



## Growth, carcass and meat quality traits in beef from Angus, Hereford and cross-breed grazing steers, and their association with SNPs in genes related to fat deposition metabolism



J. Papaleo Mazzucco <sup>a,\*</sup>, D.E. Goszczynski <sup>c</sup>, M.V. Ripoli <sup>c</sup>, L.M. Melucci <sup>a,b</sup>, A.M. Pardo <sup>a</sup>, E. Colatto <sup>b</sup>, A. Rogberg-Muñoz <sup>c,d</sup>, C.A. Mezzadra <sup>a</sup>, G.J. Depetris <sup>a</sup>, G. Giovambattista <sup>c</sup>, E.L. Villarreal <sup>a</sup>

<sup>a</sup> Área de Investigación en Producción Animal, Estación Experimental Agropecuaria Balcarce, Instituto Nacional de Tecnología Agropecuaria (INTA), Ruta Nac. 226 km 73.5, 7620 Balcarce, Buenos Aires, Argentina

<sup>b</sup> Departamento de Producción Animal, Facultad de Ciencias Agrarias, Universidad Nacional de Mar del Plata (UNMDP), Ruta Nac. 226 km 73.5, 7620 Balcarce, Buenos Aires, Argentina

<sup>c</sup> Instituto de Genética Veterinaria (IGEVET), UNLP-CONICET La Plata, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Calle 60 y 118 s/n, B1901AAP La Plata, Buenos Aires, Argentina

<sup>d</sup> Departamento de Producción Animal, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Ciudad de Buenos Aires, Argentina

### ARTICLE INFO

#### Article history:

Received 4 September 2015

Received in revised form 11 December 2015

Accepted 23 December 2015

Available online 28 December 2015

#### Keywords:

Angus–Hereford cross-breeds

Growth

Carcass

Meat quality

Fatty acids

Single nucleotide polymorphisms

### ABSTRACT

Grazing steers from Angus and Hereford breeds, their cross-breeds and a three-way cross-breed (Limousin × Angus–Hereford) were measured for growth, carcass and meat quality traits. Breed effects were studied, and the association of SNPs with fat deposition and fatty acid (FA) composition (leptin, melanocortin-4 receptor, stearoyl-CoA desaturase, FA synthase and thyroglobulin) was tested. Limousin cross-breed showed the greatest final body weight, ultrasound rib eye area, dressing percentage, carcass and leg length, and the lowest backfat thickness and intramuscular fat content. Genetic groups had similar pH, shear force, cooking loss, L\* and b\* and n-6:n-3 ratio. Meat from 1/2-Angus presented greater a\* than Limousin cross-breed. Whereas Angus had the highest total SFA content, Hereford had the lowest total SFA and the highest total MUFA. Limousin cross-breed had greater content of several individual PUFAs, total PUFA, n-6 and n-3 FA than Angus and 1/2-Angus. Leptin and FA synthase were associated with some FAs, supporting their influence over fat metabolism for grazing animals.

© 2015 Elsevier Ltd. All rights reserved.

### 1. Introduction

British breeds are highly distributed within the temperate areas of meat producing countries, and are the main breeds used for beef production in Argentina (Molinuevo, 2005). Crossbreeding is a frequent practice to produce calves for fattening and finishing, with the additional advantage of obtaining hybrid vigor (Gregory & Cundiff, 1980). The potential value of a biotype (pure or cross-breed) for profitable beef production over different productive systems could be estimated through the evaluation of carcass traits and meat quality. Grazing feeding is recognized for producing beef with less fat and with beneficial properties for human health, mainly fatty acid composition, when compared to more intensive production systems (French et al., 2000; Garcia et al., 2008; Latimori et al., 2008; Nuernberg et al., 2005). Furthermore, the effect of animal nutrition as well as the genetic variation on carcass characteristics and meat fatty acid composition have been demonstrated in several studies (Dinh et al., 2010; Garcia et al., 2008; Laborde, Mandell, Tosh, Wilton, & Buchanan-Smith, 2001), although

the molecular mechanisms controlling fatty acid composition are still being studied. In this regard, the growth and fattening performance of purebred and crossbred animals on pastures and the carcass and meat quality of those animals have been studied (Melucci, Mezzadra, & Villarreal, 2006; Mezzadra, Escuder, & Miquel, 1992; Nuernberg et al., 2005; Purchas & Zou, 2008; Realini, Duckett, Brito, Dalla Rizza, & De Mattos, 2004). Furthermore, in recent years, new association studies have been performed to assess whether genes and markers studied on feedlot cattle are also influencing the same traits when animals are fed on pastures, but no conclusive results are yet available (Branda Sica et al., 2014; Ferraz et al., 2009; Goszczynski et al., 2014; Melucci et al., 2012; Papaleo Mazzucco et al., 2010).

Genes that regulate metabolic pathways could influence economically important traits in farm animals, such as fatty acid composition and intramuscular fat (IMF) level. Leptin has been considered a candidate gene controlling performance, carcass and meat quality traits in beef cattle, as polymorphisms in the coding regions and its promoter have been associated with differences in serum leptin concentrations and other economically important traits (Buchanan et al., 2002; Geary et al., 2003; Nkrumah et al., 2004, 2005). The melanocortin-4 receptor (*MC4R*) is a key molecule underlying energy homeostasis and its gene was also considered a positional candidate gene for final body weight

\* Corresponding author at: EEA Balcarce-INTA, Ruta Nac. 226 km 73.5, 7620 Balcarce, Argentina.

E-mail address: [papaleo.juliana@inta.gob.ar](mailto:papaleo.juliana@inta.gob.ar) (J. Papaleo Mazzucco).

and hot carcass weight (Liu, Tian, Zan, Wang, & Cui, 2010; Zhang et al., 2009). Thyroglobulin (TG) is another important gene coding for a precursor molecule of thyroid hormones, known to affect lipid metabolism and correlated with IMF content (Barendse, 1999). On the other hand, genetic variations reported in genes related with fatty acid synthesis, namely, fatty acid synthase (FASN; Morris et al., 2007) and stearoyl-CoA desaturase (SCD; Taniguchi et al., 2004), have also been associated with fat deposition traits and fatty acid composition.

The objectives of this study were to evaluate the differences in growth, carcass characteristics, meat quality traits and fatty acid profile in beef from Angus and Hereford breeds, their cross-breeds and a three-way cross-breed (Limousin × Angus–Hereford) under grazing. Additionally, SNPs related to meat fat deposition and fatty acid composition in feedlot conditions were selected, and an association study was performed to validate their influence over these traits when animals are raised on a pasture production system.

## 2. Materials and methods

### 2.1. Animal resources and phenotypic information

A total of 845 steers born between 2000 and 2011 at the Experimental Station of the National Institute of Agricultural Technology (INTA), Balcarce, Argentina, were used for this study. The steers belonged to six different genetic groups and included purebred Angus (n = 140), purebred Hereford (n = 90), their cross-breeds: 1/4 Angus–3/4 Hereford (1/4 A; n = 93), 1/2 Angus–1/2 Hereford (1/2 A; n = 236, including reciprocal F1 and F2), 3/4 Angus–1/4 Hereford (3/4 A; n = 101); and a group of steers produced by mating Limousin sires to Angus–Hereford reciprocal F1 cows (1/2 L; n = 185). Total numbers of purebred sires were 37 Angus, 41 Hereford and eight Limousin. Periodically, commercial Angus and Hereford sires were incorporated to avoid losing genetic variability in the experimental purebred herds and to maintain a genetic link with the commercial population. All the Limousin sires were of commercial origin. Reciprocal F1 sires (n = 14 of each one) were produced within the same population.

All animals grazed a sown pasture (predominantly *Lolium multiflorum*, *Dactylis glomerata*, *Bromus catarrhicus*, *Trifolium repens* and *Trifolium pratense*). Animals were supplemented to meet their nutrient requirements when seasonal fluctuations on pasture growth or quality threatened a steady body weight gain. When supplementation was used, either maize silage, maize grain or pasture hay was offered as needed. Final body weight (FBW), ultrasound backfat thickness (BFT) and rib eye area (REA) were recorded before slaughter. Steers were progressively sent to a private abattoir as they reached an average BFT of 6 mm between the 12th and 13th ribs. In this way, 28 slaughter groups were defined. Animals were slaughtered following SENASA (National Service for Animal Health) regulations, after being kept for 24 h in paddocks deprived of feed but with full access to water. After slaughter, hot carcass weight (HCW) was used to estimate dressing percentage (DP) as  $(HCW/FBW) \times 100$ . Carcass and leg length were measured according to De Boer, Dumont, Pomeroy, and Weniger (1974), i.e., carcass length (CL) was measured from the anterior edge of symphysis pubis to the middle of the anterior edge of the visible part of the first rib, and leg length (LL) was measured from the medial malleolus of the tibia in a straight line to the anterior edge of the symphysis pubis.

### 2.2. Meat sampling and physical determinations

Twenty-four hours *post-mortem*, a section corresponding to the 12th and 13th ribs was removed from the left side, deboned, vacuum-packed and stored at  $-20^{\circ}\text{C}$  until being processed. At processing time, samples were thawed for 24 h at room temperature; all external fat and adjacent muscles were removed leaving only the *Longissimus dorsi* (LD), and pH was measured. Four 2.5 cm thick steaks were obtained from each LD

section to assess separately meat color, shear force (SF), IMF and fatty acid composition.

Colorimetric parameters (lightness, redness and yellowness;  $L^*$ ,  $a^*$  and  $b^*$ , respectively) (CIE, 1976) were measured using a Minolta colorimeter (Chroma Meter CR-300, Minolta Camera Co. Ltd., Osaka, Japan) previously calibrated against a white plate supplied by the manufacturer. The colorimeter has an 8 mm diameter measurement area and uses a light source of D65 and  $0^{\circ}$  standard observer. Determinations were done in raw meat after blooming for 1 h at  $4^{\circ}\text{C}$ . Values were recorded from three locations randomly selected from each steak and averaged to obtain a representative reading of the surface color.

