely due to the increase in muscle length with skeletal growth (Buchanan and Dolezal 1999), but this was not measured in the present study.

An increase in muscle weight was anticipated with the use of hormonal growth promotants as their effects on steer growth, efficiency and carcass yield are well established (Perry et al. 1991; Platter et al. 2003). The increase in ST muscle weight and proportion with implantation appeared to be due to an increase in the cross-sectional areas of the SO and FOG muscle fibre types, which agrees with Dreyer et al. (1977), while the increase in the GM muscle weight and proportion with implantation was associated with an increase in the proportion of SO fibres and a decrease in the proportion of FOG fibres. Previous studies involving implants that combine 200 mg progesterone and 20 mg estrogen have not been shown to change muscle fibre distribution (Ono et al. 1996; Fritsche et al. 2000), although those with trenbolone acetate may have a similar effect to corticosteroids (Fritsche et al. 2000), which have been shown to reduce fast fibres in rat muscle (Nava et al. 1996). No previous work has investigated the effect of exogenous steroidal hormone implants on the bovine GM, and Ono et al. (1996) noted a differential response among muscles to hormonal implants. Fritsche et al. (2000) suggested that the response of each muscle to exogenous steroids may be dependent upon the hormone sensitivity of each muscle. Natural testosterone in comparisons between bulls and steers has been associated with increased SO and decreased FG fibres in the m. longissimus dorsi (Seideman et al. 1986), m. semimembranosus and the m. semitendinosus (Dreyer et al. 1977). Young and Bass (1984) observed that only the proportion of FG fibres was lowered by castration in twin bovine males, and this reduction was unrelated to carcass weight. Despite the differential effect of implantation on fibre morphology and distribution between the ST and GM, synthetic sex hormones appeared to promote an overall muscle oxidative metabolism, while their absence appeared to shift muscle towards a glycolytic metabolism.

Unexpectedly, supplementation of the steers with RAC did not affect ST and GM muscle weights or proportions. Strydom et al. (2009) concluded that muscles of the round, such as the ST, are less affected by β-AA than those of the loin. An explanation for the absence of an effect on muscle by RAC supplementation may be related to its selectivity for β1-adrenergic receptors (β-AR) (Hadley 1996). β2-AR are the most abundant β-AR in cattle skeletal muscles (Sissom et al. 2007), while the β1-AR population is small (Sillence and Matthews 1994). Therefore, β1-selective agonists have much less opportunity to bind to their receptors to transmit their action than β2-selective agonists. Consequently, the effects of β1-selective agonists such as RAC are less dramatic on cattle than β2-selective agonists (Moody et al. 2000).

Although the results at the gross muscle level associated with RAC in the current study were limited, RAC had an effect on muscle fibre characteristics. Indeed, β-AA have been shown to generally cause a shift in myosin isoforms from slow to fast forms (Polla et al. 2004) and to change contractile properties and energy metabolism of fibres from oxidative to glycolytic (Vestergaard et al. 1994). In the present study, the proportion of SO fibres decreased, while the proportion of FG fibres increased in the GM in response to RAC as expected (Polla et al. 2004), but there was no direct change in fibre type distribution in the ST, which agrees with the results of Strydom et al. (2009). The ST may not have responded to RAC like the GM because it had a reduced proportion of SO fibres, and so lacked the fibres that have the highest concentration of β-AA receptors (Martin et al. 1989), although Kim and Sainz (1992), in their review, found no relationship between muscle fibre type proportions and muscle response to RAC. These results agree with those of Gonzalez et al. (2009, 2010), who found that bovine muscles had differential responses to RAC, and those of Vestergaard et al. (1994), who showed that the ST had a limited response to β-AA (cimaterol), but are the first to indicate that muscle fibres of the bovine GM are responsive to RAC.

