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Estimates of genetic parameters for triacylglycerol fatty acids in beef cattle at weaning and slaughter

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Summary

Adipose tissues from the 12th–13th rib interface were sampled at weaning (324 cattle) and slaughter (310 cattle). The animals were progeny from Hereford dams sired by Angus, Belgian Blue, Hereford, Jersey, Limousin, South Devon and Wagyu. Fatty acid composition of the triacylglycerol fraction at both stages was measured by gas–liquid chromatography. Estimates of heritability and genetic and phenotypic correlations at weaning and slaughter were computed by restricted maximum likelihood using a sire model in both univariate and multivariate analyses. Results indicated that generally, there were strong, positive genetic correlations between fatty acids at weaning and slaughter (as high as 0.98). Phenotypic correlations were however, low and poor (0.04–0.44). Heritability (h^2) estimates at weaning were low to moderate, ranging from 0–0.31. However, at slaughter, h^2 estimates were generally higher than at weaning: Stearate, oleate and total monounsaturates had h^2 estimates of 0.43, 0.37 and 0.40, respectively. Other carcass traits such as marbling score and melting point of fat had h^2 estimates of 0.20 and 0.52, respectively. Significant breed, sex and location differences in fatty acid composition were also observed at weaning and slaughter.

Introduction

Progeny testing in cattle is time-consuming and costly because of the long generation interval. Furthermore, the cattle are slaughtered to enable progeny testing for meat-quality traits. It is therefore desirable for breeders to make an early decision while the cattle are still weaners to save time and costs associated with progeny testing. The key questions this paper attempts to answer are:

(1) What is the relationship between triacylglycerol fatty acids from the adipose tissue of cattle at weaning and at slaughter?
(2) Can fatty acid composition at slaughter be predicted from weaner fatty acid data?
(3) Is there an interaction among sire-breed and age?
(4) How heritable is fatty acid composition?

Thus, the objectives of this study were firstly, to investigate genetic and nongenetic sources of variation in triacylglycerol fatty acid composition of adipose tissue within the same cattle, at weaning and at slaughter. Secondly, to estimate genetic and phenotypic correlations between fatty acids and enzyme indices at weaning and slaughter. Thirdly, to

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Table 1. **Distribution of cattle sampled at weaning and slaughter**

Breed	Number of sires	Number of progeny	
		Weaning	Slaughter
Angus × Hereford	3	39	38
Belgian Blue × Hereford	4	56	55
Hereford × Hereford	3	39	34
Jersey × Hereford	4	50	48
Limousin × Hereford	4	48	47
South Devon × Hereford	4	38	36
Wagyu × Hereford	4	54	52
Total	26	324	310

predict carcass fatty acids and enzyme indices from biopsy data at weaning, and lastly, to estimate heritabilities of fatty acids and enzyme indices at weaning and slaughter.

Materials and methods

Steers and heifers from the Southern Crossbreeding Project, Struan Research Centre, located in the south-east of South Australia were sampled in 1994. They were progeny from Hereford dams crossed to Angus, Belgian Blue, Hereford, Jersey, Limousin, South Devon and Wagyu sires. A total of 324 cattle were sampled at weaning and 310 at slaughter from 26 sires (Table 1). The animals were raised on pasture in two locations: Struan and Wandilo, and weaned at 300 days of age at which time subcutaneous fat tissue was biopsied between the 12th and 13th ribs by a technique already described (MALAU-ADULI et al. 1997). They were lot-fed on a high density diet (65% barley and 13% crude protein) for a period of 90 days (heifers) and 180 days (steers). They were grain-fed from 300 days of age. Adipose tissues at the 12th–13th rib interface from the resulting carcasses were sampled for intramuscular fat content, melting point and fatty acid composition. Marbling scores were carried out by accredited assessors according to the standard AUS-MEAT (1995) procedure. Melting point of fat was determined by the AOAC (1984) procedure and the intramuscular fat content was measured by the solvent–extraction method (AOAC, 1984). Fatty acid composition was measured by gas–liquid chromatography. The equipment, total lipid extraction, methylation, separation of triacylglycerol from phospholipid fractions and normalisation procedures have been described in detail (SIEBERT et al. 1996; MALAU-ADULI et al. 1997).

