Genetics and Molecular Biology, 29, 1, 56-61 (2006)

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Research Article

Growth and carcass traits associated with *GH1/Alu* I and *POU1F1*/*Hinf* I gene polymorphisms in Zebu and crossbred beef cattle

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Abstract

The objectives of the present study were to estimate the allele and genotype frequencies of the *GH1*/*Alu* I and *POU1F1*/*Hinf* I polymorphisms in beef cattle belonging to different genetic groups and to determine the effects of these polymorphisms on growth and carcass traits in cattle submitted to feedlot management, an intensive production model. Genotyping was performed on 384 animals, including 79 Nellore, 30 Canchim (5/8 Charolais + 3/8 Zebu), 30 Simmental x Nellore crossbred and 245 Angus x Nellore crossbred cattle. Body weight, weight gain, dressing percentage, *Longissimus dorsi* area and backfat thickness were fitted using the General Linear Model (GLM) procedure of the SAS program and the least square means of the genotypes were compared using the *F* test. The results showed significant associations between the *LL* genotype of the *GH1*/*Alu* I polymorphism and higher weight gain and body weight at slaughter ($p < 0.05$). The *POU1F1*/*Hinf* I polymorphism did not have any effect on the growth and carcass traits analyzed.

Key words: beef cattle, polymorphisms, candidate gene, growth, carcass.

Received: December 2, 2004; Accepted: July 5, 2005.

Introduction

Most traits of economic interest are of a quantitative nature and are controlled by a large number of genes which each contribute a small effect to the trait, the loci responsible for such traits being known as quantitative trait loci (QTL). However, there is debate regarding the existence of principal genes which contribute more to the phenotypic variation of a quantitative trait. Weight gain, feed efficiency, meat tenderness, marbling fat and backfat are some of the main quantitative traits evaluated in beef cattle bulls, although these analyses have been performed with little knowledge about the genetic and biochemical bases of these traits.

During the various growth phases of ruminants with different frame sizes differences in metabolism have been observed, somatotrophic axis hormones being a very important factor in such differences (Owens *et al*., 1993). The somatotrophic axis play a key role in the regulation of the metabolism and physiology of mammalian growth and essentially consists of growth hormone (GH), insulin-like growth factors 1 and 2 (IGF-1 and IGF-2) and their associated binding proteins (BP) and receptors (R), *i.e.* IGFBP, GHR, IGF-1R and IGF-2R.

The *GH1* gene codifies for circulating growth hormone which binds to the extracellular domain of specific transmembrane growth hormone receptors (GHR) which are expressed in various tissues, especially liver-tissue. This process is the signal for a cascade of intracellular metabolic events culminating in the production of IGF-1 by the target tissues, of which liver-tissue is the most important (Renaville *et al*., 2002).

Directly or indirectly, through the action of IGF-1, growth hormone is the main regulator of postnatal somatic growth, stimulating anabolic processes such as cell division, skeletal growth and protein synthesis. In addition, growth hormone is involved in the regulation of fat oxidation (lipolytic activity), inhibition of glucose transport to peripheral tissues (diabetogenic activity) and the regulation of the activity of ribosomes involved in the translation, which in turn influences protein synthesis (Goodman,

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1993). These processes are directly implicated in the metabolism of nutrient distribution to different tissues and, consequently, in carcass composition and quality (Schlee *et al.,* 1994a). The growth hormone factor 1 gene (*POU1F1*) can be considered a candidate gene for growth and carcass traits in cattle since its product, a pituitary-specific positive transcription factor 1, regulates the transcription of *GH1* and the prolactin gene in the mammalian anterior pituitary (Bodner *et al*., 1988). Pituitary-specific positive transcription factor 1 was subsequently characterized as an activator of other pituitary genes, including *POU1F1* itself (Chen *et al*., 1990) and the growth hormone releasing hormone gene (*GHRH*), among others (Lin *et al.*, 1992).