The response of the ST to RAC was more complex than that of the GM, with significant interactions indicating that the mean cross-sectional areas of the FOG and FG fibres from the ST of the British bred HAA cattle carcasses were most responsive to RAC in a calf-fed system, while those from Continental-bred steer carcasses were most responsive to RAC in a yearling-fed system. Previous studies have shown that the

effectiveness of RAC varies with animal physiological maturity. Vestergaard et al. (1994) observed a greater reduction in Friesian carcass fatness with cimaterol when it was administered late in the finishing period rather than early, while Schiavetta et al. (1990) showed that increased rib eye muscle size due to early administration of clenbuterol to Angus steers persisted for 78 d post-withdrawal. Greife et al. (1989) concluded that muscle response to β-AA was contingent upon the mobilization of body fat stores, which helps to explain why HAA steer muscles responded to RAC at an earlier age than CRA steer muscles because the ST muscles from HAA steer carcasses tended to have more fat than those from CRA steer carcasses at that time. These results suggested that, to maximize its effect, RAC has to be fed to steers when they have adequate muscle fat reserves and so response will depend upon the mature frame size of the steers and the muscles targeted.

Breed also affected ST muscle responsiveness to RAC supplementation, with RAC and hormonal growth promotant implantation additively increasing FG muscle fibre cross-sectional area of Continental-bred rather than British-bred steer carcasses. Why this occurred is unclear, as fibre populations were similar in the ST muscles of control steers of each breed. β-AA and IMP can be additive on carcass characteristics (Strydom et al. 2009; Baxa et al. 2010), but RAC and the hormonal effects of IMP have not been shown to be synergistic (Bass et al. 2009). Gonzalez et al. (2010) incorporated different breeds into a study on the effect of RAC on muscle fibre morphology, but were unable to assess breed effect as it was confounded with kill group. The present study appears to be the first research to indicate that muscle fibre growth synergy between RAC and hormonal growth promotants may be breed-specific and, given the pervasive use of hormonal growth promotants in the North American beef industry, further research is warranted. The overall muscle fibre results also indicated that RAC shifted muscle fibre metabolism from oxidative to glycolytic, while IMP shifted muscle fibres towards an oxidative metabolism, confirming that these growth promotants induce muscle growth through different mechanisms. These results support the hypothesis that muscle fibres are not static entities and that their distribution can still vary on the basis of breed cross (Jurie et al. 1995), muscle (Kirchofer et al. 2002), and production system, at least until 18 to 20 mo of age.

Because consumers will be eating the beef produced from the intensive production systems investigated in this study, it is important to satisfy their expectations of its eating quality, and tenderness forms a large part of this expectation (Huffman et al. 1996). The tenderness of beef is partly determined by the amount and heat solubility of intramuscular connective tissue (Purslow 2005). That the toughness of beef increases with animal age is well known (Shimokomaki et al. 1972), but it occurs only in muscles with moderate to high connective tissue content (Shorthose and Harris 1990). This increase in collagen toughness with advancing animal age, which is accompanied by a decline in the heat solubility of collagen, occurs because heat resistant collagen cross-links form in muscle (Shimokomaki et al. 1972). In the present study, conducted with steers between 12 and 20 mo of age, muscle collagen heat solubility decreased with animal age only for the GM and not for the ST. The active role of the ST in animal locomotion may have promoted the formation of heat insoluble collagen cross-links at an earlier age than in the GM (Gerrard et al. 1987), thereby reducing the solubility of its collagen in the calf-fed steers. Also, total collagen content of the GM increased with animal age, while that of the ST was stable over time. This result was unexpected as most studies have found that the GM had less total collagen than the ST (Rhee et al. 2004; Stolowski et al. 2006), but it agreed with the results of McKeith et al. (1985), who found that the GM had a similar intramuscular collagen concentration to the ST. The results of the present study suggest that the ST may be as tough in calf-fed steers as it is in yearling-fed steers because its collagen properties changed little with advancing age, although solubility tended to decrease. In contrast, due to its increased collagen solubility in carcasses from calf-fed steers, the GM may be a muscle that could be harvested as a premium tender muscle in young steers in order to obtain additional value from the beef carcass. A reduced age at slaughter may decrease the contribution of collagen to beef toughness by shortening the period during which collagen can accumulate or form heat-stable collagen cross-links.

In the breeds and muscles studied, manipulation of steer age at slaughter and the inclusion of hormonal growth implants in the production system had the largest impact on the inherent properties of the meat. Most importantly, the impact of RAC on muscle fibre morphology appeared dependent upon intramuscular fatness; therefore, the maturity patterns of both the steer and the target muscles (Berg and Butterfield 1976) should be taken into consideration when supplementing with dietary RAC.

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