General linear models procedure (PROC GLM) of SAS (1989) was used in analysing the data. Factors fitted in the models for biopsy (weaning) and carcass (slaughter) data included location, sex, breed and sire nested within breed (Table 2). First- and second-order interactions were dropped from the model because they were either not significant or inestimable due to confounding. Only the major individual fatty acids palmitate (16 : 0), palmitoleate (16 : 1), stearate (18 : 0) and oleate (18 : 1n-9) which constitute about 90% of the total fatty acids were tabulated (Table 2). Variance and covariance components were generated from a mixed model least-squares and maximum likelihood program (HARVEY 1990) using a sire model. These components were used in computing heritability estimates and genetic and phenotypic correlations by restricted maximum likelihood (REML) using ASREML (GILMOUR et al. 1998). To be able to make comparisons between software packages, heritability estimates from PROC MIXED (SAS 1989), HARVEY (1990) and ASREML were computed

Table 2. **Tests of significance for triacylglycerols (TAGs) at weaning and slaughter**

	Weaning (biopsy data)				Slaughter (carcass data)			
Trait	Location	Sex	Breed	Sire (Brd)	Location	Sex	Breed	Sire (Brd)
16 : 0	0.37	0.78	0.04*	0.66	0.75	0.01**	0.25	0.26
16 : 1	0.69	0.05*	0.01**	0.15	0.82	0.01**	0.05*	0.29
18 : 0	0.01**	0.13	0.01**	0.19	0.05*	0.01**	0.50	0.01**
18 : 1n-9	0.32	0.01**	0.60	0.02*	0.99	0.86	0.39	0.02*
SFA	0.08	0.06	0.01**	0.98	0.54	0.82	0.47	0.04*
MUFA	0.39	0.01**	0.05*	0.01**	0.66	0.01**	0.47	0.01**
PUFA	0.03*	0.51	0.87	0.37	0.50	0.01**	0.95	0.19
Δ^9(C16)	0.37	0.10	0.01**	0.28	0.77	0.01**	0.04*	0.32
Δ^9(C18)	0.01**	0.01**	0.04*	0.02*	0.07	0.01**	0.46	0.01**
Elongase	0.68	0.41	0.19	0.05*	0.91	0.01**	0.01**	0.02*

Values in table are F-probabilities
*$p < 0.05$; **$p < 0.01$
TAGs, triacylglycerols; SFA, total saturated fatty acids; MUFA, total mono-unsaturated fatty acids; PUFA, total polyunsaturated fatty acids; Δ^9(C16), desaturation index in C16 fatty acids; Δ^9(C18), desaturation index in C18 fatty acids; Elongase, Elongation index in chain-lengthening C16–C18 fatty acids

using a sire model in all cases. SAS estimates were from a univariate analysis, whereas multivariate analyses were performed for HARVEY (1990) and ASREML.

Results

Location of the cattle was a significant source of variation in the proportion of only one individual fatty acid: stearate (18 : 0), at weaning and slaughter (Table 2). At both stages, the adipose tissues of cattle born at Struan had higher proportions of 18 : 0 than their counterparts at Wandilo: 13.4 versus 12.2% at weaning and 13.9 versus 13.3% at slaughter (Table 3). Total polyunsaturated fatty acids (PUFA) and desaturation index in C18 fatty acids (Δ^9-C18) at weaning also significantly differed between locations (Table 2). Wandilo biopsies had higher proportions of PUFA and desaturation enzyme index (4.0 versus 3.4% and 73.3 versus 71.1%, respectively) than those in Struan (Table 3). At slaughter, the differences due to location were not detected except for 18 : 0 as mentioned earlier.

Proportions of 16 : 1, 18 : 1n-9, total mono-unsaturated fatty acids (MUFA) and desaturation index significantly differed between the sexes at weaning (Table 2). In all traits, heifers had higher proportions of 16 : 1 (5.7 versus 5.4%), 18 : 1n-9 (33.8 versus 32.4%), MUFA (46.7 versus 45.3%) and Δ^9-C18 (73.2 versus 71.2%) than steers (Table 4). At slaughter, sex differences were apparent in almost all the traits except 18 : 1n-9 and total saturated fatty acids (SFA) (Table 2). Heifers had higher proportions of 18 : 0 (15.0 versus 12.2%), PUFA (3.1 versus 1.7%), elongation index (63.3 versus 59.7%), marbling score (1.4 versus 1.2), intramuscular fat (4.3 versus 3.3%) and less 16 : 0, 16 : 1, MUFA, desaturation indices and melting point than steers (Table 4).

Breed differences at weaning were apparent in the proportions of 16 : 0, 16 : 1, 18 : 0, SFA, MUFA and desaturation indices (Table 2). Angus crosses had the most 16 : 0 (30.7%) and Wagyu crosses the least (28.7%) (Table 5). Jersey crosses had the highest proportion of 16 : 1 (6.6%) and Limousin crosses the least (4.9%). Limousin crosses also contained the least proportions of MUFA (44.1%), desaturation indices in C16 (14.2%) and C18 (69.2%) fatty acids, and the most proportions of 18 : 0 (15.0%) and SFA (52.3%) (Table 5). Wagyu

Table 3. **Location variation (% total fatty acids) in triacylglycerols (TAGs) (LSM ± SE) at weaning and slaughter**[A]

