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Towards Sustainable Sources of Omega-3 Long-Chain Polyunsaturated Fatty Acids in Northern Australian Tropical Crossbred Beef Steers through Single Nucleotide Polymorphisms in Lipogenic Genes for Meat Eating Quality

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Abstract: This study aimed to identify single nucleotide polymorphisms (SNP) in lipogenic genes of northern Australian tropically adapted crossbred beef cattle and to evaluate associations with healthy lipid traits of the *Longissimus dorsi* (loin eye) muscle. The hypothesis tested was that there are significant associations between SNP loci encoding for the fatty acid binding protein 4 (FABP4), stearoyl-CoA desaturase (SCD) and fatty acid synthase (FASN) genes and human health beneficial omega-3 long-chain polyunsaturated fatty acids (ω3 LC-PUFA) within the loin eye muscle of northern Australian crossbred beef cattle. Brahman, Charbray, and Droughtmaster crossbred steers were fed on Rhodes grass hay augmented with desmanthus, lucerne, or both, for 140 days and the loin eye muscle sampled for intramuscular fat (IMF), fat melting point (FMP), and fatty acid composition. Polymorphisms in FABP4, SCD, and FASN genes with significant effects on lipid traits were identified with next-generation sequencing. The GG genotype at the FABP4 g.44677239C>G locus was associated with higher proportion of linoleic acid than the CC and CG genotypes ($p < 0.05$). Multiple comparisons of genotypes at the SCD g.21266629G>T locus indicated that the TT genotype had significantly higher eicosapentaenoic, docosapentaenoic, and docosahexaenoic acids than GG genotype ($p < 0.05$). Significant correlations ($p < 0.05$) between FASN SNP and IMF, saturated and monounsaturated fatty acids were observed. These results provide insights into the contribution of lipogenic genes to intramuscular fat deposition and SNP marker-assisted selection for improvement of meat-eating quality, with emphasis on alternate and sustainable sources of ω3 LC-PUFA, in northern Australian tropical crossbred beef cattle, hence an acceptance of the tested hypothesis.

Keywords: meat fatty acids; omega-3 fatty acids; intramuscular fat; next-generation sequencing; tropical beef cattle; marker-assisted selection

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1. Introduction

According to the Food and Agriculture Organization of the United Nations (FAO), sustainable diets are protective and respectful of biodiversity and ecosystems, nutritionally

adequate, healthy, safe, accessible, culturally acceptable, economically fair, and affordable [1]. The fatty acid composition and intramuscular fat (IMF) content of beef contribute to sustainability due to their significant influences on shelf life [2], eating quality [3], and human health [4]. Studies suggest that dietary supplementation [5,6], nutritional alteration [7], and selective breeding [8] are management tools for manipulating meat fatty acid composition and beef quality. The nutritional composition of the diet is known to influence meat fatty acid composition and has been a subject of many literature reviews [9–15]. However, dietary manipulation of meat quality and fatty acid profile is challenging in ruminants due to rumen microbial lipolysis [16,17] and biohydrogenation of unsaturated to saturated fatty acids [18]. Muscle fatty acid composition is less diet-dependent and more largely regulated by key lipogenic enzymes in fatty acid metabolism [19,20].

Genetic selection and breeding of beef cattle provide a long-term, cumulative, and permanent approach to improving meat fatty acid composition because of their moderate to high heritability [21–26]. Heritability estimates of 0.47 was reported for total polyunsaturated fatty acids in Japanese Black cattle [27]. The identification of single nucleotide polymorphisms (SNP) in genes encoding key enzymes and proteins involved in fatty acids metabolism may improve the current fundamental understanding of underpinning genetic variants controlling muscle fatty acid composition. Several studies have shown that SNP can be used as genetic markers for improving IMF and muscle fatty acid composition in ruminant livestock. For instance, associations were reported between the growth hormone g.253 locus SNP with C14:0, C16:1, and C18:0 concentrations in Japanese Black cattle [28]; multiple autosomal SNP loci with C14:0, C16:0, and C18:0 concentrations in Nellore bulls [29]; the diacylglycerol O-acyltransferase 1 gene SNP K232A and c.947 of μ-calpain gene with IMF in meat of five beef cattle breeds in Sweden [30]; and multiple SNP in the hormone-sensitive lipase gene with IMF of the Qinchuan and Nanyang cattle [31]. Furthermore, the stearoyl-CoA desaturase (SCD) g.23881050T>C locus was significantly associated with IMF, C22:6ω-3, and C22:5ω-3, fatty acid binding protein 4 (FABP4) g.62829478A>T locus with IMF and fatty acid synthase (FASN) g.12323864A>G locus with C18:3ω-3, C18:1ω-9, C18:0, and C16:0 concentrations in Tattykeel Australian White lamb [32].

Three known candidate genes were selected for a targeted next-generation sequencing (NGS) of SNP in this study based on current knowledge of allelic substitutions encoding the FASN, SCD, and FABP4 genes. The FASN is a complex homodimeric enzyme that regulates biosynthesis of long-chain FA, and has been reported to be associated with fatty acid composition in Korean [33], crossbred Jersey and Limousin [34], Japanese Black and Limousin crossbred [20,35,36], and Angus [20] cattle. Moreover, SNP in the gene encoding stearoyl-CoA desaturase (SCD), a rate-limiting enzyme that catalyses monounsaturated fatty acid (MUFA) synthesis, is reported to influence fat melting point (FMP), SFA, MUFA, and polyunsaturated fatty acid (PUFA) composition in beef [37–40]. The fatty acid binding protein 4 (FABP4) functions include fatty acid uptake, transport, and metabolism [41], and the influence of FABP4 genotypes on fatty acid composition is documented [42]. For instance, the GG genotype of the c.388G>A, c.408G>C, and c.456A>G SNP had higher MUFA composition in Korean cattle compared to the other genotypes [43].

Meat quality measurements are often attained after slaughter making it difficult to predict meat quality in living animals [44,45]. Pewan et al. (2021) demonstrated that a combination of laboratory-based IMF, FMP, and fatty acid analyses of samples obtained through a minimally invasive biopsy sampling and next-generation sequencing of polymorphisms in lipid metabolism genes is a suitable method to directly quantify the genetic worth of live animals for IMF and fatty acid composition. Therefore, this study aimed to identify targeted SNP in lipid metabolism related genes of tropically adapted crossbred beef cattle of northern Australia and determine associations with loin eye muscle fat characteristics.

2. Materials and Methods

All the study protocols followed the Australian code of practice for the care and use of animals for scientific purposes [46] and were approved by the Commonwealth Scientific and Industrial Research Organisation Animal Ethics Committee (Approval Number 2019-38).

2.1. Animals, Diets and Experimental Design

Sample size determination, animal management, diet compositions, and experimental design were previously described [47,48], and will not be repeated herein. In summary, 48 Charbray, Brahman, and Droughtmaster crossbred steers (28–33 months old steers with an initial average liveweight of 332 ± 21 kg) were fed on isonitrogenous diets of Rhodes grass hay augmented with either desmanthus, lucerne, or both for 140 days in a completely randomised design. Steers were group-housed in 12 open outdoor pens and had unlimited access to clean water and mineral blocks with a five to ten per cent allowance for daily feed refusal. At the end of the study, steers were divided into two groups based on liveweight. The heavier steers (453 ± 15 kg) were transported to a commercial abattoir and slaughtered without feedlot finishing, while the lighter steers (406 ± 25 kg) were transferred to a commercial feedlot for finishing.