For SF assessment, each steak was weighed and placed in a plastic bag, which was immersed in a water bath, heated for 50 min to an internal temperature of  $70^{\circ}\text{C}$ , chilled under running cold water for 40 min and drained. Finally, the cooked steak was gently blotted dry with a paper towel and dry weight was measured. Cooking loss (Closs) was expressed as the percentage weight loss of the steak after cooking related to the initial weight. Four round cores (2.54 cm diameter) were removed from each steak parallel to the muscle fibers and sheared at their mid-point using a 50 kg compression load cell and a Warner-Bratzler V-notch blade mounted on an Instron model 4442 testing machine (Canton, MA, USA) at a crosshead speed of 50 mm/min. SF was recorded as peak force (kg) and the value reported for each steak was the average of the four evaluated cores.

### 2.3. Lipid extraction and fatty acid composition

IMF was measured in another steak; it was extracted according to the official method of AOAC (1990) and expressed as the amount of fat in 100 g of fresh muscle excluding external adipose tissue. The fourth steak was used to measure fatty acid composition; total lipids of muscle samples were extracted according to Folch, Lees, and Sloane-Stanley (1957). Fatty acid composition was measured as fatty acid methyl esters (FAMES) using a gas chromatography (Shimadzu GC14B) on a  $100\text{ m} \times 0.25\text{ mm}$  capillary column (Restek) and helium as carrier gas. The injector and detector were kept at  $260^{\circ}\text{C}$  and the chromatograph was set initially at a temperature of  $140^{\circ}\text{C}$  during one minute; temperature was thereafter increased from 140 to  $240^{\circ}\text{C}$  at  $4^{\circ}\text{C}$  per min, and finally held constant at  $240^{\circ}\text{C}$  for 20 min. Data were recorded using GCSolution Software and the amount of each fatty acid was quantified by the internal standard technique (Supelco 37 FAME MIX), expressed as percentage of total fatty acids. All fatty acid components were used to calculate total concentrations of saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA), n-6 PUFA, and n-3 PUFA.

### 2.4. DNA extraction and genotyping

Blood samples were obtained from animals born in 2006, 2008 and 2009 (n = 260), from the jugular vein using 6% EDTA as anticoagulant and stored at  $-18^{\circ}\text{C}$ . Total DNA was then extracted using the Wizard® Genomic DNA purification kit (Promega, Madison, WI, USA) following the manufacturer's instructions. Alternatively, when blood sample was not available or DNA could not be obtained (n = 34), a freshly 1 cm side cube was separated from the previously mentioned section of LD muscle and DNA was extracted according to the methods previously reported by Wagner, Schild, and Geldermann (1994) and Giovambattista, Lirón, Villegas Castagnasso, Peral-García, and Lojo (2001). The polymorphisms of five lipid metabolism-related genes were studied: leptin (two SNPs, one in exon II [*LEP-E*; rs29004488] and the other in the promoter region [*LEP-P*; rs109406937]), melanocortin-4 receptor (*MC4R*; rs108968214), fatty acid synthase (*FASN*; rs41919985), stearoyl-CoA desaturase (*SCD*; rs41255693) and thyroglobulin (*TG*; rs135751032). The importance of those genes on lipid metabolism has already been reported (Ibeagha-Awemu, Kgwatalala, & Zhao, 2008) and explained in the Introduction. The SNPs over those genes were selected from the

data available at NCBI SNP database (<http://www.ncbi.nlm.nih.gov/gquery/>), considering their gene position (exon or promoter located) and their previous association with beef quality traits. Genotyping was performed with a customized assay using the Sequenom platform ([www.sequenom.com](http://www.sequenom.com)), Neogen genotyping service (USA, [www.neogen.com](http://www.neogen.com)).

2.5. Statistical analysis

Growth performance, carcass characteristics, physical determinations, IMF and fatty acid composition were analyzed with a linear model as follows:

$$Y_{ijk} = \mu + GGR_i + CGR_j + e_{ijk}$$

where  $Y_{ijk}$  is the trait of interest,  $\mu$  is the overall mean,  $GGR_i$  and  $CGR_j$  were the fixed effects of the  $i$ th genetic group ( $i = 1$  to 6) and the  $j$ th contemporary group ( $j = 1$  to 28), respectively, and  $e_{ijk}$  was the residual error associated with the  $ijk$  observation. The Contemporary Group includes animals born at the same year and slaughtered in the same group, hence the effect contains variations due to possible differences in diets, transporting or slaughtering conditions. The sire random effect was not included in the model, because previous analyses indicated that it was not significant for these variables (data not shown).

Fatty acid composition and SNPs information was available only for animals born in 2006, 2008 and 2009 ( $n = 260$ ). Hence, fatty acid composition and the preliminary exploration of its association with SNPs were analyzed using only data from those years. For the exploration analysis, all fatty acids were previously adjusted for the fixed effects mentioned above, and the estimation of SNPs effects was performed on the obtained residuals. Separate analyses were carried out for each SNP. False discovery rate (FDR) was calculated for the five SNPs of each fatty acid, using the Benjamini and Hochberg (1995) method.

Allele frequencies and Hardy-Weinberg equilibrium (HWE) were estimated using GENEPOP 4 software (Rousset, 2008). Additive and dominance effects were estimated for traits that were different ( $P < 0.05$ ) between genotypes. Additive genetic effects were computed as half the difference between the two homozygous genotypes. Dominance deviation was computed by subtracting the average of homozygous genotypes from that of the heterozygote genotype (Falconer & Mackay, 1996).

All statistical analyses were carried out using SAS PROC GLM procedure (SAS Inst. Inc., Cary, NC, 1998). For statistically significant main effects ( $P < 0.05$ ), least square means were reported and Tukey mean separation test at  $P < 0.05$  was used to determine differences between them.

3. Results and discussion

3.1. Growth performance and carcass characteristics

Grazing is the most common feeding production system adopted by producers in Argentina (Rearte & Pordomingo, 2014). It is based on the

utilization of annual or perennial pastures with supplementation, mainly silage, to cover the deficiency of fodder at times of the year when the supply decreases. Under these conditions, a differential response of biotypes with different growth potential and size is expected (Mezzadra, Corva, & Melucci, 1996).

Differences in growth performance and carcass characteristics between genetic groups were as expected, according to their respective breed composition and expected level of heterosis (Table 1): size-related traits (REA, FBW and HCW) were greatest for 1/2 L, intermediate for the Angus–Hereford cross-breed and smallest for both purebreds. Regarding BFT, whereas 1/2 L and Hereford had the least, Angus and Angus–Hereford had the highest fatness. Similar results were found by Villarreal, Melucci, and Mezzadra (2006) using a sub-sample of the same population under grazing, and are consistent with previous studies where British breeds were found to be smaller in mature size, had an earlier maturing and produced lighter carcasses with more fat (particularly BFT) and a smaller REA and percentage of lean muscle than Continental breeds and cross-breeds (Bureš, Bartoň, Zahrádková, Teslík, & Krejčová, 2006; Laborde et al., 2001; Villarreal, 1987). Regarding British cross-breeds, Mezzadra, Melucci, Villarreal, and Faverin (2003) found that the three-way cross with Shorthorn under semi-intensive and intensive fattening systems had greater FBW and lowest BFT than Angus and Hereford purebred animals and their cross-breeds.

In the present study, crossbred animals had greater ( $P < 0.05$ ) CL than purebred, with the exception of 3/4 A, which was not different from Hereford, and greater LL ( $P < 0.05$ ), except for 3/4 A and 1/2 A, that did not differ from Hereford (Table 1). Similar results were found by Maggioni et al. (2010) comparing Nellore with various Nellore–European crossbred young bulls and by Miguel et al. (2014) comparing Nellore and Nellore–Angus males under intensive fattening systems. In both researches, a greater CL was reported for crossbred animals as compared with their purebred counterparts. However, these authors documented greater LL for purebred Nellore animals finished in feedlot than for crossbred ones under similar management. In the current work, 1/2 L presented greater CL and LL than the rest of the genetic groups, possibly because these characteristics, which represent carcass conformation, are strongly influenced by the paternal genetic component of frame size, the slaughter weight and, probably, heterosis. No other reports were found concerning these measurements under grazing. Limousin sired steers had higher DP than both British breeds and their cross-breeds in agreement with results found by Wheeler, Cundiff, Shackelford, and Koochmariaie (2005).

In summary, the Limousin cross-breed showed superiority over the rest of the genetic groups for all traits (weight, muscularity, size) excepting BFT (finishing), not only because it is a leaner biotype, but probably because the greater nutritional requirements of this cross-breed were not sufficiently satisfied under grazing conditions.

3.2. pH, shear force, muscle color and intramuscular fat

Results of physical meat quality determinations and IMF content are shown in Table 2. No differences were observed between genetic groups

**Table 1**  
Effect of genetic group on growth performance and carcass characteristics.

Traits <sup>2</sup>	A <sup>1</sup>	H	3/4 A	1/2 A	1/4 A	1/2 L
FBW, kg	345 ± 3 e	362 ± 4 d	371 ± 4 cd	379 ± 2 bc	386 ± 4 ab	396 ± 3 a
BFT, mm	6.2 ± 0.1 a	5.6 ± 0.1 b	6.5 ± 0.1 a	6.4 ± 0.1 a	6.2 ± 0.1 a	5.3 ± 0.1 b
REA, cm <sup>2</sup>	48.0 ± 0.6 c	45.0 ± 0.7 d	52.0 ± 0.7 b	51.0 ± 0.5 b	51.6 ± 0.7 b	56.3 ± 0.6 a
HCW, kg	180 ± 2 c	186 ± 2 c	196 ± 2 b	199 ± 1 b	203 ± 2 b	213 ± 2 a
CL, cm	114.0 ± 0.3 d	114.9 ± 0.4 cd	116.2 ± 0.4 bc	116.4 ± 0.3 b	117.2 ± 0.4 b	118.9 ± 0.3 a
LL, cm	68.7 ± 0.2 d	71.1 ± 0.3 c	70.7 ± 0.3 c	71.5 ± 0.2 bc	72.3 ± 0.3 b	73.9 ± 0.2 a
DP, %	52.23 ± 0.15 b	51.33 ± 0.18 c	52.83 ± 0.18 b	52.53 ± 0.12 b	52.41 ± 0.18 b	53.73 ± 0.14 a

<sup>1</sup> A: Angus; H: Hereford; 3/4 A: 3/4 Angus–1/4 Hereford; 1/2 A: 1/2 Angus–1/2 Hereford; 1/4 A: 1/4 Angus–3/4 Hereford; 1/2 L: Limousin sires × Angus–Hereford reciprocal F1 cows.  
<sup>2</sup> FBW: Final body weight, BFT: ultrasound backfat thickness, REA: ultrasound rib eye area, HCW: hot carcass weight, CL: carcass length, LL: length of leg, DP: Dressing Percentage. Within a row, means with different letters differ significantly ( $P < 0.05$ ).