	Weaning (biopsy data)			Slaughter (carcass data)		
Fatty acid	Struan (n = 172)	Wandilo (n = 152)	Sig.	Struan (n = 168)	Wandilo (n = 152)	Sig.
16 : 0	30.2 ± 0.2	29.9 ± 0.3	NS	29.5 ± 0.2	29.4 ± 0.3	NS
16 : 1	5.5 ± 0.1	5.6 ± 0.1	NS	4.6 ± 0.2	4.5 ± 0.2	NS
18 : 0	13.4 ± 0.3	12.2 ± 0.3	**	13.9 ± 0.2	13.3 ± 0.3	*
18 : 1n-9	32.8 ± 0.3	33.3 ± 0.4	NS	40.8 ± 0.3	40.8 ± 0.3	NS
SFA	50.6 ± 0.3	50.0 ± 0.4	NS	47.8 ± 0.3	47.5 ± 0.4	NS
MUFA	46.0 ± 0.4	46.0 ± 0.4	NS	49.9 ± 0.3	50.1 ± 0.4	NS
PUFA	3.4 ± 0.2	4.0 ± 0.3	*	2.3 ± 0.1	2.4 ± 0.2	NS
Δ^9(C16)	15.5 ± 0.2	15.8 ± 0.3	NS	13.2 ± 0.3	13.3 ± 0.4	NS
Δ^9(C18)	71.1 ± 0.5	73.3 ± 0.6	**	74.7 ± 0.4	75.5 ± 0.4	NS
Elongase	56.4 ± 0.3	56.2 ± 0.4	NS	61.5 ± 0.3	61.4 ± 0.3	NS

[A]Abbreviation of traits as in Table 2
*p < 0.05; **p < 0.01; NS, not significant
LSM, Least squares means; SFA, 14 : 0+16 : 0+17 : 0+18 : 0; MUFA, 14 : 1+16 : 1+17 : 1+18 : 1n-9+18 : 11n-7; PUFA, 18 : 2+18 : 3n-3+18 : 3n-6+18 : 4; Δ^9(C16), 100[(16 : 1)/(16 : 0+16 : 1)]; Δ^9(C18), 100[(18 : 0)/(18 : 0+18 : 1n-9)]; Elongase, 100[(18 : 0+18 : 1n-9)/(16 : 0+16 : 1+18 : 0+18 : 1n-9)]

Table 4. **Sex variation (% total fatty acids) in TAGs (LSM ± SE) at weaning and slaughter**[A]

	Weaning (biopsy data)			Slaughter (carcass data)		
Fatty acid	Steers (n = 174)	Heifers (n = 150)	Sig.	Steers (n = 172)	Heifers (n = 138)	Sig.
16 : 0	30.1 ± 0.3	30.0 ± 0.3	NS	30.7 ± 0.2	28.3 ± 0.2	**
16 : 1	5.4 ± 0.1	5.7 ± 0.1	*	5.2 ± 0.1	3.9 ± 0.1	**
18 : 0	13.1 ± 0.3	12.5 ± 0.3	NS	12.2 ± 0.3	15.0 ± 0.3	**
18 : 1n-9	32.4 ± 0.4	33.8 ± 0.4	**	40.9 ± 0.3	40.8 ± 0.3	NS
SFA	50.9 ± 0.4	49.5 ± 0.4	NS	47.7 ± 0.3	47.6 ± 0.3	NS
MUFA	45.3 ± 0.4	46.7 ± 0.4	**	50.6 ± 0.3	49.3 ± 0.3	**
PUFA	3.8 ± 0.2	3.8 ± 0.2	NS	1.7 ± 0.2	3.1 ± 0.2	**
Δ^9(C16)	15.4 ± 0.2	15.9 ± 0.3	NS	14.5 ± 0.3	12.0 ± 0.3	**
Δ^9(C18)	71.2 ± 0.6	73.2 ± 0.6	**	77.0 ± 0.4	73.2 ± 0.4	**
Elongase	56.1 ± 0.4	56.4 ± 0.4	NS	59.7 ± 0.3	63.3 ± 0.3	**
Marbling	–	–		1.2 ± 0.01	1.4 ± 0.01	**
IM Fat	–	–		3.3 ± 0.18	4.3 ± 0.14	**
Melting Pt.	–	–		40.3 ± 0.30	39.0 ± 0.30	**

[A]Abbreviation of traits as in Table 2
*p < 0.05; **p < 0.01; NS, not significant

crosses contained the highest proportions of MUFA (49.0%) and as expected, the lowest SFA (47.4%).

