**ABSTRACT**

*Bos indicus* (*n* = 67) and crossbred *Bos taurus × Bos indicus* (*n* = 67) bulls were finished in extensive or intensive conditions to evaluate the effect of genetic differences and finishing system on the fatty acid (FA) composition of intramuscular fat. Finishing system had a more pronounced effect on FA profiles than the genetic group, but the two factors often interacted for both individual and groups of FA. When compared with animals finished intensively, those finished on pasture produced meat with higher concentration of CLA and polyunsaturated n-3 FA, in particular of 18:3, 20:5 and 22:5. Meat from animals finished intensively had higher amounts of 14:0, 16:0, 18:1 *trans*-10, 18:1 *trans*-11, monounsaturated *trans* FA and 18:2. When the two genetic groups were compared under intensive finishing, *B. indicus* animals showed lower amounts of 20:4 (synthesised from 18:2) and 20:5 (synthesised from 18:3), suggesting that they may have a lower ability in biochemical pathways involved in the metabolism of n-6 and n-3 long chain fatty acids. Overall, meat from animals finished on pasture had a higher amount of the FA considered desirable for human health.

**Introduction**

The consumption of red meat originating from ruminants has often been considered to be associated with cardiovascular disease in humans, and it is believed that this is mostly a consequence of the high content of saturated fatty acids (SFA) and low content of polyunsaturated fatty acids (PUFA) in intramuscular fat (IMF), particularly when compared with monogastric animals (Wood et al. 2008; Scollan et al. 2014). However, factors such as diet and genotype have a well-known effect on the amount of IMF and its fatty acid profile (Pitchford et al. 2002; Gruffat et al. 2013). On the contrary, some fatty acids (FA) have a beneficial role in human health, including n-3 PUFA, which reduce the incidence of heart diseases, and some specific isomers of conjugated linoleic acid (CLA), which have an inhibitor role in the development of atherosclerosis and cancer (Gebauer et al. 2011). The WHO (2003) recommends that total fat, saturated fatty acids (SFA), n – 6 polyunsaturated fatty acids (PUFA), n – 3 PUFA and *trans* fatty acids should contribute <15–30, <10, <5–8, <1–2 and <1% of total energy intake, respectively.

In general, meat from beef cattle finished on pasture has a more desirable fatty acid profile than when finishing is with grain (French et al. 2000; Alfaia et al. 2009; Daley et al. 2010; Rossato et al. 2010; Bressan et al. 2011; Rosa et al. 2014). On the other hand, genetic effects play an important role in fatty acid profiles of ruminant tissues and products (Pitchford et al. 2002; De Smet et al. 2004), e.g. by influencing the activity of enzymes involved in lipid metabolism, including elongase, Δ⁹ desaturase and Δ⁶, Δ⁵ and Δ⁴ desaturase (Oosterveer et al. 2009; Gama et al. 2013; Gruffat et al. 2013). Also, cattle breeds with lower levels of IMF are expected to produce meat with a higher amount of PUFA, given the negative association of these two variables (De Smet et al. 2004).

Cattle in the Americas was originally brought from the Iberian Peninsula by Portuguese and Spanish
discoverers in the transition of the fifteenth to the sixteenth centuries, originating locally adapted populations commonly known as Creole (Delgado et al. 2012). Nevertheless, in many regions in the American continent where tropical climate prevails, the good adaptation of B. indicus allowed its expansion through vast areas, either as purebred or in crosses with B. taurus (Ferraz & Felicio 2010; Lobato et al. 2014). However, a decline in meat quality, especially meat tenderness, when B. indicus are compared with B. taurus has been widely documented (Wheller et al. 2001), and B. indicus also tends to have a slower growth rate than B. taurus (Ferraz & Felicio 2010). Still, results regarding genetic differences in lipid profiles between zebuine and taurine cattle are scarcer, but there are indications that fatty acid profiles differ between B. taurus and B. indicus (Huerta-Leidenz et al. 1996). However, these differences are largely dependent on the finishing system used, such that, with grain finishing, meat from B. indicus has higher levels of SFA, but that is not the case with pasture finishing (Bressan et al. 2011). Nevertheless, the results until now do not provide conclusive evidence regarding the benefits for FA profiles of using crossbred B. taurus × B. indicus animals comparatively with straightbred B. indicus, and if the possible effects of crossbreeding depend on the finishing system used. Moreover, different ingredients used for finishing ruminants, such as various agricultural by-products, may determine differences in FA profiles of IMF. Therefore, the objectives of this work were to assess differences in FA profiles between B. indicus and F1 B. taurus × B. indicus bulls, and investigate how finishing animals on pasture or with concentrate affects these differences.