Lucy *et al.* (1991) described a C → G exchange at codon 127 in the bovine *GH1* gene (*GH1*/*Alu* I polymorphism) leading to a leucine (*L* allele) to valine (*V* allele) substitution which have been associated with several production traits in cattle such as growth and carcass composition and quality (Schlee *et al*., 1994a, b; Regitano *et al*., 1999; Sartore and Di Stasio, 2000). Moody *et al.* (1995) identified in bovines the *A* and *B* alleles of the *POU1F1*/*Hinf* I polymorphism, which is an exon 6 A → G silent mutation of the bovine *POU1F1* gene (Dierkes *et al.*, 1998) which probably is not the direct responsible by phenotypic variation, although relationships have been observed between *POU1F1* polymorphisms and body weight and somatic measures (Renaville *et al*., 1997), weaning and yearling weight (Carrijo *et al*., 2003).

The objectives of the present study were to estimate the allele and genotype frequencies of the different alleles of the *GH1*/*Alu* I and *POU1F1*/*Hinf* I polymorphisms of beef cattle belonging to different genetic groups and to determine associations between these polymorphisms and the performance of the animals when submitted to an intensive production model.

Material and Methods

Cattle

The study was carried out in the experimental feedlot facility of the Animal Science Department of São Paulo State University (Unesp, Botucatu-SP, Brazil) during three consecutive years (2000 = feedlot 1, 2001 = feedlot 2 and 2002 = feedlot 3) using samples of cattle from commercial herds belonging to six different farms. The sample group consisted of 384 bull calves belonging to four different genetic groups differing in frame size, these groups being *Bos indicus* (Zebu) Nellore pure-bred cattle (n = 79) and *Bos taurus* (European)/Zebu cross-breeds consisting of Canchim cattle (5/8 Charolais + 3/8 Zebu, n = 30) and 1/2 Simmental (n = 30) and 1/2 Angus (n = 245) cross-breeds resulting from crosses between Simmental or Angus sires and Nellore dams.

The bull calves were weaned at 210 days using a creep-feeding system. At the beginning of the experiment the bulls were individually identified, treated against endo- and ectoparasites, divided into groups of five animals in each feedlot pen according to breed , where they were fed diets formulated according to the norms of the National Research Council (NRC, 1996) for an average daily gain in excess of 1.2 kg. After entering the pen, the bulls were allowed to adapt for about 20 days. When they were slightly over one year old, and after an average feedlot (fattening) period of 110 days, the bulls were slaughtered at a commercial abattoir.

For growth traits the bulls were weighed to assess their body weight (BW) when first penned (BW_0) and also at the beginning of their feedlot period (BW_1) and close to the time of slaughter (BW_{END}). Average daily weight gain (ADWG) was calculated for the interval between the last two weight measurements. For carcass traits, ribeye area (REA) or *Longissimus dorsi* area and backfat thickness (BT) were assessed at BW_{END} by ultrasonography using the method of Perkins as modified by Gresham (1998) and carcass weight (CW) was measured at slaughter with dressing percentage (DP) being taken as CW divided by BW_{END}.

Extraction of DNA and genotyping

For each bull, 5 mL of total blood was collected from the left jugular vein using vacuum tubes containing 7.5 mg of EDTA and genomic DNA extracted from a 300-μL aliquot using the Genomic Prep™ Blood DNA Isolation kit according to the manufacturer's instructions (Amersham Biosciences, Piscataway, NJ, USA).

Bulls were genotyped for the *GH1* and *POU1F1* genes by using the polymerase chain reaction and restriction fragment length polymorphism (PCR-RFLP). The chromosome 19 *GH1*/*Alu* I forward primer was 5'-GCT GCT CCT GAG GGC CCT-3' and the reverse primer 5'-GCG GCG GCA CTT CAT GAC CCT-3' and the annealing temperature 58 °C while the chromosome 1 *POU1F1*/*Hinf* I forward primer was 5'-CAA TGA GAA AGT TGG TGC-3' and the reverse primer 5'-TCT GCA TTC GAG ATG CTC -3'with an annealing temperature of 54 °C.