At slaughter, Wagyu crosses had the highest C18 desaturation index of 76.0%, whereas Jersey crosses had the highest proportions of 16 : 1 (5.3%), Δ^9-C16 (15.0%) and the lowest elongation index of 59.8% (Table 5). Purebred Herefords had the lowest Δ^9-C18 enzyme index of 73.7% and Limousin crosses the lowest Δ^9-C16 of 12.1%. Sire nested within breed

Table 5. **Sire-breed variation (% total fatty acids) in TAGs (LSM ± SE) at weaning and slaughter**[A]

	Angus	B. Blue	Hereford	Jersey	Limousin	S. Devon	Wagyu
Weaning							
16 : 0	**30.7 ± 0.5**	30.0 ± 0.4	30.5 ± 0.5	30.6 ± 0.5	30.2 ± 0.5	29.5 ± 0.5	**28.7 ± 0.4**
16 : 1	5.3 ± 0.2	5.9 ± 0.2	5.4 ± 0.2	**6.6 ± 0.2**	**4.9 ± 0.2**	5.4 ± 0.2	5.6 ± 0.2
18 : 0	13.1 ± 0.6	12.4 ± 0.5	13.7 ± 0.6	**11.1 ± 0.5**	**15.0 ± 0.5**	12.8 ± 0.6	11.5 ± 0.5
18 : 1n-9	32.9 ± 0.8	33.3 ± 0.7	32.6 ± 0.8	33.3 ± 0.7	32.7 ± 0.7	32.3 ± 0.8	34.2 ± 0.7
SFA	51.4 ± 0.7	49.7 ± 0.6	51.7 ± 0.7	49.1 ± 0.6	**52.3 ± 0.6**	50.2 ± 0.7	**47.4 ± 0.6**
MUFA	45.3 ± 0.9	46.5 ± 0.7	44.4 ± 0.9	47.2 ± 0.8	**44.1 ± 0.8**	45.9 ± 0.8	**49.0 ± 0.8**
PUFA	3.3 ± 0.3	3.8 ± 0.3	3.9 ± 0.4	3.7 ± 0.3	3.6 ± 0.3	3.9 ± 0.3	3.6 ± 0.3
Δ^9(C16)	14.6 ± 0.5	16.5 ± 0.4	15.0 ± 0.5	**17.7 ± 0.5**	**14.2 ± 0.4**	15.3 ± 0.5	16.4 ± 0.4
Δ^9(C18)	71.7 ± 1.3	73.0 ± 1.1	70.6 ± 1.3	**75.0 ± 1.2**	**69.2 ± 1.1**	71.9 ± 1.2	73.8 ± 1.1
Elongase	56.1 ± 0.8	56.0 ± 0.7	56.4 ± 0.8	54.6 ± 0.7	57.4 ± 0.7	56.4 ± 0.8	56.9 ± 0.7
Slaughter							
16 : 0	28.9 ± 0.2	28.9 ± 0.4	29.9 ± 0.5	30.0 ± 0.4	29.1 ± 0.4	29.5 ± 0.5	29.9 ± 0.4
16 : 1	4.4 ± 0.3	4.4 ± 0.2	4.2 ± 0.3	**5.3 ± 0.3**	**4.1 ± 0.3**	4.5 ± 0.3	5.1 ± 0.3
18 : 0	13.7 ± 0.2	13.9 ± 0.5	14.2 ± 0.6	12.9 ± 0.5	14.2 ± 0.5	13.3 ± 0.6	13.2 ± 0.5
18 : 1n-9	41.4 ± 0.7	41.3 ± 0.6	39.6 ± 0.7	40.2 ± 0.6	41.2 ± 0.6	40.5 ± 0.7	41.4 ± 0.6
SFA	47.2 ± 0.7	47.3 ± 0.6	49.2 ± 0.7	47.5 ± 0.6	47.8 ± 0.6	47.4 ± 0.7	47.3 ± 0.6
MUFA	50.7 ± 0.7	50.3 ± 0.6	48.5 ± 0.8	50.1 ± 0.7	49.7 ± 0.7	50.4 ± 0.7	50.3 ± 0.7
PUFA	2.1 ± 0.3	2.4 ± 0.3	2.3 ± 0.3	2.4 ± 0.3	2.5 ± 0.3	2.2 ± 0.3	2.4 ± 0.3
Δ^9(C16)	13.1 ± 0.6	13.1 ± 0.6	12.3 ± 0.7	**15.0 ± 0.6**	**12.1 ± 0.6**	13.1 ± 0.6	13.9 ± 0.6
Δ^9(C18)	75.2 ± 0.8	75.1 ± 0.7	73.7 ± 0.9	75.9 ± 0.8	74.4 ± 0.8	75.4 ± 0.8	76.0 ± 0.8
Elongase	62.3 ± 0.5	62.4 ± 0.5	61.1 ± 0.6	**59.8 ± 0.5**	**62.7 ± 0.5**	60.8 ± 0.6	61.2 ± 0.5

Figures in bold depict the highest and lowest values
[A]Abbreviation of traits as in Table 2

was a significant source of variation in the proportions of 18 : 1n-9, total MUFA, Δ^9-C18 and elongation indices at weaning (Table 2). At slaughter, similar significant effects were observed in the proportions of 18 : 0, 18 : 1n-9, SFA, MUFA and Δ^9-C18 and elongation indices.