2.2. Loin Eye Muscle Sampling and Chemical Analysis

A minimally invasive biopsy technique was used to collect loin eye muscle samples from the 12th–13th rib interface of the steers transported to the feedlot after forage-feeding phase according to the protocol described earlier [49]. Samples from the steers slaughtered immediately after the forage-feeding phase were collected from the 12th–13th rib interface of the chilled carcasses 12 h after slaughter. The IMF of the biopsy and carcass samples was extracted as described by Flakemore et al., (2014) [50], and FMP was determined with the slip-point method [51]. The fatty acid composition was evaluated using a gas chromatography-mass spectrometry procedure [52].

2.3. Blood Sampling and Genomic DNA Extraction

Blood samples were collected into 10 mL EDTA-containing vacutainer tubes (BD, Sydney, Australia) via jugular venipuncture, transported in dry ice and stored at −80 °C until needed for laboratory analysis. Blood samples were thawed at room temperature and genomic DNA was extracted from a 2 mL aliquot using the NucleoSpin Blood Kit (Macherey-Nagel GmbH and Co. KG, Duren, Germany) according to the manufacturer's instructions. DNA yield and purity were determined with NanoDrop ND-1000 (Thermo Fisher Scientific Australia Pty Ltd., Scoresby, VIC, Australia).

2.4. Primer Design, Amplification of Target Genes, Clean-Up of PCR Products, Library Preparation, Sequencing and Data Analysis

The procedures were carried out as described previously [32] with slight modifications on the gene amplification conditions. The target genes were amplified using the primer sequences presented in Table S1 and the gel image of the amplification products is presented in Supplementary Figure S1. The amplification reactions were executed in a SimpliAmp Thermal Cycler (Thermofisher Scientific, Scoresby, VIC, Australia) in a total volume of 50 µL consisting of 25 µL of PCR master mix, 100 ng of DNA template, and 0.5 µM of each primer in a 3-step procedure: single initial denaturation at 98 °C for 1 min, 35 cycles of denaturation, annealing and extension at 98 °C for 15 s, 60 °C for 15 s, and 72 °C for 9 min, respectively, followed by a final extension at 72 °C for 9 min and a 4 °C hold. The FASN gene was amplified with PrimeSTAR GXL Master Mix (TaKaRa Bio Inc., Kusatsu, Shiga, Japan) in a 2-step protocol. The amplification reaction mix consisted of 1.25 units of polymerase, 10 µL of 5 × buffer, 0.2 µM of each primer, 200 µM of dNTP mixture, and 100 ng of DNA template in a total volume of 50 µL. The amplification reaction conditions included initial denaturation for 1 min at 98 °C and 30 cycles of denaturation and annealing combined with extension at 98 °C for 10 s and 68 °C for 10 min, respectively. The Hereford cattle breed

sequences NC_ 037353.1, NC_ 037346.1, and NC_ 037341.1 obtained from the GenBank database were used as the SCD, FASN, and FABP4 reference sequences, respectively.

2.5. Calculations and Statistical Analysis

Data analyses and the plotting of figures were conducted with the R software v.4.0.2 (R Foundation for Statistical Computing, Vienna, Austria). The GDIcall online calculator (http://www.msrcall.com/Gdicall.aspx (accessed on 14 January 2022)) was used to calculate SNP polymorphism information content (PIC). Hardy-Weinberg equilibrium (HWE) and expected heterozygosity (He) were calculated according to the methods described by Nei and Roychoudhury (1974) [53]. The HWE was tested for each identified SNP locus with the Chi-square test. Summary statistics including range, means, and standard deviations were computed and checked for data entry errors and outliers. The degree of linkage disequilibrium between each pair of loci was examined with distance-based hierarchical clustering of SNP loci [54] and the results presented as dendrograms and heatmaps. Linear correlations between genomic variants and muscle IMF, FMP, and fatty acid composition were estimated with Spearman's ρ correlations. Generalised least square procedure was used to fit linear models to investigate SNP associations with the loin eye muscle IMF, FMP, and fatty acid composition. Differences between means were compared using the Tukey-adjusted multiple comparisons test with a threshold for significance set at $p < 0.05$.

3. Results

3.1. Genetic Diversity of the Identified Single Nucleotide Polymorphisms

In total, 88 SNP, comprising 16, 42 and 30 SNP for FABP4, SCD, and FASN genes respectively, were identified (Supplementary Table S2). Thirty-five of the 88 SNP were not found in the Bovine Genome Variation Database (BGVD) (http://animal.nwsuaf.edu.cn/code/index.php/BosVar, (accessed on 28 January 2022)), and were deemed novel. All SNP had 0.11–0.50 minor allele frequency, 0.20–0.50 He, and 0.18–0.38 PIC. All the SNP were in HWE except FASN g.50784824G>A (rs209227647), g.50785253C>T (novel), g.50786977A>G (novel), g.50788575T>C (rs41919993), and g.50790973C>A (rs109149276) ($p \leq 0.04$). Many of the identified SNP were located in the introns. The distance-based hierarchical clustering of SNP loci indicated the presence of linkage disequilibrium between SNP loci (Figures S1–S4). The FABP4 SNP loci formed three clusters but g.44677611G>C (rs41729172) was not in linkage disequilibrium with other FABP4 loci (Supplementary Figure S1). A similar trend was observed for the SCD gene SNP loci (Supplementary Figure S2) but not for the FASN gene. All the FASN SNP loci were in linkage disequilibrium with at least one other locus (Supplementary Figure S3). Only nine SNP were non-synonymous amino acid substitutions (Table 1).

Table 1. Single nucleotide polymorphisms of the FABP4, SCD, and FASN genes, protein coding sequence positions and non-synonymous amino acid substitutions.

Gene [1]	SNP (Variant ID) [2]	PCS Position [4]	Amino Acid Substitution
FABP4	g.44677959 T>C (rs110757796)	220	Isoleucine to Valine
SCD	g.21272422 C>T (rs41255693)	878	Alanine to Valine
FASN	g.50782773 G>A (rs715140536)	1243	Alanine to Threonine
	g.50784533 C>G (rs481622676)	2066	Alanine to Glycine
	g.50784824 G>A (rs209227647)	2252	Arginine to Histidine
	g.50786496A>G [3]	3145	Serine to Glycine
	g.50788575T>C (rs41919993)	4168	Tyrosine to Histidine
	g.50789448C>T (rs516607144)	4693	Leucine to Phenylalanine
	g.50790973C>A (rs109149276)	5572	Leucine to Isoleucine

[1] FABP4: Fatty acid binding protein 4, SCD: Stearoyl-CoA desaturase, FASN: Fatty acid synthase. [2] SNP: Single nucleotide polymorphism. Variant dbSNP ID are based on the Bovine Genome Variation Database (BGVD). [3] SNP not listed in BGVD. [4] PCS: Protein coding sequence.