Materials and methods

Animals and treatments

An experiment was carried in the state of Mato Grosso, Central Brazil, with 134 intact males representing the B. indicus (n = 67) and F1 B. taurus × B. indicus (n = 67) genetic groups. The experimental animals were produced in a commercial herd by a group of Nelore cows, which were randomly assigned to be inseminated either with Nelore semen to produce purebred B. indicus or with Simmental semen to produce F1 B. taurus × B. indicus. The Nelore and the Simmental semen were from animals born in Brazil and supplied by local companies. The calves born were weaned at 8 months of age and, from these, a group of 134 males (of which half were indicus and half were F1) were selected to be raised on pasture until the age of about 20 months. At this time, the experimental bulls were randomly assigned within the genetic group to be finished either remaining on the same pasture for an additional period of 225 d (n = 40, of which 22 were indicus and 18 were F1) or with a total mixed ration for a period of 90 d (n = 94, of which 45 were indicus and 49 were F1). As the experiment was carried out in a commercial farm where the majority of the animals are usually finished on grain, the experimental use of pasture finishing required some adjustments, and the number of pasture-finished animals was what was feasible with the available pasture resources. The pasture was rainfed cultivated Brachiaria brizantha cv. marandu, which has a height above 1 m and a yield ranging from about 8 to 20 tons of DM/ha/year. Animals were distributed in fenced parks with natural shade at a stocking rate of 0.8 bulls/ha, and had permanent access to fresh water. The animals finished intensively received a total mixed ration formulated according to National Research Council (2000), and two different diets were distributed over the finishing period, with the composition shown in Table 1. Initially, animals received a starter diet for a period of 15 d of adaptation to concentrate, followed by a trial period of 45 d with the same diet. At this point, they were switched to a finishing diet and remained on this diet for an additional 45 d. The total mixed ration was distributed two times daily with a mixer feeder and, depending on the period considered, animals received an average of 10.5–13.6 kg of dry matter daily. The intake was maintained by adjusting the offered amounts of feed on a weekly basis, depending on the amount of feed refused during the previous week. The feed amounts were adjusted so that the amount refused corresponded to 7–8% of the offered feed.

The proportion represented by different feedstuffs differed somewhat between the starter and finishing diets, but in both of them, the whole cottonseed represented nearly 11% (Table 1). The FA composition of the finishing diet was determined, and the results are summarised for the major FA and groups of FA in Table 1. The chemical composition and FA profiles of Brachiaria brizantha cv. Marandu, which were reported by Oliveira et al. (2014) in a different study, are also included in Table 1 for completeness.

Slaughter and sample collection

Pre-slaughter, slaughter and inspection management of the animals from which meat samples were obtained was performed according to the current standards for animal welfare and inspection in Brazil (Ministério da Agricultura, Pecuária e Abastecimento
Experimental animals were considered to be ready for slaughter when their body condition score, visually assessed by experienced judges, indicated a minimum fat cover of 3 mm between the 6th and 12th ribs. As the group finished on grain had a faster growth rate, animals reached the target finishing point nearly 3 months before the pasture-finished group. When the majority of the animals in a finishing group reached the end-point, the whole group in that finishing system was sent for slaughter in a commercial abattoir certified for meat export. Therefore, all the animals in a given finishing system were slaughtered on the same day. After a period of 12 h of resting and fasting of solid feed, animals were slaughtered, and carcasses were submitted to electrical stimulation before evisceration, and the half carcasses were then refrigerated to a temperature of 2.1°C ± 0.1°C. The mean carcass weight for the whole group of 134 animals in the study was 293.3 ± 30.2 kg.

At 48 h post mortem, a sample of the M. longissimus thoracis was collected between the 11th and the 13th rib of the left carcass for analyses of cholesterol and fatty acids. Samples were individually packaged, fast frozen and stored at −20°C until further analyses.

For lipid extraction, samples were thawed at 4°C for 24 h, and trimmed of subcutaneous fat and connective tissue on the surface. Meat samples were then minced in a commercial mixer-blender until a homogeneous mass was obtained.

### Fat extraction and cholesterol determination

For the analysis of cholesterol and FA, lipids were extracted as described by Folch et al. (1957), and then esterified and separated according to the procedures described by Hartman and Lago (1973). Cholesterol was quantified by colorimetry, according to Bohac et al. (1988), and the results were expressed in mg/100 g of meat.

### Lipid profile

The preparation of fatty acid methyl esters was carried out according to Raes et al. (2001), using NaOH/MeOH and HCl/MeOH. The FA methyl esters were submitted to Gas Liquid Chromatography on an Agilent HP 6890 chromatograph (Agilent Technologies Inc., Palo Alto, CA) equipped with a flame ionisation detector, using a

| Supplement | Ingredient/composition | Starter diet | Finishing diet | Brachiaria |
|------------|------------------------|--------------|---------------|------------|
| Formulation, % of raw matter | | | | |
| Sorghum grain | 39.27 | 30.61 | | |
| Soybean hulls | 22.33 | 34.71 | | |
| Sorghum silage | 19.00 | 14.91 | | |
| Whole Cottonseed | 11.00 | 11.24 | | |
| Soybean residues | 5.83 | 5.92 | | |
| Minerals and vitamins | 2.57 | 2.61 | | |
| Chemical composition | | | | |
| Dry matter, % | 78.61 | 81.17 | 67.93 | |
| Crude protein, % | 11.29 | 12.07 | 6.09 | |
| Digestible energy, Mcal/kg DM | 2.65 | 2.74 | 2.20 | |
| Fatty acid profile, % | | | | |
| 14:0 | 2.90 | 1.13 | | |
| 16:0 | 26.01 | 18.92 | | |
| 18:0 | 13.13 | 5.81 | | |
| 18:1 cis-9 | 28.20 | 16.79 | | |
| 18:2 n-6 | 14.85 | 34.63 | | |
| 18:3 n-3 | 0.17 | 9.55 | | |
| Saturated FA | 46.83 | 25.85 | | |
| Monounsaturated FA | 35.35 | 21.03 | | |
| Polyunsaturated FA | 17.82 | 53.13 | | |
| Polyunsaturated FA n-6 | 17.11 | 37.71 | | |
| Polyunsaturated FA n-3 | 0.71 | 15.42 | | |