To determine the *GH1* gene *L* and *V* alleles we amplified a 223-bp fragment located between intron 4 and exon 5 and digested it with the *Alu* I restriction enzyme (Schlee *et al*., 1994a). The *POU1F1* gene *A* and *B* alleles were identified by amplification of a 1301-bp sequence corresponding to fragments of exons 5 and 6 followed by digestion with *Hinf* I (Moody *et al*., 1995).

Each PCR was performed in 25 μL of amplification mixture consisting of 50 ng genomic DNA, 0.20 μM of each primer, 10 mM Tris-HCl, pH 8.0, 50 mM KCl, 2.0 mM $MgCl_2$, 0.2 mM of each dNTP and 1 unit of *Taq* DNA polymerase. The amplification protocol was initial double- strand denaturation at 94 °C for 4 min, followed by denaturation at 94 °C for 1 min, primer annealing at 54 to 58 °C for 45 s (depending on the primer), extension at 72 °C

for 1 min, a final extension at 72 °C for 4 min. Steps 2, 3 and 4, corresponding to one cycle, were repeated 35 times. The amplified fragments were digested in a reaction mixture containing 10 μL of PCR product and 3 units of the restriction enzyme and the digested fragments separated by 3% (w/v) agarose gel horizontal electrophoresis using a 100 base pair (bp) molecular weight standard (Invitrogen, São Paulo, SP, Brazil) to calculate the size of the amplified and digested fragments which were visualized by ethidium bromide staining and exposure to ultraviolet light. The genotypes of the individual cattle were determined for each polymorphism by analyzing the size of the fragments reported as base pairs.

Statistical analysis

Genotype and allele frequencies were calculated for each polymorphism according to Weir (1996). Differences in the allele frequencies of the polymorphisms within and between genetic groups were determined by the method of Goodman adapted by Curi and Moraes (1981).

The traits of interest were analyzed by least square analysis of variance ($p = 0.05$) using the General Linear Model (GLM) procedure of the SAS program (Statistical Analysis System, 1999). The linear model used to fit the quantitative variables included, in addition to the genotype effect, the contemporary group effect which considered the interaction between genetic groups (1, ..., 4), feedlots (1, ..., 3) and farms of origin (1, ..., 6) as follows: $Y_{ijk} = \mu + G_i + GC_j + e_{ijk}$, where Y_{ijk} = production trait, μ = overall mean, G_i = fixed effect of the i^{th} genotype, GC_j = fixed effect of the j^{th} contemporary group, and e_{ijk} = random error.

Genotypes with very low frequency (less than 0.10) in the total sample of bulls or genetic groups showing a single genotype were not included in the analysis in order to avoid unreliable results or confounding the influence of genetic groups and genotype effects on traits of interest. The sire effect was not included in the linear model since the number of genotyped bulls which were progenies of the same sire was very small (8.5 on average). The possibility of confounding the influence of genotype effect and sire effect on production traits was low because of the large number of small half-sib families.

Results

We detected the *L* and *V* alleles of the *GH1/Alu I* polymorphism in our sample of bulls, but although the *LL* and *LV* genotypes were present the VV genotype was not (Figure 1). The *A* and *B* alleles of the *POU1F1*/*Hinf* I polymorphism were present in our sample as the *AA*, *AB* and *BB* genotypes (Figure 2). The *GH1/Alu I* and *POU1F1*/*Hinf* I polymorphism allele frequencies are shown in Table 1 and the genotype frequencies in Table 2.

The *GH1*/*Alu* I polymorphism showed segregation in the Canchim, 1/2 Simmental and 1/2 Angus genetic groups. The *GH1*/*Alu* I polymorphism *L* allele was fixed in Nellore bulls, resulting in the occurrence of the *LL* genotype only, and its frequency was significantly higher than that of the *V* allele in all the other genetic groups studied. Nellore animals presented a significantly higher frequency of the *L* allele than the Canchim and 1/2 Angus groups, which in turn

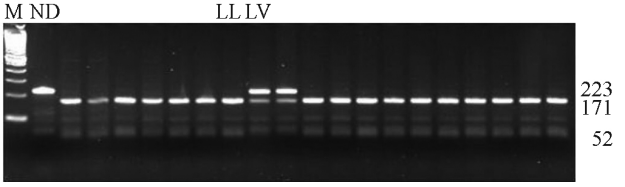

Figure 1 - Bovine *GH1* gene *Alu* I restriction fragment length polymorphisms. M = 100-bp molecular weight standard; ND = 223 bp undigested *GH1* PCR product; *LL* = genotype characterized by the presence of 171 and 52 bp restriction fragments; *LV* = heterozygous genotype characterized by 223, 171 and 52 bp fragments.