3.2. Correlations between Single Nucleotide Polymorphisms, Intramuscular Fat, Fat Melting Point, and Fatty Acid Composition

The clustering patterns of the SNP loci among steers with regard to the FABP4, SCD, and FASN genes are presented in Figures 1A, 2A and 3A, respectively. There was less variability in heterozygosity and homozygosity of closely related individuals for the FASN gene SNP compared to the FABP4 and SCD genes. Most SNP were in linkage disequilibrium but a few SNP depicted no linkage (Figures 1B, 2B and 3B). Four FABP4 gene SNP–g.44677205A>G (rs109388335), g.44677239C>G (rs110383592), g.44678114G>C (novel), and g.44678641T>C (rs110490217) were positively correlated with linoleic acid (C18:2n6). One SNP (g.44680048A>G; rs468994137) on the other hand, was negatively correlated with linoleic acid concentration, while g.44677587G>C (rs723716479) was positively correlated with conjugated linoleic acid (CLA) (Figure 1B; $p < 0.05$). Fourteen SCD SNP were negatively correlated, while g.21266629G>T (novel) and g.21271645G>A (rs380628677) were positively correlated with eicosapentaenoic acid (EPA), docosapentaenoic acid (DPA), docosahexaenoic acid (DHA) (Figure 1B; $p < 0.05$). No correlation was observed between FABP4 and SCD SNP with IMF, FMP, SFA, or MUFA. In contrast, FASN g.50784242C>T (rs800844468) SNP was positively correlated with IMF, palmitic acid (16:0), oleic acid (18:1), SFA, and MUFA (Figure 3B; $p < 0.05$). CLA concentration was negatively correlated with g.50787886A>G (novel), g.50788691T>C (rs526036338), and g.50788956C>T (novel) while g.50792445C>T (novel) was negatively correlated with EPA and the sum of EPA and DHA ($p < 0.05$). Several fatty acids were positively correlated ($p < 0.05$), and no significant negative correlations between quantified fatty acids were observed. Highly positive correlations ($\geq$0.7) between palmitic acid, palmitoleic acid, stearic acid, and oleic acid with the CLA, SFA, and MUFA levels were observed ($p < 0.01$).

(**A**)

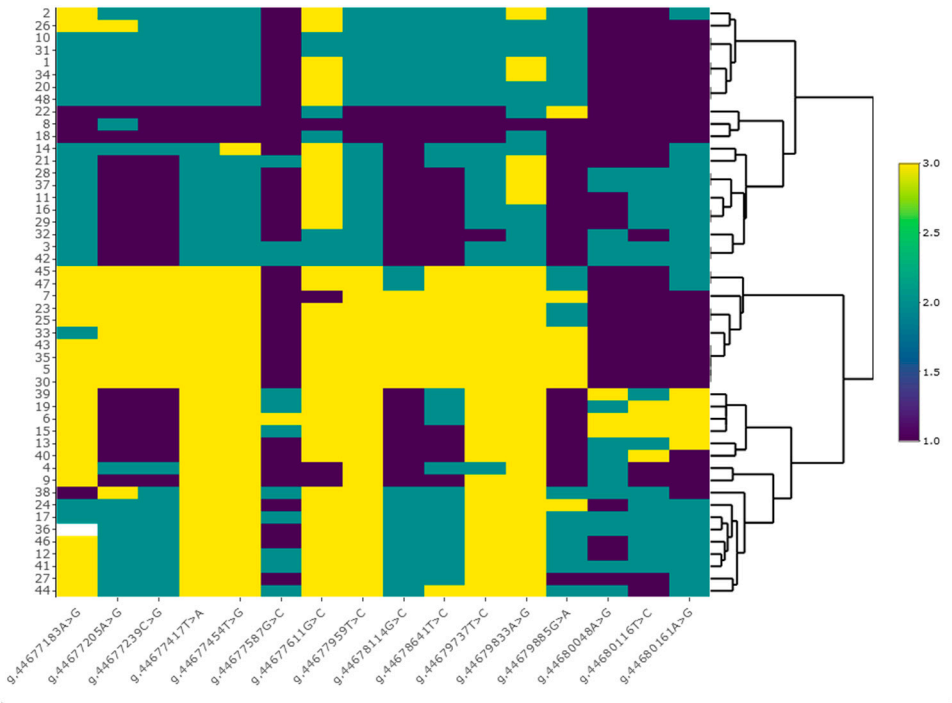

Figure 1. *Cont.*

(**B**)

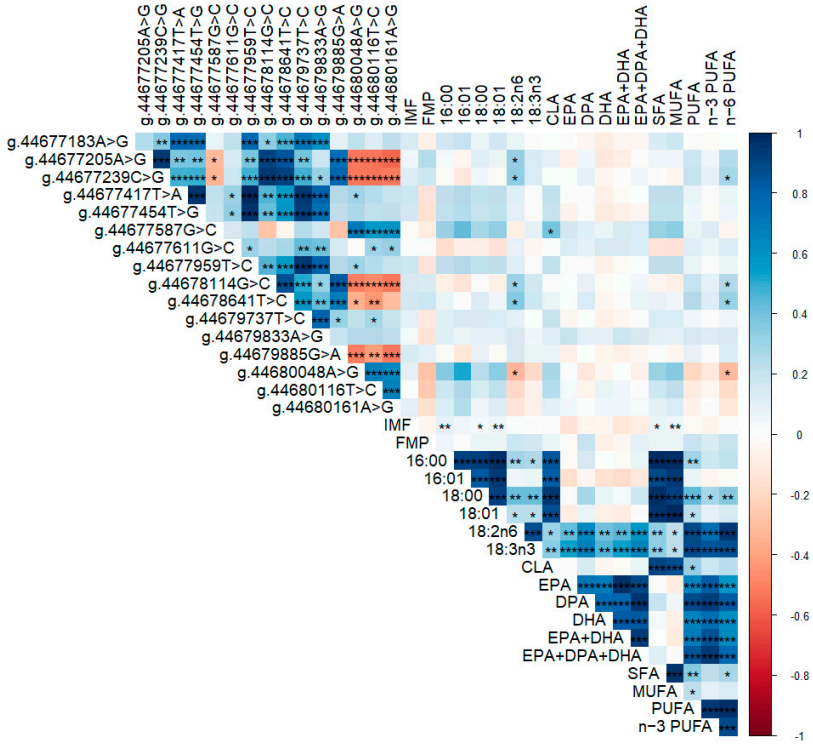

Figure 1. Single nucleotide polymorphisms in the FABP4 gene. (**A**) Clustering map of genetic variants; homozygotes similar to the reference sequence genotype (Hereford), heterozygotes and alternative allele homozygotes. (**B**) Correlations between SNP and IMF, FMP and fatty acids. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

(**A**)

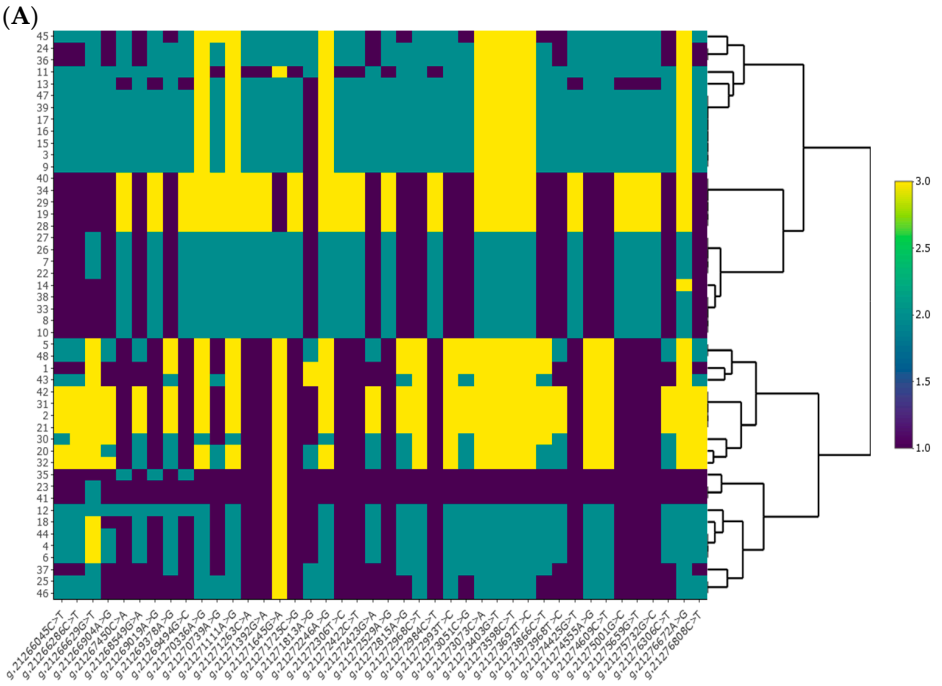

Figure 2. *Cont.*

(**B**)