*aDiet used for 15 d of adaptation plus 45 d of growth.
*bDiet used for 45 d of finishing.
*cChemical composition and fatty acid profile of Brachiaria, adapted from Oliveira et al. (2014).
*dResidues of pre-cleaning soybeans.
*eMinerals and vitamins: Ca: 235 g; P: 45 g; S: 23 g; Na: 80.18 g; Zn: 2.38 mg; Cu: 625 mg; Fe: 1.18 mg; Mn: 312 mg; Co: 2 mg; I: 41.6 mg; Se: 11.25 mg; Vit. A: 70,000 U; Vit. D3: 5000 U; Vit. E: 15 U; and Niacin: 3.33 mg.
split injector ratio of 1:10 and a 100 m capillary column (CP-Sil 88, 100 m × 0.25 mm i.d. × 0.20 µm film thickness; Varian Inc., Walnut Creek, CA). The temperature and other chromatograph settings were as follows: initial column temperature of 100 °C for 1 min, increase to 150 °C in 1 min and maintenance for 20 min; increase by 1 °C per minute up to 190 °C and maintenance for 5 min; increase by 1 °C per minute up to 200 °C and maintenance for 35 min. The temperature was kept at 250 °C for the injector and 280 °C for the detector. Helium was the carrier gas, at a constant pressure of 32.78 psi. Identification of FAMEs after GLC analysis was accomplished by comparing sample peak retention times with those of FAME standard mixtures. The trans-6, trans-7 and trans-8 18:1 isomers coeluted in one peak and are hereafter named 18:1 trans-6,-7,-8. The chromatographic resolution of the trans 18:2 isomers was not complete, and are thus considered as 18:2 isomers. Individual FA were expressed as a percentage of total identified FA.

Indices of fatty acids and estimated activity of enzymes involved in lipid metabolism

The totals for SFA, monounsaturated FA (MUFA), MUFA cis-9, MUFA trans, PUFA, PUFA n-3 and PUFA n-6 were calculated from the sum of individual fatty acids, as outlined in Table 2. The estimated enzymatic activity of Δ⁹ desaturase and elongase were calculated as outlined by Pitchford et al. (2002) and the combined effect of desaturase/elongase on the n-6 and n-3 metabolic pathways was estimated from different ratios of FA, as shown in Table 2.

Statistical analysis

Data were considered to have originated from a 2 × 2 factorial, with two genetic groups (B. indicus and F1 B. taurus × B. indicus) and two finishing systems (pasture and grain). The animal was considered the sampling unit in all analyses. The GLM procedure of SAS (version 9.3, SAS Institute Inc., Cary, NC) was used in analyses of variance of the various response variables, with a linear model including the effects of the genetic group, finishing system and their interaction. To account for the possible effect of IMF on FA profiles, a second set of analyses was performed, adding to the statistical model the linear effect of IMF.

Results

The levels of significance of the factors considered in statistical analyses and the corresponding coefficients of determination for the various traits analysed are in Table 2.

The IMF affected (p < 0.05) some of the individual SFA and PUFA, as well as the corresponding total SFA and PUFA, but no effect of IMF (p > 0.05) was detected on the computed indices of FA, except for the P/S ratio and the joint activity of desaturase and elongase n-6 (p < 0.05, Table 2). Notwithstanding, the general pattern observed when the two models were compared was that the change in the coefficient of determination was minor when IMF was added to the model. Moreover, among the 129 factor-trait combinations analysed, only 13 combinations changed their degree of significance (p < 0.05) from one model to the other, but the changes in p values were very small in most cases. Under these circumstances, the simplest model, which did not include the linear effect of IMF, was kept throughout the statistical analyses, but in a few very particular cases, where it was deemed important, the influence of IMF was also considered in our discussion.

The results of the analyses of variance indicate that, among the 43 individual FA and indices of FA, 14 were affected (p < 0.05) by the interaction between the genetic group and the finishing system. This interaction was also significant (p < 0.05) for IMF, but not for cholesterol. For major groups of FA, the interaction of the genetic group and the finishing system influenced (p < 0.05) total SFA and PUFA, while for MUFA only the effect of genetic group was significant (p < 0.05). Of the 29 FA and indices of FA where the interaction was not significant, 11 were influenced (p < 0.05) by the genetic group and 25 by the finishing system (p < 0.05). Overall, with the only exceptions of cholesterol, 18:1 trans-6,-7,-8, 18:1 trans-12 and the ratio 22:5 n-3/18:3 n-3, all the individual FA and indices were affected (p < 0.05) by at least one of the factors considered or their interaction.

The proportion of the observed variability explained by the main factors and interaction included in the model used in analyses of variance (Table 2) was about 23% for total SFA and PUFA, but only about 4% for MUFA. For individual FA, however, the coefficient of determination tended to be somewhat higher, and exceeded 30% in 19 of the 24 individual FA considered.

The means for IMF, cholesterol and individual FA by genetic group, finishing system and their combination are given in Table 3, and for groups and ratios of FA, the means are given in Table 4. No differences were observed among genetic groups in cholesterol level, but there was some indication (p = 0.057) that cholesterol was higher in grain-finished animals, in spite of
Table 2. Descriptive statistics, significance of factors [P(F)] and coefficient of determination (R²) obtained by fitting a linear model without or with the inclusion of intramuscular fat (IMF) as a linear covariate in the analyses of variance of intramuscular fat, cholesterol, individual fatty acids (in % of total fatty acids), groups of fatty acids, nutritional indices and estimated activity of elongase and Δ⁵ desaturase in M. longissimus of B. indicus and F1 B. taurus x B. indicus, finished on grain or pasture.