( $P > 0.05$ ), except for  $a^*$  and IMF. The difference in  $a^*$  values between 1/2 A and 1/2 L could be explained by some heterotic effects on 1/2 A (not significant when compared with purebreds) and a negative effect on  $a^*$  values of the Limousin genetics, as Continental breeds have lower  $a^*$  values than British breeds (Cuvelier et al., 2006). The lowest percentage of IMF ( $P < 0.05$ ) was obtained in 1/2 L, differing in 1.11 and 0.46 percentage points from Angus and Hereford, respectively. This was coincident with what was already shown for our BFT and REA results and with bibliography indicating that late maturing breeds (e.g. Limousin) develop more muscle mass and less fat than early maturing breeds such as Angus (Kraft, Kramer, Schoene, Chambers, & Jahreis, 2008; Scollan et al., 2006) which in time may be transmitted to their crossed progeny. Ward, Woodward, Otter, and Doran (2010) did not find significant differences in IMF between Aberdeen Angus and Limousin cross-breeds, suggesting it could be due to the low number of animals within each experimental group and/or the large variations between individual animals within each breed.

The results obtained for pH values were in the expected range for fresh meat, showing a normal *post-mortem* decrease. The SF values observed in the present study (Table 2) were higher than those reported in the literature for similar breeds (King, Dikeman, Wheeler, Kastner, & Koohmaraie, 2003; Shackelford, Wheeler, & Koohmaraie, 1999). This could be consequence of the lack of an aging period, the cooking method and the round core size. In this sense, Wheeler, Koohmaraie, Cundiff, and Dikeman (1994) reported that variations in cooking, coring and shearing resulted in highly different SF values. Nevertheless, the genetic group effect was not significant. In general, tenderness reported differences among *Bos taurus* cross-breed have been smaller (Koch, Dikeman, Lipsey, Allen, & Crouse, 1979) than differences between *Bos indicus* × *Bos taurus* cross-breed (Crouse, Cundiff, Koch, Koohmaraie, & Seideman, 1989), possibly because *Bos indicus* breeds have a lower content of IMF than *Bos taurus* ones (Marshall, 1994). This is consistent with Schor et al. (2008) who reviewed several researches from Argentina and concluded that breed had a minor effect in terms of the physical and nutritional parameters of meat. They also concluded that when steers from British and Continental purebreds were compared with *Bos indicus* crossed steers, SF values of *Bos indicus* were higher, depending on their proportion in the cross. On the other hand, when British purebreds were compared with British × Continental cross-breed, no differences in SF values were detected.

In summary, the lack of differences between genetic groups may be explained by their common origin (*Bos taurus*). IMF was the exception, probably a consequence of Limousin being a later maturing breed, with a greater adult weight than Hereford and Angus. Under the pasture conditions of this experiment, the Limousin progeny could not express its potential for fat deposition.

### 3.3. Fatty acid composition

The predominant SFA in meat are 14:0 (myristic acid), 16:0 (palmitic acid) and 18:0 (stearic acid) (Scollan et al., 2006). In the present work, similar results were observed (Table 3). The genetic group affected 16:0 and total SFA content, with Angus purebreds having

the highest values and Hereford the lowest ( $P < 0.05$ ). Interestingly, crossbred animals with at least 50% Angus blood also showed higher values than Hereford, while 1/2 L animals presented intermediate contents of 16:0 and total SFA and significantly differed from Angus ( $P < 0.05$ ). Other studies have also reported differences between genetic groups. Rule, MacNeil, and Short (1997) found more 16:0, 18:0 and total SFA in Hereford-cross than in Charolais-cross steers. In contrast, Bureš et al. (2006) found higher 18:0 content in Charolais than in Simmental bulls, and a tendency towards more content than in Angus and Hereford. The importance of the fatty acid composition of food is related to the fact that the human consumption of SFA raises total cholesterol and LDL-cholesterol and increases the risk of cardiovascular heart disease. However, it has been suggested that not all SFA have the same hypercholesterolemic effect: 18:0 has a neutral effect on plasma cholesterol level while 16:0 is less potent than 12:0 (lauric acid) and 14:0 (Daley, Abbott, Doyle, Nader, & Larson, 2010; Ulbricht & Southgate, 1991).

When analyzing the MUFA profile, total MUFA values were greater ( $P < 0.05$ ) in Hereford than in 3/4 A and 1/2 L, possibly associated with a greater but not significant ( $P > 0.05$ ) content of oleic acid (18:1 n-9) in Hereford (Table 3). In a review, Smith, Gill, Lunt, and Brooks (2009) suggested that breed types differ in their ability to accumulate MUFA in their adipose tissues. Purchas and Zou (2008) found differences in the concentrations of several MUFAs between breeds, including Angus, Friesian, Charolais-cross and Wagyu-cross. These authors attributed such differences to a higher activity of the delta-9 desaturase enzyme present in Wagyu than in Angus or other cross-breeds. Huerta-Leidenz et al. (1996) reported that Brahman steers contain a greater proportion of MUFA than Hereford under identical production systems. However, Laborde et al. (2001) found no breed differences in oleic acid and overall MUFA content between the Angus and Simmental cross-breeds.

The PUFAs profile includes the n-6 and n-3 fatty acids classes, which have been found to be essential for human normal growth, development and overall health. Genetic group effects ( $P < 0.05$ ) were detected for several PUFAs contents (Table 3); in most of them 1/2 L appears to be the group with greater values. In particular, 18:2 n-6, 18:3 n-3, 20:4 n-6 and 20:5 n-3 contents were greater in 1/2 L than in Angus and 1/2 A; 20:3 n-6 and 22:5 n-3 values differed between 1/2 L and 3/4 A; and 22:6 n-3 did between 1/2 L and 1/2 A. The total PUFA and overall content of n-6 and n-3 were greater in 1/2 L than in Angus and 1/2 A. These differences could be due to the low IMF of 1/2 L animals, as some researches had indicated that PUFA proportion decreased as IMF increased (De Smet, Raes, & Demeyer, 2004; Dinh et al., 2010; Scollan et al., 2006; Warren et al., 2008). On the other hand, De Smet et al. (2004) reviewed a decrease in the relative proportion of PUFA and consequently in the PUFA:SFA ratio with increasing fatness. Consistently, in this work 1/2 L presented leaner carcasses and greater PUFA:SFA ratio ( $0.18 \pm 0.01$ ) than Angus and 1/2 A ( $0.14 \pm 0.01$  for both). The n-6:n-3 ratio is an index utilized to evaluate the nutritional value of fat; a ratio below 4.0 in the diet is recommended to prevent diseases such as coronary heart disease and cancers (Simopoulos, 2004). All values obtained for this ratio were within the recommended range and no significant differences between genetic groups were observed (Table 3).

**Table 2**  
Effect of genetic group on pH, shear force, cooking loss, muscle color and intramuscular fat of meat.

Traits <sup>2</sup>	A <sup>1</sup>	H	3/4 A	1/2 A	1/4 A	1/2 L
pH	5.53 ± 0.01	5.52 ± 0.02	5.52 ± 0.02	5.51 ± 0.01	5.51 ± 0.02	5.56 ± 0.01
SF, kg	9.64 ± 0.24	10.09 ± 0.29	9.89 ± 0.28	9.69 ± 0.19	9.93 ± 0.29	9.68 ± 0.23
Closs, %	24.12 ± 0.27	24.63 ± 0.33	24.02 ± 0.32	24.35 ± 0.21	24.86 ± 0.33	24.23 ± 0.26
L*	37.25 ± 0.22	37.23 ± 0.26	36.69 ± 0.26	36.86 ± 0.18	37.35 ± 0.26	36.90 ± 0.21
$a^*$	20.69 ± 0.21 ab	20.69 ± 0.25 ab	20.90 ± 0.24 ab	21.09 ± 0.17 a	21.05 ± 0.25 ab	20.23 ± 0.20 b
$b^*$	10.56 ± 0.15	10.58 ± 0.18	10.56 ± 0.18	10.62 ± 0.12	10.76 ± 0.18	10.27 ± 0.15
IMF, %	3.09 ± 0.09 a	2.44 ± 0.11 c	3.00 ± 0.11 a	2.87 ± 0.07 ab	2.58 ± 0.11 bc	1.98 ± 0.09 d

<sup>1</sup> A: Angus; H: Hereford; 3/4 A: 3/4 Angus–1/4 Hereford; 1/2 A: 1/2 Angus–1/2 Hereford; 1/4 A: 1/4 Angus–3/4 Hereford; 1/2 L: Limousin sires × Angus–Hereford reciprocal F1 cows.

<sup>2</sup> SF: shear force; Closs: cooking loss; L\*: lightness;  $a^*$ : redness;  $b^*$ : yellowness; IMF: intramuscular fat. Within a row, means with different letters differ significantly ( $P < 0.05$ ).