There were strong and positive genetic correlations (r_g) between triacylglycerol fatty acids and enzyme indices at weaning and slaughter (Table 6). The highest r_g of 0.98 was obtained for 18 : 1n-9, whereas the lowest r_g of 0.11 was for elongation index. Individual fatty acids 16 : 1 and 18 : 0 at weaning and slaughter were also highly positively correlated (0.88 for 16 : 1 and 0.75 for 18 : 0, respectively). On the other hand, 16 : 0, the most abundant saturated fatty acid, was poorly correlated (0.15) at weaning and slaughter.

For the most part, phenotypic correlations (r_p) were very low, ranging from 0.04 in 16 : 1 to 0.44 in total SFA (Table 6). Simple regression equations for predicting carcass fatty acids at slaughter from biopsy data at weaning were derived (Table 7). The highest coefficient of determination (R^2) value of 0.74 was obtained from the prediction of 18 : 0, whereas the lowest R^2 values of 0.06 were from the predictions of 16 : 0 and total PUFA.

Estimates of heritability (h^2) for triacylglycerol fatty acids at weaning and slaughter were calculated (Table 8). At weaning, individual fatty acids 16 : 0, 16 : 1, 18 : 0 and 18 : 1n-9 had h^2 values of 0.13, 0.12, 0.10 and 0.26, respectively. A summation of total SFA, MUFA and PUFA produced h^2 values of 0.15, 0.31 and 0.03, respectively. Calculated enzyme indices had h^2 values of 0.06, 0.25 and 0.21 for Δ^9-C16, Δ^9-C18 and elongase, respectively (Table 8). In general, the results show that triacylglycerol fatty acids in the adipose tissue of weaner cattle have a low to moderately low heritability. Heritability estimates were generally higher at slaughter than at weaning for most traits (Table 8). The h^2 estimates at slaughter using

Table 6. **Genetic (r_g) and phenotypic (r_p) correlations between TAG fatty acids at weaning and slaughter**[A]

Trait	r_p	r_g
16 : 0	0.11 ± 0.04	0.15 ± 0.33
16 : 1	0.04 ± 0.02	0.88 ± 0.42
18 : 0	0.10 ± 0.03	0.75 ± 0.52
18 : 1n-9	0.10 ± 0.04	0.98 ± 0.80
SFA	0.44 ± 0.04	0.21 ± 0.43
MUFA	0.21 ± 0.04	0.86 ± 0.50
PUFA	0.08 ± 0.03	0.67 ± 0.42
Δ^9(C16)	0.07 ± 0.04	0.72 ± 0.56
Δ^9(C18)	0.13 ± 0.03	0.76 ± 0.36
Elongase	0.16 ± 0.04	0.11 ± 0.59

[A]Abbreviation of traits as in Table 2

Table 7. **Simple regression equations for the prediction of carcass fatty acids at slaughter (Y) from biopsy data at weaning (x)**[A]

Trait	Prediction equation	R^2
16 : 0	$Y = 34.45 - 0.17x$	0.06
16 : 1	$Y = 0.91 + 0.66x$	0.61
18 : 0	$Y = 9.38 + 0.33x$	0.74
18 : 1n-9	$Y = 23.98 + 0.51x$	0.20
SFA	$Y = 37.81 + 0.20x$	0.23
MUFA	$Y = 40.41 + 0.21x$	0.24
PUFA	$Y = 1.74 + 0.16x$	0.06
Δ^9(C18)	$Y = 50.30 + 0.34x$	0.68
Elongase	$Y = 18.87 + 0.76x$	0.41

[A]Abbreviation of traits as in Table 2
R^2, coefficient of determination

SAS (1989) for 16 : 0, 16 : 1, 18 : 0 and 18 : 1n-9 were 0.10, 0.16, 0.43 and 0.28, respectively. With the exception of 16 : 1, h^2 estimates obtained using HARVEY (1990) were similar (0.17, 0.06, 0.37 and 0.30 for 16 : 0, 16 : 1, 18 : 0 and 18 : 1n-9, respectively) to the SAS (1989) estimates. ASREML estimates were however, generally lower than those obtained using both SAS (1989) and HARVEY (1990) (Table 8), indicating that it is a more conservative estimation than either SAS and HARVEY.

Summations of saturated, mono-unsaturated and polyunsaturated fatty acids portrayed significant increases in h^2 estimates at slaughter, regardless of the analytical software used (Table 8). SFA, MUFA and PUFA had h^2 estimates of 0.21, 0.40 and 0.18 (SAS, 1989), 0.22, 0.40 and 0.09 (HARVEY, 1990) and 0.30, 0.20 and 0.05 (ASREML), respectively. It is obvious that total MUFA, which are highly desirable in human diets in view of their cholesterol-lowering ability, are moderate to highly heritable at slaughter. Of equal importance too, are the individual fatty acids 18 : 0 and 18 : 1n-9 with moderate to high heritabilities of 0.37–0.43 and 0.28–0.30, respectively.