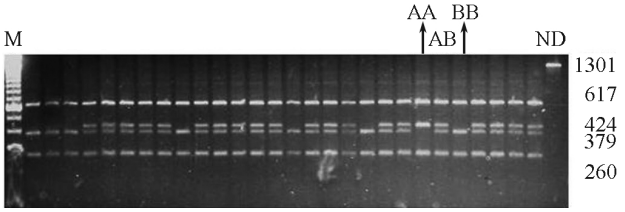

Figure 2 - Bovine *POU1F1* gene *Hinf* I restriction fragment length polymorphisms. M = 100-bp molecular weight standard; ND = undigested *POU1F1* PCR product of 1301 bp; *AA* = genotype characterized by the presence of 617, 424 and 260 bp fragments; *AB* = heterozygous genotype characterized by 617, 424, 379 and 260 bp fragments; *BB* = genotype characterized by 617, 379 and 260 bp fragments. The small 45 bp fragment of allele *B* is not visible in the gel.

Table 1 - Allele frequencies of the *GH1*/*Alu* I and *POU1F1*/*Hinf* I *loci* for the four genetic groups and for the sample as a whole.

		Genetic group and allele frequency				
Locus	Allele	Nellore	Canchim	1/2 Simmental	1/2 Angus	Total
GH1/*Alu* I	*L*	$1.000^{A,a}$	$0.933^{A,b}$	$0.717^{A,c}$	$0.922^{A,b}$	0.923
	V	$0.000^{B,c}$	$0.067^{B,b}$	$0.283^{B,a}$	$0.078^{B,b}$	0.077
POU1F1/*Hinf* I	*A*	$0.897^{A,a}$	$0.883^{A,a}$	$0.867^{A,a}$	$0.641^{A,b}$	0.731
	B	$0.103^{B,b}$	$0.117^{B,b}$	$0.133^{B,b}$	$0.359^{B,a}$	0.269

^{A,B} Within the same column values with different letters are significantly different at ($p < 0.05$). ^{a,b,c}Within the same lines values with different letters are significantly different at ($p < 0.05$).

Table 2 - Genotype frequencies of the *GH1*/*Alu* I and *POU1F1*/*Hinf* I *loci* for the four genetic groups and for the sample as a whole. The number of observations of each genotype is given in parentheses.

		Genetic group and allele frequency				
Locus	Genotype	Nellore	Canchim	1/2 Simmental	1/2 Angus	Total
GH1/*Alu* I	*LL*	1.000 (79)	0.867 (26)	0.433 (13)	0.845 (207)	0.846 (325)
	LV	0.000 (0)	0.133 (4)	0.567 (17)	0.155 (38)	0.154 (59)
POU1F1/*Hinf* I	*AA*	0.795 (63)	0.800 (24)	0.733 (22)	0.295 (72)	0.472 (181)
	AB	0.205 (16)	0.167 (5)	0.267 (8)	0.693 (170)	0.517 (199)
	BB	0.000 (0)	0.033 (1)	0.000 (0)	0.012 (3)	0.011 (4)

showed higher frequencies than the 1/2 Simmental group. The *LL* genotype predominated in Canchim and 1/2 Angus bulls, while a higher frequency of the *LV* genotype occurred in the 1/2 Simmental group.

The *POU1F1*/*Hinf* I polymorphism segregated in all four genetic groups, with the *A* allele showing a significantly higher frequency than the *B* allele in all groups. The frequency of the *A* allele was significantly higher in the Nellore, Canchim and 1/2 Simmental groups compared to the 1/2 Angus group. We did not detect the *POU1F1*/*Hinf* I polymorphism *BB* genotype in either the Nellore or 1/2 Simmental bulls and its frequency was very low in the other two groups.