**Table 3**  
Major fatty acid composition by genetic group.

Fatty acid <sup>2</sup>	A <sup>1</sup>	H	3/4 A	1/2 A	1/4 A	1/2 L
14:0	2.56 ± 0.09	2.35 ± 0.11	2.51 ± 0.11	2.57 ± 0.06	2.40 ± 0.12	2.40 ± 0.09
16:0	28.12 ± 0.27 a	25.96 ± 0.34 c	28.17 ± 0.34 a	27.66 ± 0.19 ab	27.29 ± 0.37 abc	26.74 ± 0.28 bc
18:0	14.47 ± 0.30	13.88 ± 0.39	13.84 ± 0.40	14.01 ± 0.21	13.29 ± 0.42	14.05 ± 0.32
18:1 n-9	39.48 ± 0.39	40.75 ± 0.50	39.20 ± 0.50	40.19 ± 0.27	40.79 ± 0.54	39.27 ± 0.40
18:2 n-6	2.65 ± 0.18 b	3.00 ± 0.23 ab	3.33 ± 0.23 ab	2.67 ± 0.12 b	2.94 ± 0.24 ab	3.40 ± 0.18 a
18:3 n-3	0.73 ± 0.04 b	0.84 ± 0.05 ab	0.79 ± 0.05 ab	0.77 ± 0.03 b	0.79 ± 0.05 ab	0.92 ± 0.04 a
20:3 n-6	0.18 ± 0.02 b	0.19 ± 0.02 ab	0.16 ± 0.02 b	0.18 ± 0.01 b	0.18 ± 0.03 ab	0.26 ± 0.02 a
20:4 n-6	0.93 ± 0.09 b	1.24 ± 0.11 ab	1.08 ± 0.11 ab	0.94 ± 0.06 b	1.12 ± 0.12 ab	1.34 ± 0.09 a
20:5 n-3	0.39 ± 0.04 b	0.54 ± 0.06 ab	0.47 ± 0.06 ab	0.41 ± 0.03 b	0.49 ± 0.06 ab	0.58 ± 0.05 a
22:5 n-3	0.50 ± 0.05 b	0.72 ± 0.07 ab	0.51 ± 0.07 b	0.53 ± 0.04 b	0.55 ± 0.07 ab	0.81 ± 0.05 a
22:6 n-3	0.07 ± 0.01 ab	0.10 ± 0.01 ab	0.10 ± 0.01 ab	0.07 ± 0.01 b	0.08 ± 0.02 ab	0.12 ± 0.01 a
SFA	46.61 ± 0.41 a	43.65 ± 0.52 c	45.93 ± 0.53 ab	45.65 ± 0.29 ab	44.33 ± 0.56 bc	44.82 ± 0.42 bc
MUFA	47.31 ± 0.39 ab	49.09 ± 0.50 a	46.98 ± 0.51 b	48.12 ± 0.28 ab	48.91 ± 0.54 ab	47.05 ± 0.41 b
PUFA	6.22 ± 0.43 b	7.82 ± 0.56 ab	7.23 ± 0.56 ab	6.35 ± 0.31 b	6.92 ± 0.60 ab	8.06 ± 0.45 a
n-6	3.98 ± 0.27 b	4.64 ± 0.35 ab	4.78 ± 0.35 ab	3.97 ± 0.19 b	4.39 ± 0.38 ab	5.29 ± 0.28 a
n-3	1.70 ± 0.13 b	2.20 ± 0.16 ab	1.87 ± 0.17 ab	1.79 ± 0.09 b	1.91 ± 0.18 ab	2.43 ± 0.13 a
n-6:n-3 ratio	2.62 ± 0.14	2.26 ± 0.18	2.58 ± 0.18	2.34 ± 0.01	2.31 ± 0.19	2.28 ± 0.15

Within a row, means with different letters differ significantly ( $P < 0.05$ ).

<sup>1</sup> A: Angus; H: Hereford; 3/4 A: 3/4 Angus–1/4 Hereford; 1/2 A: 1/2 Angus–1/2 Hereford; 1/4 A: 1/4 Angus–3/4 Hereford; 1/2 L: Limousin sires × Angus–Hereford reciprocal F1 cows.

<sup>2</sup> Expressed as percentage of total fatty acids. 14:0 (myristic acid), 16:0 (palmitic acid), 18:0 (stearic acid), 18:1 n-9 (oleic acid), 18:2 n-6 (linoleic acid), 18:3 n-3 (linolenic acid), 20:3 n-6 (eicosatrienoic acid), 20:4 n-6 (arachidonic acid), 20:5 n-3 (eicosapentaenoic acid; EPA), 22:5 n-3 (docosapentaenoic acid; DPA), 22:6 n-3 (docosahexaenoic acid; DHA), SFA (sum of total saturated fatty acids), MUFA (sum of total monounsaturated fatty acids), PUFA (sum of total polyunsaturated fatty acids), n-6 (sum of total n-6 PUFA), n-3 (sum of total n-3 PUFA).

In summary, the fatty acid profile study suggests an effect of breeds over the FA composition of meat. SFA differences were observed between Hereford and Angus with lower values of palmitic acid and total SFA detected in the former. Hereford had the greatest MUFA content while 1/2 L and 3/4 A had the lesser, while 1/2 L had consistently more PUFA, n-6 and n-3 than Angus and 1/2 A. The low n-6:n-3 ratio observed was rather uniform among genetic groups and consistent with the hypothesis that beef produced on pastures determine a fatty acid profile that makes meat better for human health. Moreover, this seems to be independent of the genetic constitution of the animals. Dietary n-6 for human consumption can be obtained from several foods, but consumers have access to relatively few sources of n-3, such as fish or other sources which have relatively low n-3 content. Thus, beef – especially that obtained from grass-fed cattle – can be an important alternative source of n-3 fatty acids.

### 3.4. Genotype and allele frequencies

As previously mentioned in Section 2.4, this and the following section correspond to a limited subset of data ( $n = 260$ ), i.e. steers born in 2006, 2008 and 2009. Allele and genotype frequencies of the SNPs evaluated are shown in Tables 4 and 5, respectively. *TG* was monomorphic for the C allele in the population studied.

No significant departures from HWE were identified for leptin in exon II (*LEP-E*;  $P = 0.9675$ ) and the promoter region (*LEP-P*;  $P = 0.2282$ ), *MC4R* ( $P = 0.9063$ ), *SCD* ( $P = 0.1592$ ) and *FASN* ( $P = 3638$ ). For certain genetic groups, some genotypes were at low frequencies, e.g., the TT genotype of *LEP-P* in 1/2 L and GG of *MC4R* in 3/4 A. Other genotypes were absent, such as TT genotype of *LEP-P* in Angus, GG in both purebreds and CC genotype of *SCD* in all breeds, except in Angus (Table 5).

For *LEP-E* markers, Buchanan et al. (2002) found greater frequency of T allele in Angus and Hereford (0.58 and 0.55, respectively) than in Charolais and Simmental (0.34 and 0.32, respectively), and Nkrumah et al. (2004) found a frequency of 0.71 for T allele in Angus and 0.55 in Hereford. Motter et al. (2006) in a population of Angus, Hereford and their cross-breed found similar frequencies to those obtained in this work. All of these authors indicated that the T allele was positively correlated with rapid fat deposition. Concerning *LEP-P*, Anton et al. (2011) found CC frequencies slightly higher (0.56) in purebred Angus; Schenkel et al. (2005) found similar frequencies to those found in the present study for the C and T alleles (0.73 and 0.27, respectively).

*MC4R* was significantly associated with live weight, carcass weight, BFT and marbling in Korean and Angus cattle (Liu et al., 2010; Seong, Suh, Park, Lee, & Kong, 2012). In our work, most of the animals had genotype CC, and genotype GG only appeared in cross-breeds but at a very low frequency. For *SCD*, only 71% of the animals were genotyped and genotype CC was detected in only two purebred Angus steers, the frequency of CT being greater in purebreds and 3/4 A and smaller in 1/4 A, 1/2 A and 1/2 L. Inostroza, Larama, and Sepúlveda (2013) found similar allele frequencies for *FASN* in Angus ( $A = 0.52$  and  $G = 0.48$ ) to those observed by us, but different from those observed by Oh et al. (2012) in Korean cattle.

### 3.5. Association of SNPs with fatty acid composition

#### 3.5.1. Leptin

Leptin is a hormone mainly produced in adipose tissue and involved in the regulation of body homeostasis, fat deposition, feed intake, immune function and reproduction (Chilliard, Delavaud, & Bonnet, 2005). Associations of SNPs in the leptin and leptin receptor genes with economically relevant traits have been reported in cattle by several authors (Buchanan et al., 2002; Geary et al., 2003; Nkrumah et al., 2004,

**Table 4**  
Allele frequencies of SNPs by genetic group.

Locus <sup>2</sup>	Allele	A <sup>1</sup>	H	3/4 A	1/2 A	1/4 A	1/2 L
LEP-E	n	44	25	30	93	23	41
	C	0.27	0.32	0.30	0.27	0.44	0.24
	T	0.73	0.68	0.70	0.73	0.57	0.76
LEP-P	n	44	26	30	95	23	41
	C	0.74	0.67	0.72	0.73	0.65	0.81
	T	0.26	0.33	0.28	0.27	0.35	0.20
MC4R	n	44	26	30	95	24	41
	C	0.92	0.85	0.85	0.85	0.81	0.77
	G	0.08	0.15	0.15	0.15	0.19	0.23
SCD	n	30	19	21	66	20	28
	C	0.32	0.29	0.33	0.19	0.10	0.23
	T	0.68	0.71	0.67	0.81	0.90	0.77
FASN	n	42	25	28	94	23	41
	A	0.69	0.28	0.59	0.52	0.26	0.52
	G	0.31	0.72	0.41	0.48	0.74	0.48

<sup>1</sup> A: Angus; H: Hereford; 3/4 A: 3/4 Angus–1/4 Hereford; 1/2 A: 1/2 Angus–1/2 Hereford; 1/4 A: 1/4 Angus–3/4 Hereford; 1/2 L: Limousin sires × Angus–Hereford reciprocal F1 cows.

<sup>2</sup> LEP-E: Leptin in exon, LEP-P: leptin in promoter, MC4R: melanocortin-4 receptor, SCD: stearoyl-CoA desaturase, FASN: fatty acid synthase.