| Variable | Genetic group (GG) | Finishing system (FS) | P(F) unadjusted for IMF | P(F) adjusted for IMF |
|----------|--------------------|-----------------------|------------------------|----------------------|
| IMF      | 0.246              | <0.001                | 0.022                  | 0.331                |
| Cholesterol | 0.414              | 0.057                | 0.941                 | 0.033                |
| 12:0     | 0.076              | <0.001                | 0.499                 | 0.378                |
| 16:1     | <0.001             | 0.012                | 0.337                 | <0.001               |
| 16:2     | 0.017              | 0.001                | 0.803                 | 0.143                |
| 18:0     | 0.124              | <0.001                | 0.001                 | 0.399                |
| 18:1 c-9 | <0.001             | 0.001                | 0.165                 | 0.001                |
| 18:1 c-7 | 0.395              | <0.001                | 0.011                 | 0.852                |
| 18:1 c-9 | 0.011              | 0.001                | 0.498                 | 0.358                |
| 17:1 c-9 | 0.670              | <0.001                | 0.103                 | 0.549                |
| 18:1 c-11| 0.564              | <0.001                | 0.091                 | 0.421                |
| 18:1 c-12| 0.056              | <0.001                | 0.109                 | 0.452                |
| 18:1 c-13| 0.007              | <0.001                | 0.006                 | 0.897                |
| 18:1 c-13| 0.447              | <0.001                | 0.548                 | 0.616                |
| 18:1 n-6 | 0.425              | 0.714                | 0.143                 | 0.035                |
| 18:1 n-9 | 0.554              | 0.019                | 0.564                 | 0.051                |
| 18:1 n-10| 0.189              | <0.001                | 0.242                 | 0.668                |
| 18:1 n-11| 0.600              | 0.001                | 0.235                 | 0.112                |
| 18:1 n-12| 0.436              | 0.655                | 0.591                 | 0.817                |
| 18:2 n-6 | <0.001             | 0.010                | 0.479                 | <0.001               |
| 18:2 n-9 | 0.016              | <0.001                | 0.753                 | 0.396                |
| 18:2 n-11| 0.090              | <0.001                | 0.114                 | 0.591                |
| 18:3 n-3 | 0.475              | <0.001                | 0.001                 | 0.905                |
| 20:4 n-6 | <0.001             | 0.001                | 0.041                 | 0.480                |
| 20:5 n-3 | 0.195              | <0.001                | 0.107                 | 0.670                |
| 22:5 n-3 | 0.801              | <0.001                | 0.229                 | 0.306                |
| 22:5 n-6 | <0.001             | 0.011                | 0.003                 | 0.282                |
| 22:5 n-3 | 0.883              | <0.001                | 0.217                 | 0.628                |
| 22:6 n-3 | 0.059              | <0.001                | 0.186                 | 0.748                |
| P/S      | 0.012              | <0.001                | 0.003                 | 0.247                |
| Elongase 16-18 | 0.029            | 0.863                | 0.002                 | 0.162                |
| Elongase 13-16 | 0.031            | 0.001                | 0.122                 | 0.157                |
| Δ⁵ desaturase general | 0.323          | 0.322                | 0.231                 | 0.548                |
| Δ⁵ desaturase 14° | 0.004          | 0.001                | 0.229                 | 0.265                |
| Δ⁵ desaturase 16° | 0.001          | 0.001                | 0.444                 | 0.476                |
| Δ⁵ desaturase 18° | 0.567          | 0.001                | 0.041                 | 0.493                |
| Δ⁵ desaturase CLA/t-11 | 0.009         | 0.001                | 0.117                 | 0.292                |
| Desaturation rate | 0.073        | <0.001                | 0.001                 | 0.116                |
| Desaturation rate | 0.125        | 0.001                | 0.028                 | 0.150                |
| Desaturation rate | 0.512        | 0.001                | 0.086                 | 0.092                |

Notes:
- Total percentage of r-6, r-7, and t-8 18:1 isomers.
- Sum of isomers of 18:2 (unidentified).
- SFA = (12:0 + 14:0 + 16:0 + 18:0).
- MUFA = (14:1c-9 + 16:1c-7 + 16:1c-9 + 17:1c-9 + 18:1c-7 + 18:1c-9 + 18:1c-10 + 18:1c-11 + 18:1c-12 + 18:1c-13).
- MUFA c-9 = (14:1c-9 + 16:1c-9 + 17:1c-9 + 18:1c-9).
- MUFA c-9 = (18:1c-7 + 18:1c-9 + 18:1c-10 + 18:1c-11 + 18:1c-12 + 18:1c-13).
- PUFAs = (18:2 n-6 + 20:4 n-6 + 18:3 n-3 + 20:5 n-3 + 22:5 n-3).
- SFAs = (18:2 n-6 + 18:4 n-6 + 18:5 n-3 + 20:4 n-6 + 20:6 n-3 + 20:6 n-3).
- S/P = PUFAs/SFAs.

This information is derived from the text and represents the extracted data as structured tables and formatted for clear readability.
the large variability observed among animals in the same treatment, as reflected by the residual standard deviation. Overall, even though there was a significant interaction between finishing system and genetic group for IMF, the means were consistently higher for animals finished intensively. The total amount of SFA essentially reflected the pattern mentioned above for individual SFA, such that the interaction between genetic group and finishing system was significant (p < 0.05), with minor differences among genetic groups on pasture (p > 0.05) and a total amount of SFA in grain-finished animals higher by about 1.9% in B. indicus relative to F1 crosses (p < 0.05). For 16:0, the interaction was not significant, but the main effects were important (p < 0.05), with higher levels in animals finished intensively and in B. indicus.

