

Effects of breed and a concentrate or grass silage diet on beef quality in cattle of 3 ages. I: Animal performance, carcass quality and muscle fatty acid composition

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Abstract

An increase in the intake of the *n*-3 series polyunsaturated fatty acids (PUFA) is recommended by nutritionists for the human diet and beef is a significant source of these fatty acids. Enhancing the *n*-3 PUFA content of beef is important in view of the generally saturated nature of fatty acids in ruminant meats and the potentially negative effect this can have on human health. This study examined the effects of breed and diet on the fatty acid composition of beef *M. longissimus*. Ninety-six steers were used, 48 Aberdeen Angus cross (AA) and 48 Holstein–Friesian (HF). At 6 months of age, 3 groups were identified, to be slaughtered at 14, 19 and 24 months, respectively. Each group consisted of eight steers of each breed fed on a concentrate or a grass silage diet, rich in *n*-6 and *n*-3 PUFA, respectively. The intake of the concentrate diet was restricted so that steers of each breed grew at a similar rate on each diet. The early maturing AA produced heavier, fatter carcasses with better conformation. Animals fed grass silage had higher carcass fatness and conformation scores and higher levels of neutral lipid and total lipid in muscle than those fed concentrate. When all animals were pooled, a decline in PUFA% as total muscle lipid increased was evident. Feeding a grass silage diet rich in α -linolenic acid (18:3*n*-3) increased levels of this fatty acid in muscle neutral lipid by a factor of about 3.0 compared with the concentrate diet, as well as enhancing the synthesis of the *n*-3 series long-chain C20–22 PUFA in the phospholipid fraction, including docosahexaenoic acid (DHA, 22:6*n*-3). In contrast, both levels and proportions of linoleic acid (18:2*n*-6) and the *n*-6 series C20–22 PUFA were higher in animals fed the concentrate diet. The proportions of 18:1*trans* and conjugated linoleic acid (CLA) in muscle neutral lipid were higher in animals fed concentrate compared with silage in all 3 groups. This was partly due to increased consumption of 18:2*n*-6. The ratio of PUFA to saturated fatty acids (P:S) in muscle was reduced by feeding grass silage, partly as the result of increased fat deposition. However, the increase in levels of *n*-3 series fatty acids with silage-feeding resulted in beneficially low *n*-6:*n*-3 ratios in muscle in all age groups (approximately 1.2 compared with 12.0 in the concentrate diet). Subtle breed differences in PUFA amounts and proportions were noted. Holstein–Friesians had higher proportions of PUFA and higher P:S ratios compared with AA, partly due to a higher proportion of phospholipid in total lipid. In phospholipid itself, HF in the 19 and 24 months groups had higher proportions of most *n*-3 PUFA. In all age groups the ratio of DHA to its precursor, 18:3*n*-3 was higher in HF.

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1. Introduction

The fatty acid composition of meat (muscle and adipose tissue) is important for two main reasons: it determines

nutritional value and it affects various aspects of meat quality, including shelf life and flavour (Wood et al., 2003). Nutritional value is determined primarily by the ratio between saturated fatty acids (SFA) and polyunsaturated fatty acids (PUFA) in meat and the balance between fatty acids of the *n*-6 and *n*-3 series. In general, a ratio of PUFA to SFA (termed P:S) above about 0.45 and a ratio of *n*-6:*n*-3 below about 4.0 are required in the diet to

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combat various “lifestyle diseases” such as coronary heart disease and cancers (Simopoulos, 2004; Williams, 2000).

Several factors in beef production affect fatty acid composition, including breed and diet. Breed affects the fat content of meat and fat content itself is a factor determining fatty acid composition (Choi, Enser, Wood, & Scollan, 2000; Scollan et al., 2006). Ruminants naturally consume a diet which is low in fat but high in PUFA, whether in fresh grass, conserved grass or the concentrate portion of the diet. However, a high proportion of PUFA undergoes microbial biohydrogenation in the rumen, leading to predominantly SFA being absorbed in the intestine and deposited in tissues. Despite this, dietary manipulation of muscle and adipose tissue is possible and the potential to enrich ruminant tissues with *n*-3 PUFA has been demonstrated (Marmer, Maxwell, & Williams, 1984; Ponnampalam, Sinclair, Egan, Ferrier, & Leury, 2002; Scollan et al., 2001; Scollan et al., 2006). Of particular interest is the use of grass and forages to increase the concentration of α -linolenic acid (18:3*n*-3) in meat. This fatty acid is then converted by desaturase and elongase enzymes into the desirable long-chain (C20–22) *n*-3 PUFA such as eicosapentaenoic acid (EPA, 20:5*n*-3) and docosahexaenoic acid (DHA, 22:6*n*-3). In contrast, concentrate diets based on grains and protein supplements are high in linoleic acid (18:2*n*-6), the precursor of the *n*-6 series of PUFA. Grass feeding has also been shown to enhance levels of conjugated linoleic acid (CLA) (Dannenberger et al., 2005), particularly the *cis*-9, *trans*-11 isomer, which has anti-carcinogenic properties (Steen & Porter, 2003).