**Table 5**  
Genotype frequencies of SNPs by breed.

Locus <sup>2</sup>	Genotype	A <sup>1</sup>	H	3/4 A	1/2 A	1/4 A	1/2 L
LEP-E	CC	0.07	0.08	0.07	0.08	0.22	0.10
	CT	0.41	0.48	0.47	0.40	0.44	0.29
	TT	0.52	0.44	0.47	0.53	0.35	0.61
LEP-P	CC	0.48	0.42	0.53	0.52	0.52	0.63
	CT	0.52	0.50	0.37	0.42	0.26	0.34
MC4R	TT	0.00	0.08	0.10	0.06	0.22	0.02
	CC	0.84	0.69	0.73	0.74	0.67	0.61
	CG	0.16	0.31	0.23	0.22	0.29	0.32
SCD	GG	0.00	0.00	0.03	0.04	0.04	0.07
	CC	0.07	0.00	0.00	0.00	0.00	0.00
	CT	0.50	0.58	0.67	0.38	0.20	0.46
FASN	TT	0.43	0.42	0.33	0.62	0.80	0.54
	AA	0.50	0.08	0.32	0.20	0.09	0.24
	AG	0.38	0.40	0.54	0.64	0.35	0.56
	GG	0.12	0.52	0.14	0.16	0.57	0.20

<sup>1</sup> A: Angus; H: Hereford; 3/4 A: 3/4 Angus–1/4 Hereford; 1/2 A: 1/2 Angus–1/2 Hereford; 1/4 A: 1/4 Angus–3/4 Hereford; 1/2 L: Limousin sires × Angus–Hereford reciprocal F1 cows.

<sup>2</sup> LEP-E: Leptin in exon, LEP-P: leptin in promoter, MC4R: melanocortin-4 receptor, SCD: stearoyl-CoA desaturase, FASN: fatty acid synthase.

2005). They indicated associations of the T allele with improvement in fat thickness, daily gain, and backfat carcass score. In this study, *LEP-E* was associated with IMF, with significant differences ( $P < 0.05$ ) between CT and TT (CT:  $-0.258 \pm 0.101$ ; TT:  $0.174 \pm 0.090$ ). Genotype CC was not different from the others (CC:  $0.216 \pm 0.213$ ), possibly due to the large standard error. However, no differences ( $P > 0.05$ ) between genotypes were found for FBW, BFT and HCW. *LEP-P* was not significantly associated with those traits and IMF ( $P > 0.05$ ; data not shown).

Concerning fatty acid composition, the effect of *LEP-E* was detected for 18:1 n-9 and 22:5 n-3 and for total content of SFA and MUFA (Table 6). For 18:1 n-9 and MUFA, genotype TT presented a significantly higher content than CT, while for 22:5 n-3 the differences were detected between the homozygotes and the heterozygote. Finally, for SFA, genotype TT showed less significant content than CC, and the CT genotype presented an intermediate but not significant value with any of the homozygotes. There are few works reporting the effect of leptin on fatty acid composition. Orrù et al. (2011) worked in Simmental bulls and found three SNPs on the leptin gene (g.3157A > G; g.3100C > T and g.978C > T) that affected the desaturation of fatty acid into MUFA, but they found no evidence of the effect of these markers on PUFA. Additionally, Tian et al. (2013) studied Simmental crossbred steers, and found an association of genotypes CC and TC of E2-169 T > C with higher

content of 14:0, 16:0, 17:1 and 18:0, and genotypes TA and TT of E3-299 T > A with higher content of 14:0, 14:1, 16:0 and 16:1.

The same as *LEP-E*, *LEP-P* was associated with oleic acid and MUFA, but in this case CC differed from CT and TT (Table 6) and showed the higher content. *LEP-P* also was associated with 20:5 n-3 and differences were detected between the homozygotes (Table 6), with TT presenting higher content. After FDR correction, only the association of *LEP-E* and *LEP-P* with 18:1 n-9 and of *LEP-E* with 22:5 n-3 remained significant ( $p = 0.0078$ ,  $p = 0.0078$  and  $p = 0.0120$ , respectively).

### 3.5.2. FASN

Fatty acid synthase is a multifunctional enzyme complex that catalyzes the synthesis of long-chain SFA. One of those functions is achieved by the thioesterase domain which is responsible for the final elongation of fatty acid synthesis and release of newly synthesized SFA, mainly palmitic acid (Zhang, Knight, Reecy, & Beitz, 2008). Herein, *FASN* was associated with IMF and with some fatty acid content: 14:0, 16:0 16:1 and 18:1 c9 (Table 6), even after FDR correction (adjusted p values: 0.0255, 0.0195, 0.0135 and 0.0220 for 14:0, 16:0, 16:1 and 18:1 n-9, respectively). Genotype AG presented a higher percentage ( $p < 0.05$ ) of IMF than genotype GG (AG:  $0.168 \pm 0.089$ ; GG:  $-0.281 \pm 0.135$ ) and the homozygote AA did not differ from the others (AA:  $-0.024 \pm 0.130$ ). Regarding fatty acids content, genotype AA presented higher contents of 14:0, 16:0 and 16:1 than GG, whereas for 18:1 c9, genotype AA presented lower content than AG. Similar results were found by Abe et al. (2009) and Matsuhashi et al. (2011) who reported significant effects of the *FASN* genotype on 14:0, 14:1, 16:0, 16:1, and 18:1 content and on intramuscular fat in Japanese Black cattle populations. They indicated that when the AR haplotype was substituted for TW, the proportion of 16-C or shorter fatty acids was decreased, and the proportion of 18:1 was increased. Similarly, Oh et al. (2012) found that homozygous genotypes with C, T, A, T, and G allele at g.12870, g.13126, g.15532, g.16907, and g.17924 increased the proportion of 18:1 and decreased the proportion of 16:0 in Korean cattle. Moreover, Zhang et al. (2008) found that Angus bulls with the g.17924GG genotype had lower 14:0, 16:0 and total SFA and higher 18:1 and total MUFA in the total lipid and triacylglycerol fraction than did those with the g.17924AA genotype.

### 3.5.3. MC4R

*MC4R* is a G-protein-coupled receptor. In previous analyses, it has been associated with live weight, carcass weight, backfat thickness and marbling (Liu et al., 2010; Seong et al., 2012; Zhang et al., 2009) but we did not find reports evaluating the association of this SNP with fatty acids. In the present association analysis performed using this

**Table 6**  
Averages of residuals, additive effect and dominance deviation of SNPs on fatty acids that showed differences ( $P < 0.05$ ) among genotypes.

SNP <sup>1</sup>	Alleles (N° of animals)			Additive effect	Dominance effect	
LEP-E	CC (23)	CT (102)	TT (129)			
	18:1 n-9 <sup>2</sup>	$-0.365 \pm 0.495$ ab	$-0.583 \pm 0.235$ b	$0.483 \pm 0.209$ a	$-0.847 \pm 0.537$ ( $p = 0.1449$ )	$-0.642 \pm 0.357$ ( $p = 0.1220$ )
	22:5 n-3	$-0.136 \pm 0.066$ b	$0.074 \pm 0.031$ a	$-0.044 \pm 0.028$ b	$-0.092 \pm 0.072$ ( $p = 0.8691$ )	$0.165 \pm 0.048$ ( $p = 0.0030$ )
	SFA	$1.174 \pm 0.519$ a	$0.222 \pm 0.247$ ab	$-0.288 \pm 0.219$ b	$1.462 \pm 0.564$ ( $p = 0.0500$ )	$-0.221 \pm 0.374$ ( $p = 0.6935$ )
MUFA	$-0.490 \pm 0.500$ ab	$-0.462 \pm 0.238$ b	$0.438 \pm 0.211$ a	$-0.928 \pm 0.543$ ( $p = 0.1110$ )	$-0.436 \pm 0.361$ ( $p = 0.2854$ )	
LEP-P	CC (134)	CT (106)	TT (17)			
	18:1 n-9	$0.475 \pm 0.206$ a	$-0.421 \pm 0.232$ b	$-1.035 \pm 0.578$ b	$1.511 \pm 0.614$ ( $p = 0.0593$ )	$-0.141 \pm 0.384$ ( $p = 0.7134$ )
	20:5 n-3	$-0.023 \pm 0.024$ b	$0.013 \pm 0.027$ ab	$0.145 \pm 0.067$ a	$-0.174 \pm 0.072$ ( $p = 0.0780$ )	$-0.045 \pm 0.045$ ( $p = 0.5318$ )
	MUFA	$0.542 \pm 0.206$ a	$-0.496 \pm 0.232$ b	$-1.019 \pm 0.579$ b	$1.561 \pm 0.615$ ( $p = 0.0585$ )	$-0.259 \pm 0.385$ ( $p = 0.5025$ )
FASN	AA (63)	AG (131)	GG (57)			
	14:0	$0.145 \pm 0.069$ a	$0.024 \pm 0.048$ ab	$-0.179 \pm 0.072$ b	$0.324 \pm 0.100$ ( $p = 0.0065$ )	$0.041 \pm 0.069$ ( $p = 0.9189$ )
	16:0	$0.384 \pm 0.207$ a	$0.089 \pm 0.143$ a	$-0.596 \pm 0.217$ b	$0.980 \pm 0.300$ ( $p = 0.0060$ )	$0.194 \pm 0.208$ ( $p = 0.7956$ )
	16:1	$0.110 \pm 0.089$ a	$0.073 \pm 0.062$ a	$-0.282 \pm 0.093$ b	$0.392 \pm 0.129$ ( $p = 0.0130$ )	$0.160 \pm 0.089$ ( $p = 0.1860$ )
	18:1 n-9	$-0.818 \pm 0.303$ b	$0.235 \pm 0.210$ a	$0.181 \pm 0.318$ ab	$-0.999 \pm 0.439$ ( $p = 0.0593$ )	$0.553 \pm 0.304$ ( $p = 0.1220$ )

Within a row, means with different letters differ significantly ( $P < 0.05$ ). For additive and dominance effects, P-values given in brackets are adjusted for FDR.

<sup>1</sup> LEP-E: Leptin in exon; LEP-P: leptin in promoter; FASN: fatty acid synthase.

