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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

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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.

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

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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 catarthicus*, *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)* 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 °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° standard observer. Determinations were done in raw meat after blooming for 1 h at 4 °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 °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 m × 0.25 mm capillary column (Restek) and helium as carrier gas. The injector and detector were kept at 260 °C and the chromatograph was set initially at a temperature of 140 °C during one minute; temperature was thereafter increased from 140 to 240 °C at 4 °C per min, and finally held constant at 240 °C for 20 min. Data were recorded using GCSolultion 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 °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), Neogen genotyping service (USA, 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:

$$Y_{ijk} = \mu + GGR_{ii} + CGR_j + e_{ijk}$$

where Y_{ijk} is the trait of interest, μ is the overall mean, GGR_i and CGR_j were the fixed effects of the ith genetic group (i = 1 to 6) and the jth contemporary group (j = 1 to 28), respectively, and e_{ijk} was the residual error associated with the ijth 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 no 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 purebreeds. 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, & Krejčovă, 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 Koohmaraie (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[2]	A[1]	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^2	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

[1] 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.
[2] 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 purebreeds 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 purebreeds were compared with British x 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 ± 0.01) than Angus and 1/2 A (0.14 ± 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[2]	A[1]	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

[1] 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.
[2] 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[2]	A[1]	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 ($P < 0.05$).
[1] 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.
[2] 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 purebreeds 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[2]	Allele	A[1]	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

[1] 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.
[2] 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[2]	Genotype	A[1]	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
	TT	0.00	0.08	0.10	0.06	0.22	0.02
MC4R	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
	GG	0.00	0.00	0.03	0.04	0.04	0.07
SCD	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
	TT	0.43	0.42	0.33	0.62	0.80	0.54
FASN	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

[1] 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.
[2] 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 ± 0.101; TT: 0.174 ± 0.090). Genotype CC was not different from the others (CC: 0.216 ± 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 ± 0.089; GG: -0.281 ± 0.135) and the homozygote AA did not differ from the others (AA: -0.024 ± 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[1]	Alleles (N° of animals)			Additive effect	Dominance effect
LEP-E	CC (23)	CT (102)	TT (129)		
18:1 n-9[2]	-0.365 ± 0.495 ab	-0.583 ± 0.235 b	0.483 ± 0.209 a	-0.847 ± 0.537 ($p = 0.1449$)	-0.642 ± 0.357 ($p = 0.1220$)
22:5 n-3	-0.136 ± 0.066 b	0.074 ± 0.031 a	-0.044 ± 0.028 b	-0.092 ± 0.072 ($p = 0.8691$)	0.165 ± 0.048 ($p = 0.0030$)
SFA	1.174 ± 0.519 a	0.222 ± 0.247 ab	-0.288 ± 0.219 b	1.462 ± 0.564 ($p = 0.0500$)	-0.221 ± 0.374 ($p = 0.6935$)
MUFA	-0.490 ± 0.500 ab	-0.462 ± 0.238 b	0.438 ± 0.211 a	-0.928 ± 0.543 ($p = 0.1110$)	-0.436 ± 0.361 ($p = 0.2854$)
LEP-P	CC (134)	CT (106)	TT (17)		
18:1 n-9	0.475 ± 0.206 a	-0.421 ± 0.232 b	-1.035 ± 0.578 b	1.511 ± 0.614 ($p = 0.0593$)	-0.141 ± 0.384 ($p = 0.7134$)
20:5 n-3	-0.023 ± 0.024 b	0.013 ± 0.027 ab	0.145 ± 0.067 a	-0.174 ± 0.072 ($p = 0.0780$)	-0.045 ± 0.045 ($p = 0.5318$)
MUFA	0.542 ± 0.206 a	-0.496 ± 0.232 b	-1.019 ± 0.579 b	1.561 ± 0.615 ($p = 0.0585$)	-0.259 ± 0.385 ($p = 0.5025$)
FASN	AA (63)	AG (131)	GG(57)		
14:0	0.145 ± 0.069 a	0.024 ± 0.048 ab	-0.179 ± 0.072 b	0.324 ± 0.100 ($p = 00.065$)	0.041 ± 0.069 ($p = 0.9189$)
16:0	0.384 ± 0.207 a	0.089 ± 0.143 a	-0.596 ± 0.217 b	0.980 ± 0.300 ($p = 0.0060$)	0.194 ± 0.208 ($p = 0.7956$)
16:1	0.110 ± 0.089 a	0.073 ± 0.062 a	-0.282 ± 0.093 b	0.392 ± 0.129 ($p = 0.0130$)	0.160 ± 0.089 ($p = 0.1860$)
18:1 n-9	-0.818 ± 0.303 b	0.235 ± 0.210 a	0.181 ± 0.318 ab	-0.999 ± 0.439 ($p = 0.0593$)	0.553 ± 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.
[1] LEP-E: Leptin in exon; LEP-P: leptin in promoter; FASN: fatty acid synthase.
[2] 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 ± 0.051; CG: 0.159 ± 0.088), 22:6 n-6 (CC: −0.005 ± 0.005; CG: 0.019 ± 0.009) and AGPI (CC: −0.214 ± 0.199; CG: 0.653 ± 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 (Matsuhashi 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.

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