Among the MUFA, the interaction between the finishing system and the genetic group was significant for 16:1 cis-7 and 18:1 cis-12, such that higher means were observed for 16:1 cis-7 in pasture-finished animals, especially in F1 bulls (p < 0.05), while for the 18:1 cis-12, the means were higher in grain-finished animals, particularly in F1 bulls. For the other MUFA, the effect of genetic group was less pronounced than for the finishing system, and only significant in 14:1 cis-9 and 16:1 cis-9, which were higher in B. indicus (p < 0.05).

On the other hand, several MUFA were affected by the finishing system (p < 0.05), with grain-finished animals showing higher means for 18:1 cis-11, 18:1 cis-13, 18:1 trans-6,-7,-8, 18:1 trans-9, 18:1 trans-10 and 18:1 trans-11, and lower means for 16:1 cis-9, 17:1 cis-9 and 18:1 cis-9. Overall, the total MUFA were not affected by the finishing system but were higher (p < 0.05) by about 0.85% in B. indicus when compared with F1 bulls. When MUFA cis-9 and trans were considered

### Table 3. Least-squares means and residual standard deviation (RSD) for intramuscular fat (IMF), cholesterol and individual fatty acids (% of total fatty acids), in M. longissimus of B. indicus and F1 B. taurus × B. indicus, finished on grain or pasture.

| Variable                  | Genetic group | Finishing system                      | Grain finishing | Pasture finishing | RSD |
|---------------------------|---------------|---------------------------------------|-----------------|-------------------|-----|
|                           | B. indicus    | F1                                    | Grain (n=67)    | Pasture (n=67)    |     |
| IMF, %                    | 1.96          | 1.81                                  | 2.32            | 1.46              |     |
| Cholesterol, mg/100 g     | 38.28         | 36.30                                 | 39.61           | 34.97             |     |
| 12:0                      | 0.14          | 0.12                                  | 0.09            | 0.18              |     |
| 14:0                      | 3.11          | 2.72                                  | 3.14            | 2.69              |     |
| 16:0                      | 24.28         | 24.86                                 | 25.00           | 24.14             |     |
| 18:0                      | 18.27         | 17.75                                 | 19.34           | 16.68             |     |
| 18:1                      | 0.49          | 0.38                                  | 0.41            | 0.46              |     |
| 18:2                      | 0.26          | 0.27                                  | 0.16            | 0.38              |     |
| 18:3 n-3                  | 0.50          | 0.45                                  | 0.27            | 0.27              |     |
| 18:4                      | 0.60          | 0.60                                  | 0.50            | 0.70              |     |
| 18:5                       | 0.35          | 0.38                                 | 0.35           | 0.46              |     |
| 18:6                       | 0.23          | 0.24                                  | 0.24            | 0.23              |     |
| 18:7                       | 0.14          | 0.19                                  | 0.18            | 0.17              |     |
| 18:8                       | 0.02          | 0.22                                  | 0.25            | 0.17              |     |
| 18:9                       | 0.79          | 0.90                                  | 1.55            | 0.14              |     |
| 19:0                       | 1.61          | 1.67                                  | 1.86            | 1.43              |     |
| 19:1                       | 0.23          | 0.24                                  | 0.24            | 0.23              |     |
| 19:2                       | 4.68          | 6.01                                  | 6.52            | 4.17              |     |
| 19:3                       | 0.29          | 0.26                                 | 0.21          | 0.33              |     |
| 19:4                       | 0.85          | 0.88                                  | 0.48            | 1.25              |     |
| 19:5                       | 0.50          | 0.45                                  | 0.27            | 0.68              |     |
| 20:4                       | 1.01          | 1.36                                  | 0.81            | 1.56              |     |
| 20:5                       | 0.35          | 0.38                                  | 0.15            | 0.58              |     |
| 22:5                       | 0.82          | 0.79                                  | 0.38            | 1.24              |     |

Means for combinations of genetic group and finishing system with different superscripts differ (p < 0.05), and no test of significance was performed for main effects. Means for genetic groups or finishing systems with different superscript differ (p < 0.05), and the interaction of genetic group and finishing system is not significant (p > 0.05).

*Total percentage of t-6, t-7 and t-8 18:1 isomers.

*Sum of isomers of 18:2 (unidentified).
Table 4. Least-squares means and residual standard deviation (RSD) for groups of fatty acids, nutritional indices, and estimated activity of elongase and Δ⁹ desaturase in *M. longissimus* of *B. indicus* and F1 *B. taurus* × *B. indicus*, finished on grain or pasture. Means for combinations of the genetic group and the finishing system with different superscripts differ (*p < 0.05*), and no test of significance was performed for main effects.