<sup>2</sup> 14:0 (myristic acid); 16:0 (palmitic acid); 16:1 (palmitoleic acid); 18:1 n-9 (oleic acid); 20:5 n-3 (eicosapentaenoic acid); 22:5 n-3 (docosapentaenoic acid); SFA (sum of total saturated fatty acids); MUFA (sum of total monounsaturated fatty acids), PUFA (sum of total polyunsaturated fatty acids).

marker, genotype GG was eliminated because it was only present in five animals. Differences between genotypes CC and CG were detected for 16:1 (CC:  $-0.069 \pm 0.051$ ; CG:  $0.159 \pm 0.088$ ), 22:6 n-6 (CC:  $-0.005 \pm 0.005$ ; CG:  $0.019 \pm 0.009$ ) and AGPI (CC:  $-0.214 \pm 0.199$ ; CG:  $0.653 \pm 0.343$ ). However, after FDR correction, no association between this SNP and fatty acids remained significant.

### 3.5.4. SCD

No differences between genotypes of SCD were detected in any of the fatty acids tested. SCD encoded for an enzyme responsible for the conversion of SFA into MUFA in mammalian adipocytes inserting a double bond between carbons 9 and 10 of the fatty acyl chain (Ntambi, 1995; Ntambi & Miyazaki, 2004). It has been suggested as a candidate gene for fatty acid composition and the studied polymorphism had been associated with MUFA content in Wagyu breed (Taniguchi et al., 2004). The lack of association observed could be the consequence of both, the studied breeds and/or the number of animals utilized for the statistical analysis. Other experiments evaluating markers in SCD found significant association with fatty acid composition in Japanese Black cattle (Matsushashi et al., 2011; Ohsaki et al., 2009), Fleckvieh bulls (Bartoň et al., 2010) and Brangus grazing steers (Baeza et al., 2013).

Finally, it must be taken into account that the association studies were not performed on the original data set used for the phenotype analysis but on a smaller subset, with larger standard errors of estimates and with some genotypes showing very low frequencies.

### 3.5.5. Additive and dominance effects

The additive effect and dominance deviation of SNPs on fatty acids showing significant differences among genotypes are presented in Table 6. After FDR correction, an additive was significant for FASN over the amount of 14:0, 16:0 and 16:1, and a dominance effect for LEP-E over 22:5 n-3 fatty acid amount. Interestingly, FASN SNP is in the coding region of the enzyme and the additive effect detected here could be consequence of a differential structure of the enzyme caused by this polymorphism or by other or others mutation(s) in LD with this one. The results obtained by Hayakawa et al. (2015) and Ji et al. (2014) studying the expression pattern of FASN gene in cattle could support this hypothesis.

## 4. Conclusion

Under grazing fattening conditions, crossbreeding between British breeds and a combination of cross-breed dams with a sire breed like Limousin may produce heavier steers even when they are unable to achieve the same degree of fatness.

Although genetic groups did not affect physical meat quality traits, differences in fatty acid composition were detected. 1/2 L presented less IMF, 16:0 and total SFA content, and greater content of total PUFA, n-6 and n-3 and some individual PUFAs, like linoleic and linolenic acids. The last two acids mentioned are the main substrates in the desaturation/elongation pathway and conversion into longer chain PUFAs, with beneficial effects on human health. Thus beef, especially from grass-fed cattle, can be an important alternative source of greater quantities of this kind of compounds, contributing to a healthier human diet.

Even when other researches with several breeds and under more intensive feeding systems have shown an association of these SNPs with IMF FA composition, we could not confirm all of them under our grazing feeding system. Only leptin and FAS were associated with some fatty acids, probably due to the small size of the molecular study data set. Hence, to validate the usefulness of these markers in selection programs, these relationships should be tested through other experiments with a larger number of animals.

## Acknowledgments

This research was funded with grants provided by ANPCYT (PICT 08-04156; PICTR2002-0017), INTA (PNPA-1126033; PNCAR-334), UNMdP (AGR456/14; AGR393/12; AGR330/10; AGR270/08; AGR202/05; AGR137/01), CONICET (PIP2010-11220090100379) and UNLP (ID V206/12, JI 9861/3/11). The authors thank A. Di Maggio for manuscript correction.

## References

- Abe, T., Saburi, J., Hasebe, H., Nakagawa, T., Misumi, S., Nade, T., ... Kobayashi, E. (2009). Novel mutations of the FASN gene and their effect on fatty acid composition in Japanese black beef. *Biochemical Genetics*, 47(5–6), 397–411. <http://dx.doi.org/10.1007/s10528-009-9235-5>.
- Anton, I., Kovács, K., Holló, G., Farkas, V., Lehel, L., Hajda, Z., & Zsolnai, A. (2011). Effect of leptin, DGAT1 and TG gene polymorphisms on the intramuscular fat of Angus cattle in Hungary. *Livestock Science*, 135(2–3), 300–303. <http://dx.doi.org/10.1016/j.livsci.2010.07.012>.
- AOAC (1990). *Official methods of analysis of the association of analytical chemists* (15th ed.). Arlington, Virginia. s.p: Association of Official Analytical Chemists, Inc.
- Baeza, M.C., Corva, P.M., Soria, L.A., Pavan, E., Rincon, G., & Medrano, J.F. (2013). Genetic variants in a lipid regulatory pathway as potential tools for improving the nutritional quality of grass-fed beef. *Animal Genetics*, 44(2), 121–129. <http://dx.doi.org/10.1111/j.1365-2052.2012.02386.x>.
- Barendse, W. (1999). Assessing lipid metabolism. *Int. Pat. Appl. PCT/AU98/00882, Int Pat Publ WO 99/23248*.
- Bartoň, L., Kott, T., Bureš, D., Řehák, D., Zahrádková, R., & Kottová, B. (2010). The polymorphisms of stearoyl-CoA desaturase (SCD1) and sterol regulatory element binding protein-1 (SREBP-1) genes and their association with the fatty acid profile of muscle and subcutaneous fat in Fleckvieh bulls. *Meat Science*, 85(1), 15–20. <http://dx.doi.org/10.1016/j.meatsci.2009.11.016>.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B. (Methodological)*, 57(1), 289–300.
- Branda Sica, A., Ravagnolo, O., Brito, G., Baldi, F., LaManna, A., Bancharo, G., ... Medrano, J. (2014). Evaluación de panel SNP en genes candidatos de vías metabólicas para carne en Hereford. *Archivos de Zootecnia*, 63(241), 73–84.
- Buchanan, F.C., Fitzsimmons, C.J., Van Kessel, V.A., Thue, T.D., Winkelman-Sim, D.C., & Schmutz, M.S. (2002). Association of a missense mutation in the bovine leptin gene with carcass fat content and leptin mRNA levels. *Genetics Selection Evolution*, 34, 105–116. <http://dx.doi.org/10.1051/gse:2001006>.
- Bureš, D., Bartoň, L., Zahrádková, R., Teslík, V., & Křečková, M. (2006). Chemical composition, sensory characteristics, and fatty acid profile of muscle from Aberdeen Angus, Charolais, Simmental, and Hereford bulls. *Czech Journal of Animal Science*, 51(7), 279–284.
- Chilliard, Y., Delavaud, C., & Bonnet, M. (2005). Leptin expression in ruminants: nutritional and physiological regulations in relation with energy metabolism. *Domestic Animal Endocrinology*, 29(1), 3–22. <http://dx.doi.org/10.1016/j.domaniend.2005.02.026>.
- CIE (Commission International de l'Éclairage) (1976). Official recommendations on uniform color spaces—color difference equations and metric color terms. *Suppl. No. 2. CIE publication no. 15 colorimetry. Paris*.
- Crouse, J.D., Cundiff, L.V., Koch, R.M., Koohmaraie, M., & Seideman, S.C. (1989). Comparisons of *Bos indicus* and *Bos taurus* inheritance for carcass beef characteristics and meat palatability. *Journal of Animal Science*, 67, 2661–2668. <http://dx.doi.org/10.2134/jas1989.67102661x>.
- Cuvelier, C., Cabaraux, J.F., Dufresne, I., Clinquart, A., Hocquette, J.F., Istasse, L., & Hornick, J.-L. (2006). Performance, slaughter characteristics and meat quality of young bulls from Belgian Blue, Limousin and Aberdeen Angus breeds fattened with a sugar-beet pulp or a cereal-based diet. *Animal Science*. <http://dx.doi.org/10.1079/ASC20057>.
- Daley, C.A., Abbott, A., Doyle, P.S., Nader, G.A., & Larson, S. (2010). A review of fatty acid profiles and antioxidant content in grass-fed and grain-fed beef. *Nutrition Journal*, 9, 10. <http://dx.doi.org/10.1186/1475-2891-9-10>.
- De Boer, H., Dumont, B.I., Pomeroy, R.W., & Weniger, J.H. (1974). *Manual on E.A.A.P. reference methods for the assessment of carcass characteristics in cattle. Livestock Production Science*, 1, 151–164.
- De Smet, S., Raes, K., & Demeyer, D. (2004). Meat fatty acid composition as affected by fatness and genetic factors: a review. *Animal Research*, 53, 81–98. <http://dx.doi.org/10.1051/anires:2004003>.
- Dinh, T.T.N., Blanton, J.R., Riley, D.G., Chase, C.C., Coleman, S.W., Phillips, W.A., ... Thompson, L.D. (2010). Intramuscular fat and fatty acid composition of longissimus muscle from divergent pure breeds of cattle. *Journal of Animal Science*, 88(2), 756–766. <http://dx.doi.org/10.2527/jas.2009-1951>.
- Falconer, D.S., & Mackay, T.F.C. (1996). *Introduction to quantitative genetics* (4th ed.). Essex: Longman Group Ltd.
- Ferraz, J.B.S., Pinto, L.F.B., Meirelles, F.V., Eler, J.P., de Rezende, F.M., Oliveira, E.C.M., ... Nkrumah, D. (2009). Association of single nucleotide polymorphisms with carcass traits in Nellore cattle. *Genetics and Molecular Research*, 8(4), 1360–1366. <http://dx.doi.org/10.4238/vol8-4gmr650>.
- Folch, J., Lees, M., & Sloane-Stanley, H. (1957). A simple method for the isolation and purification of total lipids from animal tissue. *Journal of Biological Chemistry*, 226, 497–509.