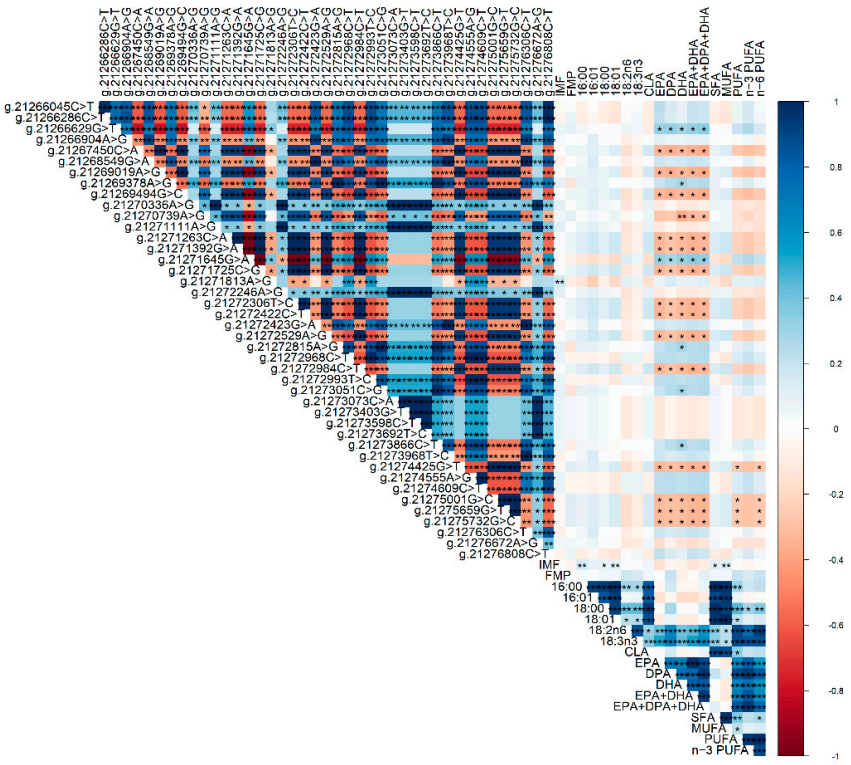

Figure 2. Single nucleotide polymorphisms in the SCD gene. (**A**) Clustering map of genetic variants; homozygotes similar to the reference sequence genotype (Hereford), heterozygotes and alternative allele homozygotes. (**B**) Correlations between SNP and IMF, FMP and fatty acids. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

(**A**)

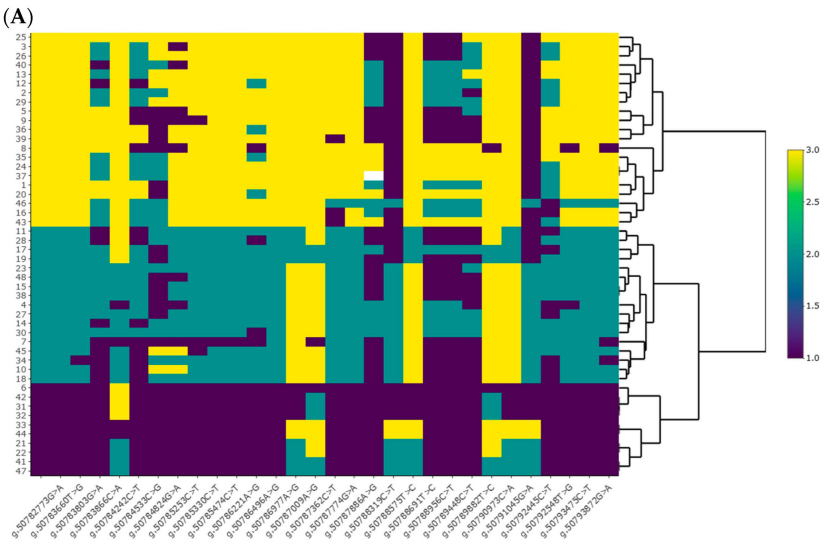

Figure 3. *Cont*.

(**B**)

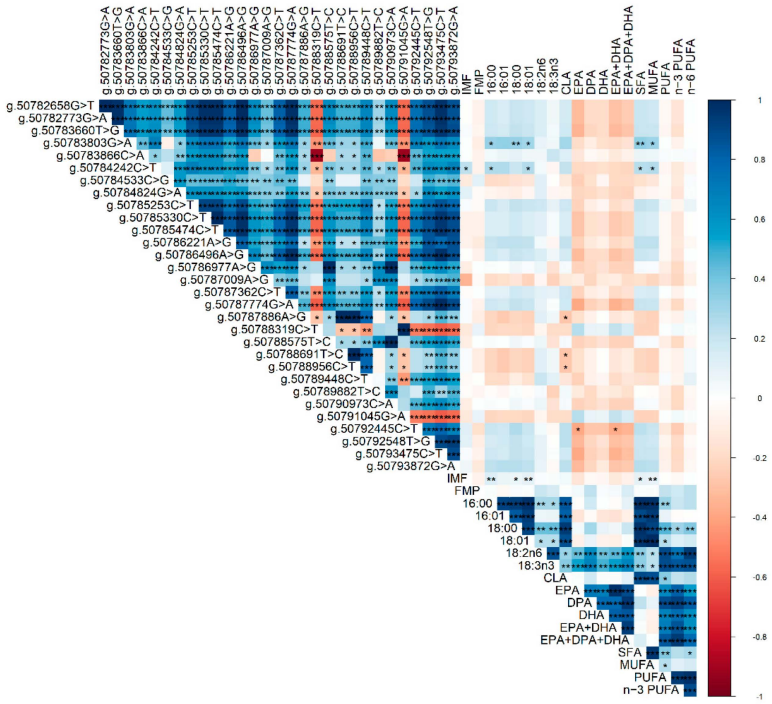

Figure 3. Single nucleotide polymorphisms on the FASN gene. (**A**) Clustering map of genetic variants; homozygotes similar to the reference sequence genotype (Hereford), heterozygotes and alternative allele homozygotes. (**B**) Correlations between SNP and IMF, FMP and fatty acids. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

3.3. Associations between Single Nucleotide Polymorphisms, Intramuscular Fat, Fat Melting Point, and Fatty Acid Composition

Associations between FABP4 g.44677239C>G (rs110383592), SCD g.21266629G>T (novel), and FASN g.50783803G>A (novel) are presented in Table 2. No significant associations were observed between the FASN g.50783803G>A with IMF, FMP, or any fatty acid examined. However, FABP4 g.44677239C>G was significantly associated with linoleic acid ($p = 0.03$). Linoleic acid was lower for the CC than the GG genotypes at 45.8 ± 10.88 mg/100 g and 54.5 ± 7.3 mg/100 g, respectively ($p = 0.02$), but CG was not significantly different from the homozygotes (Figure 4). Significant associations between the SCD g.21266629G>T SNP with DPA, DHA, EPA+DHA, and EPA+DPA+DHA were observed ($p \leq 0.02$). Multiple comparisons in Figure 5 indicate that EPA, DPA, and DHA were significantly higher for the TT compared to the GG genotypes ($p \leq 0.03$). The DHA level was lower ($p = 0.02$) while EPA and DPA tended to be lower for the TT compared to the GT variants ($p \leq 0.08$). No significant difference was observed for EPA, DPA, and DHA in GT compared to GG variants ($p \geq 0.47$). The IMF and FMP levels were not associated with either FABP4 g.44677239C>G, SCD g.21266629G>T, or FASN g.50783803G>A ($p \geq 0.38$).