| Variable* | Genetic group | Finishing system | Grain finishing | Pasture finishing |
|-----------|---------------|------------------|----------------|-----------------|
|           | *B. indicus*  | F1               | *B. indicus*  | F1              |
|           | (n = 67)      | (n = 67)         | (n = 45)      | (n = 49)        |
|           | (n = 40)      |                  | (n = 22)      | (n = 18)        |
| SFA       |               |                  |               |                 |
|           | 48.76         | 48.16            | 49.63         | 47.29           |
| MUFA      | 41.62         | 40.77            | 41.30         | 41.10           |
| MUFA cis-9| 34.22         | 33.65            | 31.21        | 36.67           |
| MUFA t    | 3.24          | 3.45             | 4.32         | 2.37            |
| PUFAs     | 10.99         | 10.69            | 9.07         | 10.82           |
| PUFAs n-6| 6.32          | 7.87             | 7.59         | 6.61            |
| PUFAs n-3| 2.20          | 2.23             | 1.00         | 3.43            |
| n-6/n-3   | 4.57          | 5.13             | 7.69         | 2.01            |
| P/S       | 0.19          | 0.22             | 0.18         | 0.23            |
| Elongase 16:18| 70.92 | 69.40            | 70.10         | 70.22           |
| Elongase n-3| 2.67         | 2.25             | 2.80         | 1.21            |
| Δ⁹ desaturase general | 0.73 | 0.71            | 0.63         | 0.81            |
| Δ⁹ desaturase 14 | 13.56       | 12.12           | 11.40        | 14.28           |
| Δ⁹ desaturase 16 | 10.30       | 9.52            | 8.87         | 10.95           |
| Δ⁹ desaturase 18 | 62.36       | 62.74           | 58.97        | 66.13           |
| Δ⁹ desaturase CLA/trans-11 | 0.19    | 0.16             | 0.12         | 0.24            |
| 20:4 n-6/18:2 n-6 | 0.24     | 0.26             | 0.12         | 0.37            |
| 20:5 n-3/18:3 n-3 | 0.36      | 0.43             | 0.31         | 0.48            |
| 22:5 n-3/18:3 n-3 | 0.86      | 0.93             | 0.80         | 0.99            |

Means for genetic groups or finishing systems with different superscripts differ (*p < 0.05*), and the interaction of the genetic group and the finishing system is not significant (*p > 0.05*).

*See Table 2 for definition of abbreviations.*

separately, the first was higher (*p < 0.05*) in pasture-finished animals by about 5.5%, while the latter was slightly higher in grain finishing (*p < 0.05*), but no differences were detected among genetic groups.

The major PUFA was 18:2 n-6, which was affected by the interaction between the finishing system and the genetic group, such that the two genetic groups did not differ from each other in pasture finishing (*p > 0.05*), but had a lower mean than in grain finishing (*p < 0.05*), and, in this system, the F1 bulls had a concentration about 2% higher than *B. indicus* (*p < 0.05*). The 20:4 n-6 was also affected by the interaction among main effects, with higher means in pasture-fishing animals (*p < 0.05*), where it was similar for the two genetic groups (*p > 0.05*), while in grain finishing, the mean was higher for F1 bulls. No interaction was detected for the remaining PUFA (*p > 0.05*), but the finishing system had a significant effect on all of them, with means which were consistently higher in pasture finishing. Among these PUFA, 18:2 cis-9, trans-11 was the only one which differed among genetic groups (*p < 0.05*), with a higher mean in *B. indicus*. Total PUFA was similar for the various genetic group × finishing system combinations, with the exception of grain-finished *B. indicus*, which had a mean PUFA nearly 3% lower than the level found in the other groups (*p < 0.05*). When n-6 PUFA were considered separately, the interaction was again significant, with similar means for the various combinations of the genetic group × finishing system, except for grain-finished F1 bulls, which had a mean about 2% higher than for the other groups (*p < 0.05*). For n-3 PUFA and for the ratio n-6/n-3, no interaction was detected and the results were similar for the two genetic groups (*p > 0.05*), but the effect of finishing system was important, with higher amounts of n-3 PUFA and lower n-6/n-3 ratio in pasture-finished animals (*p < 0.05*). The P/S ratio was affected by the interaction between the genetic group and the finishing system, with a significantly lower ratio in *B. indicus* finished on grain (*p < 0.05*), but the means were similar for the remaining combinations.

The estimated elongase activity depended on the genetic group × finishing system combination, such that the two genetic groups did not differ (*p > 0.05*) when finished on pasture, but when finishing was on grain, the *B. indicus* had the highest elongase activity (*p < 0.05*) in all combinations. On the other hand, F1 bulls finished on grain had decreased elongase activity (*p < 0.05*) when compared with those on pasture. When the n-3 elongase activity was assessed, no interaction was observed, and the highest mean values were observed in *B. indicus* finished with grain. The activity of Δ⁹ desaturase, when evaluated
either in general or for 14, 16, 18 or CLA FA, was consistently lower with grain finishing \((p < 0.05)\). Differences among genetic groups were also observed, with higher activity of \(\Delta^9\) desaturase in \(B. indicus\) for 14, 16 and CLA FA, while for 18 FA, an interaction was observed, such that F1 bulls had higher activity of \(\Delta^9\) desaturase in grain finishing \((p < 0.05)\), but the two genetic groups were similar \((p > 0.05)\) when finishing was on pasture. The joint desaturase and elongase activity for n-6, assessed by the ratio of 20:4 n-6 relative to its precursors, was only affected by the finishing system, with higher values in pasture-finished animals \((p < 0.05)\). For the joint desaturase and elongase activity for n-3, no significant effects were detected when the assessment was made by 22:5 n-3 \((p > 0.05)\), but for 20:5 n-3, there was a significant interaction, with the lowest mean observed for \(B. indicus\) finished on grain \((p < 0.05)\), while all the other groups had similar mean values.

**Discussion**

The FA profile of meat is one of the key components of meat quality, because of its implications for human health (Wood et al. 2008). The impact of finishing system and breed on FA profiles of cattle meat has been investigated by various authors (French et al. 2000; Garcia et al. 2008; Gatellier et al. 2005; Rossato et al. 2010), and there are indications that important interactions exist between the two factors (Nuernberg et al. 2005), such that \(B. indicus\) cattle tend to accumulate higher amounts of SFA than \(B. taurus\), especially when they are finished intensively (Bressan et al. 2011). On the other hand, heterosis for FA profiles has been shown to exist in crosses between \(B. taurus\) and \(B. indicus\), but it also depends on the finishing system considered (Gama et al. 2013). These results indicate that dealing with genotype x environment interactions for FA profiles is an important but unresolved issue.