- French, P., Stanton, C., Lawless, F., O'Riordan, E.G., Monahan, F.J., Caffrey, P.J., & Moloney, A.P. (2000). Fatty acid composition, including conjugated linoleic acid, of intramuscular fat from steers offered grazed grass, grass silage, or concentrate-based diets. *Journal of Animal Science*, 78(11), 2849–2855. <http://doi.org/10.1093/jas/78.11.2849>.
- García, P.T., Pensel, N.A., Sancho, A.M., Latimori, N.J., Kloster, A.M., Amigone, M.A., & Casal, J.J. (2008). Beef lipids in relation to animal breed and nutrition in Argentina. *Meat Science*, 79(3), 500–508. <http://dx.doi.org/10.1016/j.meatsci.2007.10.019>.
- Geary, T.W., McFadin, E.L., MacNeil, M.D., Grings, E.E., Short, R.E., Funston, R.N., & Keisler, D.H. (2003). Leptin as a predictor of carcass composition in beef cattle. *Journal of Animal Science*, 81(1), 1–8. <http://doi.org/10.2527/jas.2003.8111>.
- Giovambattista, G., Ripoli, M.V., Lirón, J.P., Villegas Castagnasso, E.E., Peral-García, P., & Lojo, M.M. (2001). DNA typing in a cattle stealing case. *Journal of Forensic Sciences*, 46(6), 1484–1486.
- Goszczynski, D.E., Papaleo Mazzucco, J., Ripoli, M.V., Villarreal, E.L., Rogberg-Muñoz, A., Mezzadra, C.A., ... Giovambattista, G. (2014). Characterization of the bovine gene LPE and possible influence on fatty acid composition of meat. *Meta Gene*, 2, 746–760. <http://dx.doi.org/10.1016/j.mgene.2014.09.001>.
- Gregory, K.E., & Cundiff, L.V. (1980). Crossbreeding in beef cattle: Evaluation of systems. *Journal of Animal Science*, 51(5), 1224–1242.
- Hayakawa, K., Sakamoto, T., Ishii, A., Yamaji, K., Uemoto, Y., Sasago, N., ... Sasazaki, S. (2015). The g.841G > C SNP of FASN gene is associated with fatty acid composition in beef cattle. *Animal Science Journal*, 86(8), 737–746. <http://dx.doi.org/10.1111/asj.12357>.
- Huerta-Leidenz, N.O., Cross, H.R., Savell, J.W., Lunt, D.K., Baker, J.F., & Smith, S.B. (1996). Fatty acid composition of subcutaneous adipose tissue from male calves at different stages of growth. *Journal of Animal Science*, 74(6), 1256–1264. <http://doi.org/10.2527/jas.1996.7461256x>.
- Ibeagha-Awemu, E.M., Kgwatalala, P., & Zhao, X. (2008). A critical analysis of production-associated DNA polymorphisms in the genes of cattle, goat, sheep, and pig. *Mammalian Genome*, 19(9), 591–617. <http://dx.doi.org/10.1007/s00335-008-9141-x>.
- Inostroza, K., Larama, G., & Sepúlveda, N. (2013). Polimorfismo g.17924A> G en el gen FASN y su relación con la composición de ácidos grasos (Mufa y Cla) en la carne de novillos aberdeen Angus. *Revista Científica*, XXIII(4), 329–333.
- Ji, S., Yang, R., Lu, C., Qiu, Z., Changguo Yan, C., & Zhao, Z. (2014). Differential expression of PPAR $\gamma$ , FASN, and ACADM genes in various adipose tissues and longissimus dorsi muscle from Yanbian Yellow cattle and Yan Yellow cattle. *Asian-Australasian Journal of Animal Sciences*, 27(1), 10–18. <http://dx.doi.org/10.5713/ajas.2013.13422>.
- King, D.A., Dikeman, M.E., Wheeler, T.L., Kastner, C.L., & Koohmaraie, M. (2003). Chilling and cooking rate effects on some myofibrillar determinants of tenderness of beef. *Journal of Animal Science*, 81(6), 1473–1481. <http://doi.org/10.2527/jas.2003.8161473x>.
- Koch, R.M., Dikeman, M.E., Lipsey, R.J., Allen, D.M., & Crouse, J.D. (1979). Characterization of biological types of cattle - Cycle II : III. Carcass composition, quality and palatability. *Journal of Animal Science*, 49(2), 448–460.
- Kraft, J., Kramer, J.K.G., Schoene, F., Chambers, J.R., & Jahreis, G. (2008). Extensive analysis of long-chain polyunsaturated fatty acids, CLA, trans-18:1 isomers, and plasmalogen lipids in different retail beef types. *Journal of Agricultural and Food Chemistry*, 56(12), 4775–4782. <http://dx.doi.org/10.1021/jf8001813>.
- Laborde, F.L., Mandell, I.B., Tosh, J.J., Wilton, J.W., & Buchanan-Smith, J.G. (2001). Breed effects on growth performance, carcass characteristics, fatty acid composition, and palatability attributes in finishing steers. *Journal of Animal Science*, 79(2), 355–365. <http://doi.org/10.2527/jas.2001.792355x>.
- Latimori, N.J., Kloster, A.M., García, P.T., Carduza, F.J., Grigioni, G., & Pensel, N.A. (2008). Diet and genotype effects on the quality index of beef produced in the Argentine Pampeana region. *Meat Science*, 79(3), 463–469. <http://dx.doi.org/10.1016/j.meatsci.2007.10.008>.
- Liu, H., Tian, W., Zan, L., Wang, H., & Cui, H. (2010). Mutations of MC4R gene and its association with economic traits in qinchuan cattle. *Molecular Biology Reports*, 37(1), 535–540. <http://dx.doi.org/10.1007/s11033-009-9706-0>.
- Maggioli, D., Marques, J.D.A., Rotta, P.P., Perotto, D., Ducatti, T., Visentainer, J.V., & do Prado, I.N. (2010). Animal performance and meat quality of crossbred young bulls. *Livestock Science*, 127(2–3), 176–182. <http://dx.doi.org/10.1016/j.livsci.2009.09.006>.
- Marshall, D.M. (1994). Breed differences and genetic parameters for body composition traits in beef cattle. *Journal of Animal Science*, 72(10), 2745–2755. <http://doi.org/10.2527/jas.1994.72102745x>.
- Matsuhashi, T., Maruyama, S., Uemoto, Y., Kobayashi, N., Mannen, H., Abe, T., ... Kobayashi, E. (2011). Effects of bovine fatty acid synthase, stearoyl-coenzyme A desaturase, sterol regulatory element-binding protein 1, and growth hormone gene polymorphisms on fatty acid composition and carcass traits in Japanese Black cattle. *Journal of Animal Science*, 89(1), 12–22. <http://dx.doi.org/10.2527/jas.2010-3121>.
- Melucci, L.M., Mezzadra, C.A., & Villarreal, E.L. (2006). Genetic components for breeding system traits in Angus–Hereford crossing. *8th World Congress on Genetics Applied to Livestock Production*.
- Melucci, L.M., Panarace, M., Feula, P., Villarreal, E.L., Grigioni, G., Carduza, F., ... Miquel, M.C. (2012). Genetic and management factors affecting beef quality in grazing Hereford steers. *Meat Science*, 92(4), 768–774. <http://dx.doi.org/10.1016/j.meatsci.2012.06.036>.
- Mezzadra, C.A., Corva, P.M., & Melucci, L.M. (1996). Evaluación de dos líneas de novillos Angus de diferente tamaño estructural. I: producción de carne bajo distintos niveles nutricionales. *Investigación Agraria: Producción y Sanidad Animales*, 11(2), 135–147.
- Mezzadra, C.A., Escuder, J., & Miquel, M.C. (1992). Effects of genotype and stocking density on post-weaning daily gain and meat production per hectare in cattle. *Animal Production*, 55(01), 65–72. <http://dx.doi.org/10.1017/S0003356100037284>.
- Mezzadra, C.A., Melucci, L.M., Villarreal, E.L., & Faverin, C. (2003). Comparación del desempeño productivo de novillos puros y cruce británicos bajo sistemas de engorde semi-intensivos e intensivos. *Revista Argentina de Producción Animal*, 23(1), 45–52.
- Miguel, G.Z., Faria, M.H., Roça, R.O., Santos, C.T., Suman, S.P., Faltarone, A.B.G., ... Savian, T.V. (2014). Immunocastration improves carcass traits and beef color attributes in Nellore and Nellore  $\times$  Aberdeen Angus crossbred animals finished in feedlot. *Meat Science*, 96(1), 884–891. <http://dx.doi.org/10.1016/j.meatsci.2013.08.030>.
- Molinueva, H.A. (2005). *Genética bovina y producción en pastoreo*. Argentina: Ediciones INTA.
- Morris, C.A., Cullen, N.G., Glass, B.C., Hyndman, D.L., Manley, T.R., Hickey, S.M., ... Lee, M.A.H. (2007). Fatty acid synthase effects on bovine adipose fat and milk fat. *Mammalian Genome*, 18(1), 64–74. <http://dx.doi.org/10.1007/s00335-006-0102-y>.
- Motter, M., Corva, P.M., Soria, L., Villarreal, E.L., Schor, A., Cervini, M.L., ... Grigera Naón, J.J. (2006). Efecto de un SNP del gen de la leptina sobre aptitudes carniceras de novillos. *Revista Argentina de Producción Animal*, 26(Supl.1), 269–270.
- Nkrumah, J.D., Li, C., Basarab, J.B., Guercio, S., Meng, Y., Murdoch, B., ... Moore, S.S. (2004). Association of a single nucleotide polymorphism in the bovine leptin gene with feed intake, feed efficiency, growth, feeding behaviour, carcass quality and body composition. *Canadian Journal of Animal Science*, 84(2), 211–219. <http://dx.doi.org/10.4141/A03-033>.
- Nkrumah, J.D., Li, C., Yu, J., Hansen, C., Keisler, D.H., & Moore, S.S. (2005). Polymorphisms in the bovine leptin promoter associated with serum leptin concentration, growth, feed intake, feeding behavior, and measures of carcass merit. *Journal of Animal Science*, 83(1), 20–28. <http://doi.org/10.2527/jas.2005.83120x>.
- Ntambi, J.M. (1995). The regulation of stearoyl-CoA desaturase (SCD). *Progress in Lipid Research*, 34(2), 139–150. [http://dx.doi.org/10.1016/0163-7827\(94\)00010-J](http://dx.doi.org/10.1016/0163-7827(94)00010-J).
- Ntambi, J.M., & Miyazaki, M. (2004). Regulation of stearoyl-CoA desaturases and role in metabolism. *Progress in Lipid Research*, 43(2), 91–104. [http://dx.doi.org/10.1016/S0163-7827\(03\)00039-0](http://dx.doi.org/10.1016/S0163-7827(03)00039-0).
- Nuernberg, K., Dannenberger, D., Nuernberg, G., Ender, K., Voigt, J., Scollan, N.D., ... Richardson, R.I. (2005). Effect of a grass-based and a concentrate feeding system on meat quality characteristics and fatty acid composition of longissimus muscle in different cattle breeds. *Livestock Production Science*, 94(1–2), 137–147. <http://dx.doi.org/10.1016/j.livprodsci.2004.11.036>.
- Oh, D., Lee, Y., La, B., Yeo, J., Chung, E., Kim, Y., & Lee, C. (2012). Fatty acid composition of beef is associated with exonic nucleotide variants of the gene encoding FASN. *Molecular Biology Reports*, 39(4), 4083–4090. <http://dx.doi.org/10.1007/s11033-011-1190-7>.
- Ohsaki, H., Tanaka, A., Hoashi, S., Sasazaki, S., Oyama, K., Taniguchi, M., ... Mannen, H. (2009). Effect of SCD and SREBP genotypes on fatty acid composition in adipose tissue of Japanese black cattle herds. *Animal Science Journal*, 80(3), 225–232. <http://dx.doi.org/10.1111/j.1740-0929.2009.00638.x>.
- Orrù, L., Cifuni, G.F., Piasentier, E., Corazzin, M., Bovolenta, S., & Moiola, B. (2011). Association analyses of single nucleotide polymorphisms in the LEP and SCD1 genes on the fatty acid profile of muscle fat in simmental bulls. *Meat Science*, 87(4), 344–348. <http://dx.doi.org/10.1016/j.meatsci.2010.11.009>.
- Papaleo Mazzucco, J., Melucci, L.M., Villarreal, E.L., Mezzadra, C.A., Soria, L., Corva, P., ... Miquel, M.C. (2010). Effect of ageing and  $\mu$ -calpain markers on meat quality from Brangus steers finished on pasture. *Meat Science*, 86(3), 878–882. <http://dx.doi.org/10.1016/j.meatsci.2010.07.015>.
- Purchas, R.W., & Zou, M. (2008). Composition and quality differences between the longissimus and infraspinatus muscles for several groups of pasture-finished cattle. *Meat Science*, 80(2), 470–479. <http://dx.doi.org/10.1016/j.meatsci.2008.01.013>.
- Realini, C.E., Duckett, S.K., Brito, G.W., Dalla Rizza, M., & De Mattos, D. (2004). Effect of pasture vs. concentrate feeding with or without antioxidants on carcass characteristics, fatty acid composition, and quality of Uruguayan beef. *Meat Science*, 66(3), 567–577. [http://dx.doi.org/10.1016/S0309-1740\(03\)00160-8](http://dx.doi.org/10.1016/S0309-1740(03)00160-8).
- Rearte, D.H., & Pordomingo, A.J. (2014). The relevance of methane emissions from beef production and the challenges of the argentinean beef production platform. *Meat Science*, 98(3), 355–360. <http://dx.doi.org/10.1016/j.meatsci.2014.06.021>.
- Rousset, F. (2008). Genepop'007: A complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources*, 8, 103–106. <http://dx.doi.org/10.1111/j.1471-8286.2007.01931>.
- Rule, D.C., MacNeil, M.D., & Short, R.E. (1997). Influence of sire growth potential, time on feed, and growing-finishing strategy on cholesterol and fatty acids of the ground carcass and longissimus muscle of beef steers. *Journal of Animal Science*, 75(6), 1525–1533. <http://doi.org/10.2527/jas.1997.7561525x>.
- SAS (1998). *The SAS system for windows. Version 8*. Cary, NC, USA: SAS Institute Inc.
- Schenkel, F.S., Miller, S.P., Ye, X., Moore, S.S., Nkrumah, J.D., Li, C., ... Williams, J.L. (2005). Association of single nucleotide polymorphisms in the leptin gene with carcass and meat quality traits of beef cattle. *Journal of Animal Science*, 83(9), 2009–2020. <http://doi.org/10.2527/jas.2005.8392009x>.
- Schor, A., Cossu, M. E., Picallo, A., Ferrer, J. M., Naón, J. J. G., & Colombatto, D. (2008). Nutritional and eating quality of argentinean beef: A review. *Meat Science*, 79(3), 408–422. <http://dx.doi.org/10.1016/j.meatsci.2007.10.011>.
- Scollan, N., Hocquette, J.F., Nuernberg, K., Dannenberger, D., Richardson, I., & Moloney, A. (2006). Innovations in beef production systems that enhance the nutritional and health value of beef lipids and their relationship with meat quality. *Meat Science*, 74(1), 17–33. <http://dx.doi.org/10.1016/j.meatsci.2006.05.002>.
- Seong, J., Suh, D.S., Park, K.D., Lee, H.K., & Kong, H.S. (2012). Identification and analysis of MC4R polymorphisms and their association with economic traits of Korean cattle (Hanwoo). *Molecular Biology Reports*, 39(4), 3597–3601. <http://dx.doi.org/10.1007/s11033-011-1133-3>.
- Shackelford, S.D., Wheeler, T.L., & Koohmaraie, M. (1999). Evaluation of slice shear force as an objective method of assessing beef longissimus tenderness. *Journal of Animal Science*, 77(10), 2693–2699. <http://doi.org/10.2527/jas.1999.77102693x>.
- Simopoulos, A.P. (2004). Omega-6/omega-3 essential fatty acid ratio and chronic diseases. *Food Reviews International*, 20(1), 77–90. <http://dx.doi.org/10.1081/FRI-120028831>.
- Smith, S., Gill, C., Lunt, D., & Brooks, M. (2009). Regulation of fat and fatty acid composition in beef cattle. *Asian-Australasian Journal of Animal Sciences*, 22(9), 1225–1233. <http://dx.doi.org/10.5713/ajas.2009.10>.