Table 2. Least Square Means ± SD of loin eye muscle IMF (%), FMP (°C) and fatty acid concentrations (mg/100 g fresh muscle) by genotype at the FABP4 g.44677239C>G, SCD g.21266629G>T and FASN g.50783803G>A SNP loci.

Gene/SNP [1] **FABP4 g.44677239C>G**	**Total (*n* = 48)**	**CC (*n* = 19)**	**CG (*n* = 19)**	**GG (*n* = 10)**	***p*-Value** [2]
IMF	2.3 ± 0.75	2.1 ± 0.62	2.5 ± 0.9	2.2 ± 0.67	0.38
FMP	43.9 ± 4.79	42.7 ± 4.58	44.6 ± 4.83	44.9 ± 5.13	0.53
16:0 (Palmitic acid)	209.1 ± 149.68	194.3 ± 113.24	238.7 ± 185.99	179.5 ± 133.59	0.72

Table 2. *Cont.*

Gene/SNP [1] **FABP4 g.44677239C>G**	**Total (*n* = 48)**	**CC (*n* = 19)**	**CG (*n* = 19)**	**GG (*n* = 10)**	***p*-Value** [2]
16:1 (Palmitoleic acid)	34.6 ± 34.72	40.5 ± 47.35	34.5 ± 25.6	23.3 ± 16.87	0.52
18:0 (Stearic acid)	128.6 ± 78.22	119.2 ± 66.31	139.4 ± 83.68	125.1 ± 92.35	0.61
18:1 (Oleic acid)	263.1 ± 195.31	244.6 ± 143.89	302.4 ± 245.96	221.4 ± 170.23	0.74
18:2ω6 (Linoleic acid)	50.1 ± 10.2	45.8 ± 10.88[a]	52.0 ± 9.62 [ab]	54.5 ± 7.3[b]	0.03
18:3ω3 (α-linolenic acid)	16.3 ± 3.14	15.7 ± 3.69	16.4 ± 2.85	16.9 ± 2.73	0.73
CLA	4.3 ± 3.33	4.2 ± 3.11	4.4 ± 3.49	4.1 ± 3.77	0.79
EPA	9.4 ± 2.18	9.2 ± 2.13	9.8 ± 2.31	9.1 ± 2.12	0.58
DPA	14.0 ± 3.37	13.0 ± 3.61	15.0 ± 2.64	13.9 ± 3.92	0.12
DHA	2.3 ± 0.8	2.3 ± 0.93	2.5 ± 0.69	2.2 ± 0.79	0.28
EPA+DHA	11.8 ± 2.77	11.5 ± 2.81	12.3 ± 2.76	11.4 ± 2.86	0.33
EPA+DPA+DHA	25.8 ± 5.79	24.6 ± 5.88	27.4 ± 5.23	25.3 ± 6.53	0.14
SFA	376.9 ± 254.18	351.5 ± 201.61	420.0 ± 298.96	340.8 ± 260.83	0.75
MUFA	313.4 ± 228.69	294.7 ± 173.9	358.2 ± 285.22	261.9 ± 199.01	0.69
PUFA	142.8 ± 26.51	134.2 ± 28.71	149.6 ± 23.23	146.3 ± 25.98	0.41
ω3 PUFA	48.2 ± 8.92	47.0 ± 10.06	49.9 ± 7.84	47.5 ± 8.96	0.55
ω6 PUFA	79.6 ± 16.18	73.0 ± 18.67	83.6 ± 13.12	84.5 ± 13.17	0.11
SCD g.21266629 G>T	**Total (*n* = 48)**	**GG (*n* = 11)**	**GT (*n* = 22)**	**TT (*n* = 15)**	
IMF	2.3 ± 0.75	2.2 ± 0.55	2.2 ± 0.62	2.5 ± 1.03	0.64
FMP	43.9 ± 4.79	42.9 ± 3.64	44.1 ± 6.17	44.3 ± 3.26	0.78
16:0 (Palmitic acid)	209.1 ± 149.68	182.2 ± 111.02	201.0 ± 116.16	240.2 ± 209.36	0.86
16:1 (Palmitoleic acid)	34.6 ± 34.72	27.4 ± 16.93	38.4 ± 44.8	34.2 ± 27.7	0.91
18:0 (Stearic acid)	128.6 ± 78.22	125.6 ± 76.49	122.6 ± 60.52	139.2 ± 102.52	0.82
18:1 (Oleic acid)	263.1 ± 195.31	241.6 ± 164.92	255.0 ± 152.87	290.1 ± 266.99	0.82
18:2ω6 (Linoleic acid)	50.1 ± 10.2	50.0 ± 5.35	48.0 ± 10.93	53.2 ± 11.52	0.66
18:3ω3 (α-linolenic acid)	16.3 ± 3.14	16.5 ± 2.66	15.5 ± 3.24	17.1 ± 3.28	0.49
CLA	4.3 ± 3.33	4.7 ± 4.46	4.3 ± 2.71	4.0 ± 3.4	0.57
EPA	9.4 ± 2.18	8.6 ± 1.61 [a]	9.2 ± 2.43 [ab]	10.3 ± 1.93 [b]	0.08
DPA	14.0 ± 3.37	12.9 ± 1.78 [a]	13.4 ± 3.75 [ab]	15.7 ± 3.2 [b]	0.03
DHA	2.3 ± 0.8	2.1 ± 0.51 [a]	2.2 ± 0.88 [a]	2.8 ± 0.74 [b]	0.02
EPA+DHA	11.8 ± 2.77	10.8 ± 1.89 [a]	11.4 ± 3.07 [ab]	13.1 ± 2.48 [b]	0.03
EPA+DPA+DHA	25.8 ± 5.79	23.7 ± 3.21 [a]	24.8 ± 6.31 [ab]	28.9 ± 5.51 [b]	0.02
SFA	376.9 ± 254.18	345.6 ± 210.17	360.6 ± 197.48	422.7 ± 348.72	0.89
MUFA	313.4 ± 228.69	287.2 ± 191.76	303.9 ± 181.66	345.7 ± 310.88	0.85
PUFA	142.8 ± 26.51	138.0 ± 15.98	137.8 ± 29.03	153.7 ± 26.98	0.31
ω3 PUFA	48.2 ± 8.92	45.5 ± 5.37	47.2 ± 10.49	51.8 ± 7.77	0.12
ω6 PUFA	79.6 ± 16.18	78.5 ± 7.52	75.9 ± 19.07	85.9 ± 15.07	0.40
FASN g.50783803G>A	**Total (*n* = 48)**	**GG (*n* = 20)**	**GA (*n* = 20)**	**AA (*n* = 8)**	
IMF	2.3 ± 0.75	2.2 ± 0.71	2.3 ± 0.60	2.5 ± 1.14	0.49
FMP	43.9 ± 4.79	44.8 ± 3.56	43.1 ± 6.01	43.8 ± 3.62	0.40
16:0 (Palmitic acid)	209.1 ± 149.68	161.3 ± 84.44	211.4 ± 131.91	323.2 ± 248.45	0.24
16:1 (Palmitoleic acid)	34.6 ± 34.72	26.0 ± 13.60	41.8 ± 46.84	45.3 ± 31.24	0.17
18:0 (Stearic acid)	128.6 ± 78.22	103.2 ± 38.01	129.8 ± 76.27	189.3 ± 123.57	0.28
18:1 (Oleic acid)	263.1 ± 195.31	196.9 ± 114.57	279.5 ± 185.13	389.2 ± 309.04	0.16
18:2ω6 (Linoleic acid)	50.1 ± 10.20	50.5 ± 10.29	48.9 ± 9.88	52.1 ± 11.72	0.95
18:3ω3 (α-linolenic acid)	16.3 ± 3.14	16.3 ± 3.00	16.1 ± 3.34	16.8 ± 3.32	0.87
CLA	4.3 ± 3.33	3.4 ± 1.70	4.8 ± 4.01	5.6 ± 4.49	0.35
EPA	9.4 ± 2.18	9.9 ± 2.25	9.0 ± 2.05	9.3 ± 2.40	0.52
DPA	14.0 ± 3.37	14.7 ± 2.78	13.1 ± 3.45	14.5 ± 4.40	0.53
DHA	2.3 ± 0.80	2.4 ± 0.78	2.3 ± 0.8	2.1 ± 0.91	0.48