Calculated enzyme indices of desaturation and elongation had low to moderately high h^2

Table 8. **Heritability (h^2) estimates ± SE of TAG fatty acids**[A]

Fatty acids	Weaning (SAS)	Slaughter (SAS)	Slaughter (HARVEY)	Slaughter (ASREML)
16:0	0.13 ± 0.10	0.10 ± 0.10	0.17 ± 0.09	0.13 ± 0.08
16:1	0.12 ± 0.07	0.16 ± 0.06	0.06 ± 0.08	0.02 ± 0.09
18:0	0.10 ± 0.16	0.43 ± 0.18	0.37 ± 0.20	0.12 ± 0.08
18:1n-9	0.26 ± 0.20	0.28 ± 0.15	0.30 ± 0.15	0.09 ± 0.07
SFA	0.15 ± 0.12	0.21 ± 0.17	0.22 ± 0.16	0.30 ± 0.06
MUFA	0.31 ± 0.18	0.40 ± 0.15	0.40 ± 0.20	0.20 ± 0.05
PUFA	0.03 ± 0.10	0.18 ± 0.09	0.09 ± 0.07	0.05 ± 0.08
Δ^9(C16)	0.06 ± 0.07	0.10 ± 0.06	0.04 ± 0.06	0.06 ± 0.08
Δ^9(C18)	0.25 ± 0.21	0.44 ± 0.15	0.40 ± 0.20	0.25 ± 0.06
Elongase	0.21 ± 0.20	0.29 ± 0.07	0.29 ± 0.09	0.14 ± 0.07
Marbling	–	0.52 ± 0.08	0.40 ± 0.10	0.15 ± 0.09
Intramuscular fat	–	0.00 ± 0.04	0.02 ± 0.03	0.00 ± 0.02
Melting point	–	0.08 ± 0.04	0.19 ± 0.10	0.20 ± 0.09

[A]Abbreviation of traits as in Table 2

values at slaughter, ranging from 0.04 (Δ^9-C16) to 0.44 (Δ^9-C18) (Table 8). Estimates obtained using SAS (1989) and HARVEY (1990) were similar, although ASREML estimates were lower than both. Marbling scores of the carcasses at slaughter had a heritability estimate of 0.52 (SAS), 0.40 (HARVEY) and 0.15 (ASREML), whereas intramuscular fat content had a zero heritability regardless of the analytical software used (Table 8). Melting point of the fat had a low heritability of 0.08 to 0.20.

Discussion

Excess fat production (SMITH et al. 1991) and inconsistent tenderness of meat (MORGAN et al. 1991; SAVELL and SHACKELFORD 1992) have been identified as major concerns to the beef industry. Beef breeders are faced with the challenge of using diverse resources to produce cattle and meat products that are in demand by consumers. To accomplish these goals, breeders need information on breed differences and genetic parameters for a wide spectrum of traits to develop effective breeding schemes (MARSHALL 1994). In this paper, location, sex and breed differences in fatty acid composition at weaning and slaughter are presented. Furthermore, heritabilities, genetic and phenotypic correlations of fatty acids and enzyme indices are reported.

Location differences

The cattle used in this study were maintained on two properties (and three management groups) at Struan and Wandilo. Struan is located on flat plains whereas Wandilo is more of a sandy terrain. Even though the cattle grazed on pasture in both locations at weaning, the adipose tissues of cattle located at Wandilo had higher proportions of total PUFA and desaturation enzyme indices and less 18:0 than those at Struan (Table 3). This observation seems to reflect differences in management practices relating to pasture quality. It is interesting that after rearing in the feedlot post-weaning, no location differences in fatty acid composition were detected, the only exception being 18:0. There doesn't seem to be a satisfactory explanation for this because 18:0 does not have a dietary origin since it is synthesized *de novo* from the elongation of 16:0 (palmitate) by the elongase enzyme. The

fact that there was no difference in elongation enzyme index between the two locations at weaning and slaughter rules out possible differences in *de novo* synthesis.

Sex differences

Sex differences were consistent with the authors' previous results (MALAU-ADULI et al. 1995; SIEBERT et al. 1996; MALAU-ADULI et al. 1997, 1998; DELAND et al. 1998; SIEBERT et al. 1998). Heifers had higher proportions of 16 : 1, 18 : 1n-9, total MUFA and desaturation enzyme index than steers at weaning. Heifers also had higher marbling scores, intramuscular fat content and elongation enzyme index than steers at slaughter (Table 4). An explanation lies in differences in fatness and maturity between heifers and steers. Heifers reach physiological maturity and begin to deposit intramuscular fat earlier than steers. ZEMBAYASHI et al. (1995) and HUERTA-LEIDENZ et al. (1996) demonstrated that changes in fatty acid composition were related to fatness and rate of fat deposition such that fatter animals contain higher proportions of MUFA than lean animals. This is supported by the results herein showing that at the same age at weaning, heifers had more MUFA and a higher desaturation index than steers.