In many tropical regions, beef production is largely based on \(B. indicus\) cattle and their crosses, given their superior adaptation to tropical conditions (Hansen 2004). For example, in Brazil, which is among the leading beef producers and exporters in the world (Lobato et al. 2014), \(B. indicus\) and their crosses represent nearly 80% of the cattle population (Ferraz & Felicio 2010). However, given the less desirable FA profile of \(B. indicus\) and their lower meat tenderness (Wheller et al. 2001), crossbreeding with \(B. taurus\) would be a possible way to improve meat quality, including FA profile, without losing the adaptation characteristics of \(B. indicus\).

In our study, the most prominent feature is the impact of the finishing system on IMF and FA profile, as would be anticipated (French et al. 2000), but differences among genetic groups were important. The higher amount of IMF reported here for grain-finished animals would be expected, given the increased availability of energy in the diet. On the other hand, an increased deposition of IMF in \(B. indicus\) was also detected, which could be due to their lower energy requirements for maintenance, estimated to be about 20% below those of \(B. taurus\) (Commonwealth Scientific and Industrial Research Organisation 2007).

The total amount of SFA was highest in \(B. indicus\) finished on grain and lowest in pasture-finished \(B. indicus\) and F1 bulls, a result which is in line with that reported by Bressan et al. (2011) for purebred \(B. indicus\) and \(B. taurus\). Other authors, however, have reported less consistent results when the amount of SFA was compared among different feeding systems in cattle, as reviewed by Daley et al. (2010). The increased amount of SFA in grain-finished animals in our study, especially of the \(B. indicus\) type, was mostly due to an increased amount of 18:0, 16:0 and 14:0. While higher levels of 16:0 and 14:0 are commonly detected in grain-finished animals (Daley et al. 2010), the higher amount of 18:0 reported here for this type of animals was somewhat unexpected, as this FA usually has a higher concentration in pasture-finished animals (Raes et al. 2004; Nuernberg et al. 2005; Alfaia et al. 2009).

In ruminants, the amount of 18:0 in IMF results from the supply of exogenous 18:0 derived mostly from the complete biohydrogenation of C18 unsaturated FA in the rumen, and the endogenous 18:0 obtained by elongation of 16:0 formed by de novo biosynthesis, as well as the degree of 18:0 desaturation into 18:1c9 by \(\Delta^9\) desaturase (Oosterveer et al. 2009). In our study, the estimated activity of \(\Delta^9\) desaturase and the amount of 18:1 cis-9 were lower in grain-finished animals, indicative of a lesser ability for desaturation of 18:0 in this group of animals. This may be due to diet-related factors, because the group of animals finished intensively had cottonseed as part of their diet, an ingredient that normally contains cyclopropene FA, which are described to have an inhibitory role on the activity of \(\Delta^9\) desaturase (Corl et al. 2001; Gomez et al. 2003).

The higher amount of 18:0 in \(B. indicus\) finished on grain could also be a consequence of an increased ability for elongation of 16:0, as indicated by the higher estimated activity of elongase in this group of animals and by the lower amount of 16:0 in \(B. indicus\) when compared with F1 cattle. On the other hand, when the activity of \(\Delta^9\) desaturase is assessed by the
relationship of 18:0 and 18:1 cis-9 in grain-finished animals, the *B. indicus* show a lower desaturation activity than F1 bulls, further contributing to the accumulation of 18:0 in the IMF of grain-finished *B. indicus* bulls. Taken together, our results indicate that, especially under grain-finishing, *B. indicus* cattle accumulate higher amounts of 18:0 than F1 bulls, a pattern which is in agreement with the results reported by Bressan et al. (2011), who compared *B. taurus* and *B. indicus*.

In general, the amount of PUFA is expected to be higher in pasture-finished animals (French et al. 2000; Daley et al. 2010; Scollan et al. 2014), but the response seems to be breed dependent (Bressan et al. 2011). However, individual PUFA respond differently to the finishing system, such that 18.2 n-6 tends to be higher in grain-finished animals, while 18:3 n-3 increases with pasture-finishing (Nuernberg et al. 2005), as was also observed in our study, and total PUFA should reflect the relative importance of these components. Our results indicate that the total amount of PUFA was similar in *B. indicus* on pasture and in F1 bulls in both finishing systems, but significantly lower in *B. indicus* finished on grain. The higher than expected amount of PUFA found in grain-finished animals in our study, particularly in F1, is a consequence of the increased amounts of 18:2 n-6 in grain finishing. However, this is in contrast with previous comparisons, where PUFA tends to be higher in pasture finishing (Nuernberg et al. 2005), and could result from a grain supplement inducing higher levels of PUFA in our study, but also reflect differences in rumen microbial ecosystem, resulting either from changes induced by diet components such as cottonseed (Gomez et al. 2003) or from differences in ruminal physiology between *B. indicus* and *B. taurus* (Menezes et al. 2007).

It could also be argued that differences among groups in PUFA may essentially reflect differences in IMF, but this was not fully supported by our results. Indeed, the interaction among finishing system and genetic group, which had $P(F) = 0.006$ in the unadjusted model, approached significance [$P(F) = 0.072$] in the model including IMF, but the means for the various treatment combinations ranked essentially in the same way as for the unadjusted model, i.e. *B. indicus* on pasture still had the lowest amount of PUFA after adjusting for IMF (results not shown).