The least square means and standard errors of quantitative growth traits for the different genotypes of the *GH1*/*Alu* I and *POU1F1*/*Hinf* I polymorphisms are shown in Table 3, the same parameters for carcass traits being shown in Table 4.

A significant effect of the *GH1*/*Alu* I polymorphism genotypes was observed on BW_{END} ($p = 0.0241$), average daily weight gain ($p = 0.0220$) and carcass weight ($p = 0.0441$), with the homozygous *LL* genotype being favorable compared to the heterozygous *LV* genotype. No significant effect was observed on BW_0 ($p = 0.8982$), BW_1 ($p = 0.8704$), dressing percentage ($p = 0.3496$), ribeye area ($p = 0.8723$) or backfat thickness ($p = 0.5898$).

Only the *AA* and *AB* genotypes were considered in the comparison analysis between the *POU1F1*/*Hinf* I polymorphism genotypes and production traits. The results showed no significant effect of genotypes on the growth traits BW_0 ($p = 0.2265$), BW_1 ($p = 0.1353$), BW_{END} ($p = 0.4437$) and average daily weight gain ($p = 0.6831$) or the carcass traits

Table 3 - Least square means and standard errors of the growth traits for the *GH1*/*Alu* I and *POU1F1*/*Hinf* I genotypes.

		Growth trait[1] (kg)			
Locus	Genotype	BW_0	BW_1	BW_{END}	ADWG
GH1/*Alu* I	*LL*	293.51 ± 2.75	322.13 ± 1.94	479.43 ± 2.42[a]	1.60 ± 0.02[a]
	LV	292.90 ± 3.69	322.74 ± 3.08	468.65 ± 3.98[b]	1.53 ± 0.03[b]
POU1F1/*Hinf* I	*AA*	281.89 ± 2.31	321.39 ± 2.06	472.72 ± 2.80	1.52 ± 0.16
	AB	286.47 ± 2.81	325.95 ± 2.16	475.93 ± 2.92	1.51 ± 0.17

[1]BW_0 = body weight at penning; BW_1 = body weight at the beginning of at the start of their feedlot period; BW_{END} = body weight at slaughter; ADWG = average daily weight gain. [a,b]Within the same columns values with different letters are significantly different at $p < 0.05$

Table 4 - Least square means and standard errors of the carcass traits for the *GH1*/*Alu* I and *POU1F1*/*Hinf* I genotypes.

		Carcass[1] trait			
Locus	Genotype	CW (kg)	DP (%)	REA (cm^2)	BT (cm)
GH1/*Alu* I	*LL*	262.17 ± 1.60[a]	55.37 ± 0.13	72.34 ± 0.53	4.83 ± 0.12
	LV	255.28 ± 2.55[b]	55.13 ± 0.22	72.50 ± 0.86	4.71 ± 0.19
POU1F1/*Hinf* I	*AA*	259.60 ± 1.72	55.36 ± 0.12	72.73 ± 0.53	4.96 ± 0.12
	AB	262.37 ± 1.81	55.41 ± 0.13	72.52 ± 0.55	4.95 ± 0.12

[1]CW = carcass weight; DP = dressing percentage; REA = ribeye area; BT = backfat thickness. [a,b]Within the same columns values with different letters are significantly different at $p < 0.05$.

carcass weight (p = 0.2790), DP (p = 0.8165), ribeye area (p = 0.7855) and backfat thickness (p = 0.9514).

Discussion

The *GH1*/*Alu* I polymorphism identified by Lucy *et al.* (1991) consists of a cytosine to guanine exchange at codon 127 in the *GH1* gene and the substitution of the amino acid leucine (*L* allele) by valine (*V* allele) to produce different forms of the growth hormone which can differ in receptor-binding efficiency and thus modify physiologic processes and produce different phenotypes.