Table 2. *Cont.*

Gene/SNP [1] FABP4 g.44677239C>G	Total (*n* = 48)	CC (*n* = 19)	CG (*n* = 19)	GG (*n* = 10)	*p*-Value [2]
EPA+DHA	11.8 ± 2.77	12.3 ± 2.89	11.4 ± 2.5	11.4 ± 3.25	0.44
EPA+DPA+DHA	25.8 ± 5.79	27.1 ± 5.48	24.6 ± 5.34	26.0 ± 7.57	0.48
SFA	376.9 ± 254.18	294.0 ± 135.9	381.0 ± 229.59	574.6 ± 417.76	0.28
MUFA	313.4 ± 228.69	235.3 ± 132.97	332.1 ± 217.83	464.1 ± 359.61	0.20
PUFA	142.8 ± 26.51	143.9 ± 22.70	139.2 ± 25.97	148.9 ± 37.51	0.90
ω3 PUFA	48.2 ± 8.92	48.9 ± 8.18	47.4 ± 9.19	48.9 ± 10.91	0.82
ω6 PUFA	79.6 ± 16.18	81.5 ± 14.45	76.8 ± 16.70	79.6 ± 19.88	0.89

[1] IMF, intramuscular fat; FMP, fat melting point; CLA, conjugated linoleic acid; EPA, eicosapentaenoic acid; DPA, docosapentaenoic acid; DHA, docosahexaenoic acid; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids. SFA is the sum of 14:0, 15:0, 16:0, 17:0, 18:0, 20:0, and 21:0; MUFA is the sum of 14:1,16:1ω13t, 16:1ω9, 16:1ω7, 16:1ω7t, 16:1ω5c, 17:1ω8, 18:1ω7t,18:1ω5, 18:1ω7, 18:1ω9, 18:1a, 18:1b, 18:1c, 19:1a, 19:1b, 20:1ω11, 20:1ω9, 20:1ω7, 20:1ω5, 22:1ω9, 22:1ω11, and 24:1ω9; PUFA is the sum of 18:4ω3, 18:3ω6, 18:2ω6, 18:3ω3, 20:2ω6, 20:3, 20:3ω6, 20:4ω3, 20:4ω6, 20:5ω3, 22:4ω6, 22:5ω3, 22:5ω6, and 22:6ω3; ω3 PUFA is the sum of 18:3ω3, 18:4ω3, 20:4ω3, 20:5ω3, 22:5ω3, and 22:6ω3; ω6 PUFA is the sum of 18:2ω6, 18:3ω6, 20:2ω6, 20:3ω6, 20:4ω6, 22:4ω6, and 22:5ω6. [ab] Means followed by different lowercase superscripts differ significantly. [2] ANOVA *p*-value.

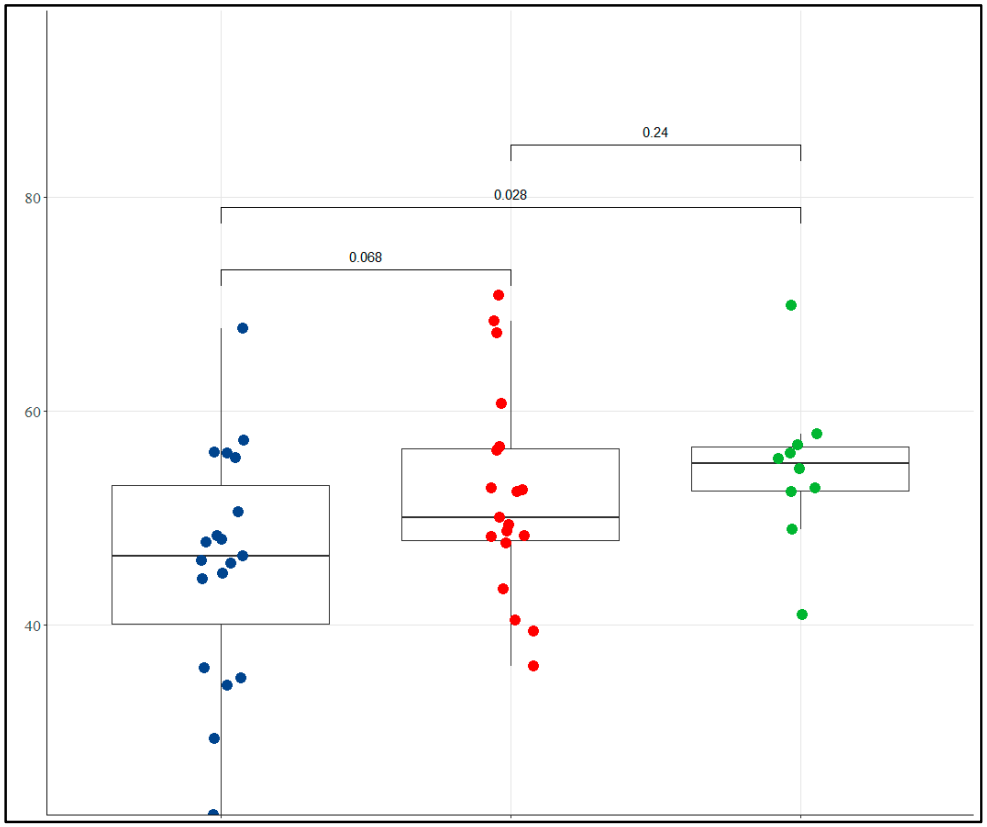

Figure 4. Multiple comparisons of loin eye muscle linoleic acid content between genotype variants at the FABP4 g.44677239C>G SNP locus CC (●), CG (●), and GG (●).