- Taniguchi, M., Utsugi, T., Oyama, K., Mannen, H., Kobayashi, M., Tanabe, Y., ... Tsuji, S. (2004). Genotype of stearyl-CoA desaturase is associated with fatty acid composition in Japanese Black cattle. *Mammalian Genome*, 15(2), 142–148. <http://dx.doi.org/10.1007/s00335-003-2286-8>.
- Tian, J., Zhao, Z., Zhang, L., Zhang, Q., Yu, Z., Li, J., & Yang, R. (2013). Association of the leptin gene E2-169 T > C and E3-299 T > A mutations with carcass and meat quality traits of the Chinese Simmental-cross steers. *Gene*, 518(2), 443–448. <http://dx.doi.org/10.1016/j.gene.2012.11.071>.
- Ulbricht, T.L.V., & Southgate, D.A.T. (1991). Coronary heart disease: Seven dietary factors. *The Lancet*, 338, 985–992.
- Villarreal, E.L. (1987). Evaluación a la faena de novillos cruza F1. *Revista Argentina de Producción Animal*, 7(3), 271–279.
- Villarreal, E.L., Melucci, L.M., & Mezzadra, C.A. (2006). Genetic components for slaughter and meat quality traits in the Angus–Hereford crossing. *8th World Congress on Genetics Applied to Livestock Production*.
- Wagner, V., Schild, T.A., & Geldermann, H. (1994). Application of polymorphic DNA sequences to differentiate the origin of decomposed bovine meat. *Forensic Science International*, 64(2–3), 89–95. [http://dx.doi.org/10.1016/0379-0738\(94\)90217-8](http://dx.doi.org/10.1016/0379-0738(94)90217-8).
- Ward, R.E., Woodward, B., Otter, N., & Doran, O. (2010). Relationship between the expression of key lipogenic enzymes, fatty acid composition, and intramuscular fat content of Limousin and Aberdeen Angus cattle. *Livestock Science*, 127(1), 22–29. <http://dx.doi.org/10.1016/j.livsci.2009.09.005>.
- Warren, H.E., Scollan, N.D., Enser, M., Hughes, S.I., Richardson, R.I., & Wood, J.D. (2008). Effects of breed and a concentrate or grass silage diet on beef quality in cattle of 3 ages. I: Animal performance, carcass quality and muscle fatty acid composition. *Meat Science*, 78(3), 256–269. <http://dx.doi.org/10.1016/j.meatsci.2007.06.008>.
- Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., & Koohmaraie, M. (2005). Characterization of biological types of cattle (Cycle VII): carcass, yield, and longissimus palatability traits. *Journal of Animal Science*, 83(1), 196–207 <http://doi:2005.831196x>.
- Wheeler, T.L., Koohmaraie, M., Cundiff, L.V., & Dikeman, M.E. (1994). Effects of cooking and shearing methodology on variation in Warner-Bratzler shear force values in beef. *Journal of Animal Science*, 72(9), 2325–2330 <http://doi:1994.7292325x>.
- Zhang, C.L., Wang, Y.H., Chen, H., Lan, X.Y., Lei, C.Z., & Fang, X.T. (2009). Association between variants in the 5'-untranslated region of the bovine MC4R gene and two growth traits in nanyang cattle. *Molecular Biology Reports*, 36(7), 1839–1843. <http://dx.doi.org/10.1007/s11033-008-9388-z>.
- Zhang, S., Knight, T.J., Reecy, J.M., & Beitz, D.C. (2008). DNA polymorphisms in bovine fatty acid synthase are associated with beef fatty acid composition. *Animal Genetics*, 39(1), 62–70. <http://dx.doi.org/10.1111/j.1365-2052.2007.01681.x>.