It was demonstrated earlier (MALAU-ADULI et al. 1997) that with increasing age, there is an increase in the proportion of MUFA and a corresponding decrease in SFA. From weaning to slaughter, it was evident that the proportions of MUFA increased and SFA decreased in both sexes (Table 4). Despite the fact that steers were fed for 90 days longer than the heifers in the feedlot, the heifers still had higher intramuscular fat content and marbling scores than steers. This is further evidence of a sex variation, regardless of age differences between heifers and steers at slaughter.

Breed differences

At both weaning and slaughter, breed differences in fatty acid composition and enzyme indices were observed. The early-maturing breeds (Jersey, Wagyu and Angus) contained higher proportions of unsaturated fatty acids and higher desaturation enzyme indices than the late-maturing Limousin, South Devon and Belgian Blue. Differences in maturity patterns have significant influences on fat deposition, desaturation and elongation enzyme indices. The Wagyu breed for example, is renowned for depositing extremely high amounts of intramuscular fat (LUNT et al. 1993). STURDIVANT et al. (1992) was of the opinion that elevated stearoyl-coA desaturation enzyme activity was responsible for the high proportions of MUFA in the adipose tissue of Wagyu cattle. MAY et al. (1993) reported that fat from Wagyu cattle had higher proportions of 16 : 1 and 18 : 1n-9 and lower 16 : 0 and 18 : 0 than Angus raised under the same conditions, although it was not clear if this difference was solely due to breed or partly due to fatness levels. However, ZEMBAYASHI et al. (1995) answered this question by reporting that at the same degree of fatness, the Wagyu breed had proportions of 16 : 0, 16 : 1 and 18 : 1n-9 that were significantly different from those of other breeds. Herein, the early maturing breeds (Jersey and Wagyu crosses) had higher proportions of unsaturated fatty acids and desaturation indices than the late-maturing breeds, and thus, the results agree with those cited above.

In other earlier studies on breed differences in fatty acid composition, GILLIS et al. (1973) used progeny from Limousin and Simmental bulls crossed with three dam breeds and reported significant breed differences in 14 : 0, 16 : 0, 16 : 1, and 18 : 0 in the adipose tissue. More recently, PERRY et al. (1998) found significant sire-breed differences in the fatty acid composition and melting point of fat in Hereford, Brahman × Hereford, Simmental × Hereford and Friesian × Hereford cattle. They reported that breed differences in fatty acid composition at the same age are associated with variation in stage of maturity at slaughter as reflected by differences in percentage fat.

There was a large variation between sires within breed because the effect of sire nested

within breed was significant for total SFA, MUFA and enzyme indices (Table 2). This indirectly suggests that the contribution of direct additive genetic variance from sires to progeny within breeds was significant.

Genetic and phenotypic correlations

There is strong evidence that a relationship exists between triacylglycerol fatty acids from the adipose tissue of cattle at weaning and slaughter (Table 6). Genetic correlations were strong and positive for almost all individual fatty acids and their summations, as well as the desaturation and elongation enzyme indices (Table 6). This implies that the additive genetic variance component contributes more to the association of these fatty acids than the environmental componet. The exceptions were 16:0, SFA and elongation enzyme index which were poorly genetically correlated (0.15, 0.21 and 0.11, respectively).

The two 18-carbon fatty acids: 18:0 and 18:1n-9, as well as total MUFA were strongly and positively correlated (0.75, 0.98 and 0.86, respectively) (Table 6). This offers hope to beef breeders that selection for these fatty acids could be made early when the cattle are weaned. Also, if the desaturation index is used in selection programmes by beef breeders, an early decision could be made at weaning, given the strong, positive correlations of 0.72 and 0.76 for Δ^9-C16 and Δ^9-C18 desaturation respectively, at weaning and slaughter. Based on the prediction equations developed in this study, 61, 74 and 68% of the variation in carcass 16:1, 18:0 and Δ^9-C18 desaturation, respectively, can be explained using biopsy fatty acid data at weaning (Table 7). The accuracy and precision of prediction could possibly be higher if selection for these fatty acids is carried out.

Generally, phenotypic correlations between individual fatty acids, their summations and enzyme indices at weaning and slaughter were very poor (Table 6). This observation seems to agree with the report of KOOTS et al. (1994) who estimated phenotypic and genetic correlations among beef cattle traits. They demonstrated that phenotypic correlation estimates for many carcass-quality traits as well as among reproductive traits were very poor.

Heritability estimates

Individual fatty acids, their summations as well as desaturation and elongation enzyme indices generally had low heritabilities at weaning, ranging from 0.03 to 0.31 (Table 8). This indicates that additive genetic variation sufficient to enable genetic progress at weaning would be low. However, total MUFA could be singled out as the exception because they had the highest h^2 value of 0.31, implying moderate genetic gain. The results at weaning also stress the importance of paying attention to environmental factors such as the feeding regime and management of weaner calves since the environment contributes more to the phenotype than the genetic component at this age.