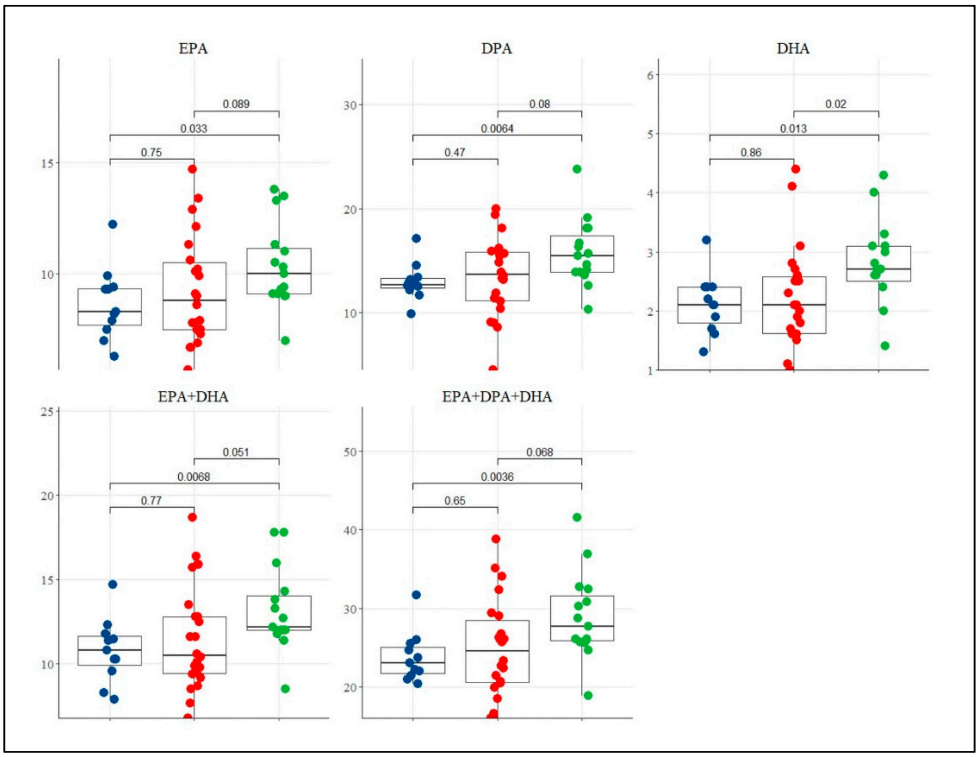

Figure 5. Multiple comparisons of loin eye muscle EPA, DPA, DHA, EPA+DHA, and EPA + DPA + DHA content between genotype variants at the SCD g.21266629G>T SNP locus GG (●), GT (●) and TT (●).

4. Discussion

Meat fatty acid composition influences meat shelf life, eating quality and consumers' health [55–57]. Although many studies have reported that diet modulation influences meat fatty acid composition, it is more difficult in ruminants compared to monogastric livestock due to microbial lipolysis [16,17] and biohydrogenation of unsaturated to saturated fatty acids in the rumen [18]. As a result, meat fatty acids are more saturated in ruminant than in monogastric animals [58,59]. On the other hand, studies have reported that fatty acid composition is heritable [21,27,60,61]. A recent study by Sakuma et al. [60] reported medium to high heritability estimates of 0.48 to 0.85 for six out of the eight fatty acids analysed. Therefore, there is an increased research interest in breeding, selecting and producing farm animals with desirable fatty acid composition [62].

Selection and breeding provide a long-term alternative to improving marbling level [63], and meat fatty acid composition [64,65]. Several SNP in genes encoding key enzymes and proteins involved in fatty acid metabolism have been reported as potential genetic markers for the improvement of IMF and fatty acid composition in different cattle breeds [33,35,41]. This study examined SNP in the FABP4, SCD, and FASN genes of northern Australian tropical crossbred beef cattle and identified SNP with significant influences on fatty acid composition of the loin eye muscle.

4.1. Fatty Acid Binding Protein 4 Gene Polymorphisms

The FABP4 gene is an important protein for long-chain fatty acid transport in mammals, and its polymorphism is associated with growth, fat deposition, and carcass traits in cattle [66–68]. Substitution of the G to C allele of the g.44677587 (rs723716479) locus was positively correlated with CLA, previously inversely linked with the risk of colorectal and breast cancer in some population-based studies [69]. The observed trend where the homozygous GG variant had the highest linoleic acid levels (almost 10 mg/100 g higher than homozygous CC in the g.44677239C>G loci) may indicate higher inflammatory eicosanoids synthesis. Linoleic acid is a building block in the synthesis of arachidonic acid,

the precursor for prostaglandins and other inflammatory eicosanoids [70]. In contrast to findings of this study, variation in the g.44677959T>C (c.220) influenced palmitoleic acid in Japanese Black cattle [71]. This discrepancy may be due to epistatic interaction of the g.44677959T>C locus with polymorphisms at another locus in line with the observations of Xu et al., (2021) [72] on the effect of polymorphisms on FABP4 protein structure. They reported that the wild type protein with isoleucine in amino acid 74 had 58.33% sheet and 29.55% loop interactions that changed to 59.09% sheet and 28.79% loop when isoleucine was substituted with valine. This discrepancy may also be due to breed differences since the Japanese Black cattle are reported to be genetically predisposed to producing carcass lipids with higher concentration of MUFA, including palmitoleic acid, compared to other cattle breeds such as Japanese Brown, Holstein or Charolais steers, likely due to the activity of the delta 9 desaturase enzyme on palmitic acid [73,74].

4.2. Stearoyl-CoA Desaturase Gene Polymorphisms

For most diets, approximately 70% to 95% and 85% to 100% ω6 PUFA and ω3 PUFA, respectively, are hydrogenated in the rumen [75]. As a result, fatty acids are absorbed almost entirely as SFA and biohydrogenation intermediates comprising conjugated di- or trienoic fatty acids and trans-11 fatty acids, notably trans-vaccenic acid, due to chemical reduction of unsaturated fatty acids in the rumen by microorganisms in ruminants [75,76]. Therefore, the composition of fatty acids stored in the fat depots mirror the action of SCD on fatty acids substrates [77]. The enzyme SCD catalyses the desaturation of SFA and MUFA by inserting a cis-double bond in the delta (Δ) 9 position of SFA substrates, with a higher preference for palmitic acid and stearic acid substrates transformed into palmitoleic acid and oleic acid, respectively [62,77,78]. Nucleotide substitution of C with T identified in the fifth exon of bovine SCD gene at the 878 CDS causes the replacement of the amino acid alanine with valine [37]. The replacement caused significantly higher MUFA and lower FMP in *M. trapezius* of CC compared to TT genotype cattle [37]. Similarly, Flekvieh bulls with the CC genotype had lower SFA and higher MUFA compared to the TT, but CC and the CT genotypes were similar [39]. The TT genotype of Chinese Simmental cattle were reported to have lower IMF compared to the CC genotype, but no difference was found between the heterozygous (CT) and either of the homozygous genotypes [79]. Additionally, the SNP had a significant association with stearic acid, oleic acid, SFA, and MUFA in Japanese black cattle with higher MUFA and lower SFA reported in animals with the CC variant [78]. In contrast, the SNP (g.21272422C>T) did not have significant effect on palmitic acid, stearic acid, palmitoleic acid, or oleic acid in the present study. However, findings of this study concur with a previous study that reported no effect of the SNP with palmitic acid, stearic acid, palmitoleic acid, or oleic acid in Canadian Angus and Charolais-based commercial crossbred beef steers [40]. Moreover, Dujková et al., (2015) [80] found that the SNP did not influence fatty acid composition in Aberdeen Angus and Blonde d'Aquitaine cattle. Unsaturated fatty acids are synthesized through the activity of Δ5, Δ6 or Δ9 desaturases [81], hence the difference between studies may be due to the activity of other desaturases or other genes [76,82]. The SCD genotype was reported to explain only 4% of the MUFA composition in Japanese Black cattle [37], and 5% in MUFA and 4% oleic acid variation, respectively, in Wagyu × Limousin cattle [38]. The significant correlations between EPA, DPA, and DHA with at least 16 SCD SNP observed in this study corroborate the findings of a previous study in sheep that recorded significant correlations between two SCD SNP and ω3 long-chain PUFA [32]. The three ω3 long-chain PUFA are synthesized from alpha-linolenic acid through the activity of Δ6 desaturase and Δ5 desaturase among other enzymes, but not Δ9 desaturase since ALA already has a double bond between C9 and C10 [83,84]. Therefore, the correlation may be due to linkage disequilibrium between the SCD SNP and other loci responsible for the synthesis of ω3 long-chain PUFA. Nonetheless, the significant correlations of SCD SNP with the EPA, DPA and DHA with no influence on the SFA and MUFA observed in this study suggests that the SNP can be used as markers to select cattle for improved health beneficial ω3 long-chain PUFA with no negative influence