In our study, the *L* allele frequencies obtained were similar to results reported in the literature which showed a fixation of this allele in Zebu breeds (Kemenes *et al*., 1999) and its predominance in the taurine breeds Charolais (Kemenes *et al*., 1999), Piedmontese (Di Stasio *et al*., 2002), Simmental and Angus (Vasconcellos *et al*., 2003), with frequencies of 0.72, 0.72, 0.82 and 0.77, respectively. Silveira (2002) obtained a frequency of 0.91 for the *L* allele in the synthetic Canchim breed.

We found significantly higher weight gain and body weight at slaughter in *LL* animals compared to *LV* animals. Because the *VV* genotype was absent from our sample the type of allele interaction could not be determined. Other authors have shown that *GH1*/*Alu* I polymorphism can influence performance traits in beef cattle, with Schlee *et al*. (1994b) having shown that in Simmental cattle the *LV* genotype is associated with higher weight gain while cattle with the *VV* genotype presented better carcass scores. Regitano *et al.* (1999) observed a significant linear increase in the *V* allele over four generations in a Canchim herd and suggested that this polymorphism may be associated with phenotypic traits that are subject to selection in this herd. Sartore and Di Stasio (2000) also suggested the occurrence of indirect selection for the *V* allele in Piedmontese cattle, although in a subsequent study (Di Stasio *et al*., 2002) these authors found no evidence of an association between this polymorphism and growth or carcass traits in this breed. Tambasco *et al*. (2003) observed that *LL* genotype Canchim x Nellore, Simmental x Nellore and Angus x Nellore crossbred cattle presented higher weight gain from birth to weaning as compared to the *LV* genotype, although from weaning to yearling the opposite was true. In a review on the molecular genetics of beef cattle, Switonski (2002) states that most studies have shown that cattle with the *VV* genotype show lower growth rates as compared to the other two genotypes. Due to these contradictory results, Switonski (2002) concluded that the use of the *GH1*/*Alu* I polymorphism in beef cattle selection programs is still premature.

The *A* and *B* alleles of the *POU1F1*/*Hinf* I polymorphism were identified by Moody *et al.* (1995). This polymorphism is a silent mutation (A → G) located in exon 6 of the bovine *POU1F1* gene (Dierkes *et al.*, 1998) and, therefore, probably does not cause any phenotypic variations.

The frequencies reported in the literature for the *A* allele of the *POU1F1*/*Hinf* I polymorphism were 0.25 for Piedmontese animals (Di Stasio *et al.*, 2002), 0.53 for Belgian Blue cattle (Renaville *et al*., 1997), 0.45 for Angus cattle (Moody *et al*., 1995), and 0.86 for the synthetic Canchim breed (Carrijo *et al*., 2003). We did not find allele frequencies of this polymorphism for pure Zebu breeds.

Our results for the *POU1F1*/*Hinf* I polymorphism showed no significant effect of the on growth or carcass traits, indicating that this is not a molecular marker associated with meat production in beef cattle and supporting the work of other published studies (Zwierzchowski *et al*., 2001; Di Stasio *et al*., 2002; Zhao *et al*., 2004). However, Renaville *et al*. (1997) reported that in taurine Belgian Blue cattle, *POU1F1*/*Hinf* I *BB* animals were significantly superior to animals with the *AB* and *AA* genotypes in terms of body weight at 7 months of age and Carrijo *et al.* (2003) found that for the mixed race taurine/zebu Canchim breed the *BB* genotype was superior to the *AB* and *AA* genotypes for weaning and yearling weight.

The differing results reported in the literature suggest that the *GH1*/*Alu* I and *POU1F1*/*Hinf* I polymorphisms are not directly responsible for phenotypic variations and these contradictions can be explained by differences in the linkage disequilibrium between markers and quantitative trait loci (QTL) in the various populations studied, by different epistatic interactions between the genetic bases of these populations and QTL, or even by the experimental design and statistical approach followed. However, the fact that our results for the *GH1*/*Alu* I polymorphism showed that the *LL* genotype was superiority to the *LV* genotype for growth and carcass traits justifies continuing studies on this polymorphism with Zebu and crossbred cattle.

Acknowledgments

The authors thank Universidade Estadual Paulista (Unesp) for providing the infrastructure for this study and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for financing the study.

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Associate Editor: Pedro Franklin Barbosa