Heritability estimates at slaughter were higher than at weaning (Table 8). This might have been partly due to differences between the breeds of cattle in maturity pattern as age increased, and not the slightly lower numbers of cattle at slaughter, because the standard errors were very similar to those at weaning. Individual fatty acids 18:0 and 18:1n-9 had reasonably high h^2 estimates of 0.43 and 0.28, respectively, implying that significant genetic progress could be made by selecting for these fatty acids. High h^2 estimates of 0.65 and 0.25 have been reported for 18:1n-9 and 18:0, respectively, in the backfat of Large White and French Landrace pigs (BOUT et al. 1991). CAMERON and ENSER (1991) found h^2 estimates for fatty acid concentrations in intramuscular fat that ranged from 0.24 to 0.73 in Duroc and British Landrace pigs. From the results of the present study in cattle, the implication is that selecting individuals with high proportions of 18-carbon fatty acids and MUFA to sire progeny would lead to moderate to high genetic gains. Furthermore, this decision could be made at weaning because of the high genetic correlation between weaner and slaughter fatty acid compositions. In selection programmes, the use of desaturation enzyme index appears

to offer a potentially reliable tool given its moderate to high heritability of 0.25 to 0.44 (Table 8).

Other traits of interest at slaughter examined herein included marbling score, intramuscular fat and melting point of fat. Marbling score was moderate to highly heritable (0.15 to 0.52). Previous studies on marbling score reported h^2 estimates of 0.52 (O'CONNOR et al. 1997), 0.47 (BENYSHEK 1981), 0.43 (VAN VLECK et al. 1992), 0.40 (KOCH et al. 1982), 0.35 (ARNOLD et al. 1991; MARSHALL 1994) and 0.23 (WOODWARD et al. 1992). Marbling is currently an important factor used by the Australian beef industry to assign carcass quality of exported beef. The high heritability suggests that breeders can make genetic gains by selecting sires with high marbling scores if they intend to meet the export market demands.

LUNT et al. (1993) reported that the Wagyu breed deposits extremely high amounts of intramuscular fat. Results from this study suggest that regardless of the method used for estimation, intramuscular fat content was not heritable (Table 8). An explanation could be that the variation between sires within breeds was not sufficiently large and hence the additive genetic variance component was zero. This implies that selecting directly for this trait would not lead to any significant genetic gains. Management factors such as energy content of grains used in feeding and the duration of feedlotting are key to improving intramuscular fat content. However, selection programmes based on marbling scores are expected to lead to a simultaneous improvement in intramuscular fat content because the two traits are positively correlated, 0.68 (MALAU-ADULI 1998) and 0.51 (BAUD et al. 1998).

It was hoped that the heritability estimates of intramuscular fat content and marbling scores would be similar, given their positive correlation, but that was not the case (Table 8). It has been demonstrated that marbling scores do not accurately match intramascular fat content (MALAU-ADULI 1998). BLUMER et al. (1962) observed that in some cases, the ether-extract value for intramuscular fat was not that expected, given the assessment of marbling. This was thought to be due to either changes in the pattern of fat deposition beneath the cut surface of the sample, or to the presence of microscopic fat deposits within the sample. More recently, BAUD et al. (1998) reported that even though marbling score and intramuscular fat were found to be moderately correlated, there was a considerable variation in intramuscular fat within any marbling score. They concluded that the variation plus the subjective nature of the marbling scoring system causes a considerable error in marbling scores and a reduced correlation with intramuscular fat percentage.

Melting point of fat was low to moderately heritable (0.08–0.20) (Table 8). Melting point is an objective measurement which indicates the hardness or softness of fat. Its moderate heritability indicates that in the beef industry, where chilled carcasses are boned and hard fat is of concern in meat processing, moderate genetic gains could be made by selecting for softer fat. This would in turn, mean more proportions of unsaturated fatty acids as they are negatively correlated with melting point.

It is also evident from this study that the use of different softwares (SAS 1989; HARVEY 1990; and ASREML) to compute heritabilities gives estimates that are very similar but not exactly the same (Table 8). A possible explanation for this could be that for the same data set, the sensitivity with which restricted maximum likelihood procedure works, varies from one software to the other. In this case, ASREML appears to be the most sensitive and conservative, then HARVEY (1990) and SAS (1989) in that order. Overall, the results of this study indicate that any of the three softwares is sufficient and reliable for the estimation of heritabilities.

In conclusion, fatty acids in the triacylglycerol fraction of bovine adipose tissue have a low to moderate heritability at weaning and moderate to high heritability at slaughter. Beef breeders can make early selection decisions for the highly desirable 18-carbon fatty acids, total MUFA and desaturation indices because these traits at weaning and slaughter have strong, positive genetic correlations. Since genetic correlations were high for key fatty acids,

producers may be able to select for fatty acid composition in carcasses by selecting on biopsy data collected at 300 days of age.

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