on meat-eating quality denoted by the lack of correlation with oleic acid; the most abundant fatty acid in beef that is reported to improve fat softness and meat palatability [85].

Seafood sources including fish, crustaceans, and molluscs are recognized as the best dietary sources of long-chain ω3 oils [86]. However, sustainability of seafood as a source of ω3 LC-PUFA is threatened by the global decline in wild-harvest fish stocks [87], high cost of seafood [88], and low availability of seafood in many geographical locations [89]. On the other hand, beef contributes significantly to meat intake as it is the third most consumed meat in the world at 6.3 kg per capita [90]. Therefore, the significant correlations of SCD SNP with the EPA, DPA, and DHA suggests that marker assisted selection can be used to provide a sustainable source of dietary ω3 LC-PUFA in communities where beef constitutes a significant proportion of the diet.

4.3. Fatty Acid Synthase Gene Polymorphisms

The FASN gene is located in the BTA19 region where quantitative trait loci affecting milk fat content, meat fatty acid composition and related traits had been previously identified [36,91]. The enzyme FASN catalyses the de novo synthesis of palmitic acid, a substrate for palmitoleic acid synthesis through desaturation, and stearic acid through elongation [92–94]. Genome-wide association studies with varying breeds of cattle have reported significant effect of FASN SNP on intramuscular composition of SFA, MUFA, and linoleic acid [91,95–98]. Previous studies had reported that FASN polymorphism significantly influenced the intramuscular composition of oleic acid, SFA and MUFA in Fleckvieh bulls [41], and palmitic acid, palmitoleic acid, oleic acid, SFA, and MUFA of the intramuscular adipose tissue in Japanese Black cattle [36,82,99]. Zhang et al., (2008) [20] reported an additive effect of the g.17924A>G SNP on fatty acid composition, where the G allele was associated with higher MUFA and lower SFA compared to the A allele in purebred Angus bulls. The SNP also influenced palmitoleic acid and oleic acid composition in commercial crossbred beef steers [40], and palmitic acid, palmitoleic acid, oleic acid, total MUFA, SFA, and marbling score in Korean cattle [100–102]. In addition, FASN polymorphisms influenced SFA, MUFA, and PUFA in Chinese Holstein cattle [98]. Oh et al., (2012) reported associations of five FASN exonic SNP with intramuscular fatty acid composition in Korean cattle. These findings align with this current study where FASN g.50784242C>T was positively correlated with IMF, palmitic acid, oleic acid, SFA, and MUFA, while g.50783803G>A was correlated with palmitic acid, stearic acid, oleic acid, SFA and MUFA. Majority of the previous studies suggested that polymorphisms influenced the tissue fatty acid composition through amino acids substitutions on the b-ketoacyl reductase domain and the thioesterase domain by changing the spatial structure of the substrate-binding site [36,100,102]. However, the g.50784242C>T was a synonymous mutation, while g.50783803G>A was in the intron, thus they did not influence the production of missense codons, but may have exerted their effect by changing the splicing regulatory sequences [33]. The effect of g.50784242C>T on palmitic acid, oleic acid, SFA and MUFA may be due to the differences in IMF content. A review by De Smet et al. [103] reported a linear increase in SFA and MUFA expressed in mg/100g muscle (r = 0.98) with IMF content.

Tissue CLA is primarily derived from endogenous synthesis from *trans-11* C18:1 (vaccenic acid) by the SCD activity [104], and to a lesser extent, as an intermediate of microbial fatty acid biohydrogenation in the rumen [105,106]. In this study, SNP of the g.50787886A>G, g.50788691T>C, and g.50788956C>T loci were found to be correlated with high CLA levels. Although these polymorphisms were either synonymous or located in the intron, they may have influenced the function of FASN in palmitic acid synthesis, the substrate for *trans-11* C18:1 and subsequently CLA synthesis. These findings suggest that these loci may be used to select cattle with high CLA composition, a fatty acid associated with lower risk for atherosclerosis, diabetes and cancer [69,106]. Put together, these findings indicate that polymorphisms on the FASN gene can be used to select individuals for improved IMF and fatty acid composition of northern Australian tropical crossbred beef cattle.

5. Conclusions

This study aimed to investigate the targeted identification of SNP in the FABP4, SCD, and FASN genes and their associations with fatty acid composition in the loin eye muscle of northern Australian tropical crossbred beef cattle. Single nucleotide polymorphisms on the FABP4 gene significantly influenced linoleic acid, SCD was associated with long-chain n3 PUFA and FASN impacted IMF, SFA, MUFA, CLA, and EPA compositions. These findings not only provide insights into the genetic role of SNP in fat deposition and lipid metabolism in tropical crossbred cattle of northern Australia, but also their potential use in marker-assisted selection and breeding for improved meat-eating quality. The tested hypothesis of significant associations between SNP loci encoding for the fatty acid binding protein 4, stearoyl-CoA desaturase and fatty acid synthase genes and human health beneficial ω3 long-chain polyunsaturated fatty acids within the loin eye muscle of northern Australian crossbred beef cattle is therefore acceptable. This is the first study that demonstrates the presence of single nucleotide polymorphisms in lipogenic genes in northern Australian crossbred beef cattle which constitute over 50% of Australian beef production and exports.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su14148409/s1, Table S1: Primer sequences for target gene amplification; Figure S1: Gel image of the amplification products of the three target genes visualised in 0.8% agarose gel.; Table S2: Genetic variants detected in the FABP4, SCD and FASN genes of tropically adapted crossbred steers; Figure S2: Correlation coefficients for all pairs of SNP loci of the FABP4 gene. The rectangles represent distance-based clustering of SNP loci; Figure S3: Correlation coefficients for all pairs of SNP loci of the SCD gene. The rectangles represent distance-based clustering of SNP loci; Figure S4: Correlation coefficients for all pairs of SNP loci of the FASN gene. The rectangles represent distance-based clustering of SNP loci.

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Institutional Review Board Statement: The study was conducted in accordance with the CSIRO Animal Ethics Committee approved guidelines (approval number 2019-38, issued on the 20 February 2020) and the Australian code of practice for the care and use of animals for scientific purposes.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available from the corresponding author on request.

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