The results obtained for 18:3 n-3 and 18:2 n-6 confirm that higher amounts of n-3 are found in pasture-finished animals, while the level of n-6 FA is increased under grain-finishing (French et al. 2000; Nuernberg et al. 2005), and this is reflected in the n-6/n-3 ratio. This occurs because forages and grain have high levels of 18:3 n-3 and 18:2 n-6, respectively, and even though the majority of these FA are biohydrogenated in the rumen, the differences in diet composition are still expressed in the FA profile of meat.

In our study, the 20:4 n-6 was higher in pasture finishing and in F1 bulls, which could again be a consequence of the lower IMF levels in these groups. Still, the differences among means were essentially maintained when the statistical model included the adjustment for IMF (results not shown). Moreover, the lower amount of 20:4 n-6 synthesised from 18:2 n-6 and of 20:5 n-3 synthesised from 18:3 n-3 observed in *B. indicus* under grain-finishing comparatively with F1 (and confirmed by differences among genetic groups in the product-substrate ratio of 20:5 n-3/18:3 n-3) suggests a limited capacity of *B. indicus* in synthesising n-3 and n-6 long-chain PUFA. These results could be a consequence of genetic differences in the expression of genes regulating the activity of enzymes involved in FA metabolism, especially those involved in the synthesis of long-chain PUFA, as recently described by Gruffat et al. (2013), who have also shown that the composition of the diet may also affect the expression of those same genes.

Large differences due to finishing system were observed in FA involved in the biohydrogenation pathways, either as substrate (18:2 n-6, 18:3 n-3 and 18:1 cis-9), product (18:0) or intermediary FA (18:1 trans-11 and 18:2 cis-9, trans-11). Generally, the 18.2 cis-9, trans-11 represents about 60–90% of the CLA isomers present in the IMF of ruminants (Alfaia et al. 2009) and results mostly from endogenous synthesis where rumen-derived 18:1 trans-11 is converted into 18:2 cis-9, trans-11 by the action of $\Delta^9$ desaturase in the muscle tissue (Corl et al. 2001). Both 18.2 cis-9, trans-11 and 18:1 trans-11 have received attention in recent years because of their potential benefits for human health (Gebauer et al. 2011), thus increasing their amount in ruminant meat is desirable. Ruminants fed with high forage/pasture in the diets generally have higher proportion of 18:2 cis-9, trans-11 in their lipids, and supplementing forage-based diets (but not concentrate-based diets) with unsaturated fat sources clearly increases the level of CLA in meat (Bessa et al. 2005). However, finishing beef cattle on pasture can result in very low IMF content, which would limit the absolute amount of CLA (mg/100 g fresh meat). Indeed, pasture-finished animals in our work presented a proportion of 18.2 cis-9, trans-11 which was about 50% higher than in grain-finished animals. Nevertheless, when expressed relative to muscle weight, the concentrations of 18.2 cis-9, trans-11 were similar for both feeding regimes (4.1 and 4.2 mg/100 g.
fresh meat, respectively, for grain- and pasture-fed animals) given the differences in IMF. Surprisingly, the 18:1 trans-11 was higher in grain-finished than in pasture-finished animals. In general, the 18:1 trans-11 is highly correlated with 18:2 cis-9, trans-11 (Bessa et al. 2000), thus the presence of higher proportions of 18:1 trans-11 coupled with lower 18:2 cis-9, trans-11 in grain-finished animals, compared with those finished on pasture, is consistent with the general pattern that suggests an inhibition of Δ9 desaturase by the presence of cyclopropene FA, resulting from the inclusion of whole cottonseed in the diet.

Differences between the two finishing systems were also observed for 18:1 trans-10, which indicates the increasing importance of biohydrogenation pathways shifted towards trans-10 in grain-finished animals. It has been shown that 18:1 trans-10 is produced in an alternate biohydrogenation route when high-concentrate diets are used (Bessa et al. 2005) and our data are fully consistent with this. The occurrence of elevated 18:1 trans-10 concentrations in meat is characteristic of intensive finishing systems for beef cattle and the putative negative health effects of 18:1 trans-10-enriched meats are currently under discussion (Aldai et al. 2013).

In our study, the differences in FA profiles between B. indicus and crossbred B. taurus × B. indicus depended on the finishing system and were higher under intensive feeding, where the largest genetic differences were observed for 18:2 n-6, n-6 PUFA, total PUFA, 18:0 and total SFA, with a more desirable FA profile generally observed in crossbred animals.

**Conclusions**

The fatty acid profiles of intramuscular fat had a large influence of the finishing system, but interactions with the genetic group (B. indicus and crossbred B. taurus × B. indicus) were also important. Differences among genetic groups were minor with pasture finishing, but in grain finishing, the B indicus showed higher amounts of SFA and 18:0, and lower concentrations of the FA synthesised from 18:2 n-6 and 18:3 n-3. Animals finished on pasture produce meat with lower intramuscular fat, higher amounts of CLA and long-chain PUFA (20:5 n-3 and 22:5 n-3), and lower amounts of trans fatty acids and SFA.

**Implications**

- Finishing system had a major impact on fatty acid profiles of intramuscular fat in B. indicus and crossbred B. taurus × B. indicus cattle, but interactions among the two factors were important.
- Meat from pasture-finished animals has healthier properties, with lower intramuscular fat, increased amounts of desirable fatty acids such as CLA and n-3 long-chain PUFA, and lower levels of trans fatty acids and SFA.
- Under pasture finishing, differences among genetic groups were minor, while in grain finishing, the crossbred bulls had a more desirable fatty acid profile, with higher amounts of n-3 PUFA and lower levels of SFA.

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