The purpose of this study was to investigate the effects of breed and diet (concentrate or grass silage, rich in *n*-6 and *n*-3 PUFA, respectively) on the fatty acid composition of beef and also on animal performance and carcass characteristics. In contrast to previous “concentrate-based” studies, the concentrate employed used full fat soya rather than extracted soya to ensure this diet was high in 18:2*n*-6. Steers were reared from 6 months to 3 ages covering the commercial range of slaughter ages. A particular aim was to rear the animals so that the steers fed concentrate and silage grew at similar rates and were slaughtered at similar weights, thus avoiding the large differences in growth rate and final carcass weight which often develop when feeding regimes are compared (Bowling, Smith, Carpenter, Dutson, & Oliver, 1977; Hedrick et al., 1983) and which affect fat content and fatty acid composition.

2. Materials and methods

2.1. Animals

Forty-eight Aberdeen Angus \times Holstein–Friesian steers (AA) (initial age 232 d and live weight 224 kg) and 48 Holstein–Friesian steers (HF) (initial age 214 d and live weight 206 kg, SD for age and live weight 2.2 d and 3.4 kg, respectively) were housed in a well-ventilated barn at the Beef

Research Unit, IGER, Aberystwyth and bedded on wood shavings with free access to fresh water. Animals were individually fed via Hoko Feeders (Insentec, Marknesse, The Netherlands). At the end of a 14 d acclimatisation period, during which all animals were fed on 1 kg of concentrates daily and *ad libitum* grass silage, animals were weighed and then allocated to treatment groups balanced for age and live weight. Twelve treatment groups comprised the two breeds (AA and HF), two dietary treatments (restricted concentrate/barley straw at 70:30 (DM basis) or *ad libitum* grass silage) and three slaughter age points (14, 19 and 24 months of age). Each treatment group contained 8 animals, which were penned together.

During the main experimental period, animal live weight was determined every 14 d on two consecutive days and data were used to calculate average daily live weight gain. All weighings were conducted at the same time of day (13:30 h) to minimise the effects of diurnal variations in feed intake. Animal weight, together with individual intake data, was used to adjust the intakes of animals fed the restricted concentrate/barley straw diet in order to achieve similar growth rates for steers of each breed given the two diets. Growth rate was, therefore, equalised across diets within breed.

2.2. Diets

The experimental concentrate was prepared by Welsh Feed Producers (Carmarthen, Wales) and consisted of barley, molassed sugarbeet pulp, molasses and full-fat soya (Table 1). A standard commercial mineral/vitamin premix was used, which resulted in a target level of 25 IU of vitamin E per kg of feed. Animals were initially offered a mix of grass silage and barley straw, in which the proportion of grass silage was decreased over three weeks prior to the main experimental period when they were offered straw alone. The straw was chopped in a mixer wagon to achieve a uniform mix and straw length (approximately 8–12 cm) before feeding.

To make the silage, perennial ryegrass was harvested with a disc mower and collected with a precision chop harvester (chop length 30 mm) after a minimum wilt (2–3 h) to minimise oxidation losses of the *n*-3 series PUFA and ensiled in a 600T concrete clamp. Formic acid (Add-F, Trouw Nutrition, Cheshire, UK) was added to the grass during collection at 4 l/T. The long-term nature of the study necessitated making the grass silage in two batches

Table 1
Formulation of experimental concentrate (g/kg as fed)

Ingredient	(g/kg as fed)
Barley	600
Molassed sugarbeet pulp	200
Molasses	50
Full-fat soyabean meal	125
Mineral/vitamin premix	25

(in mid-May 2000 and 2001) according to a similar prescription.

After a standardisation period the animals were introduced to the experimental diets mid-autumn. Grass silage and straw was fed at 14:00 h daily and the concentrate in two equal portions at 09:00 h and 16:30 h. The grass silage, straw and concentrate were sampled twice weekly for DM analysis in a forced-air oven at 105 °C. Samples of silage, straw and concentrate were accumulated over 4-week periods and chemical composition assessed as described by Dewhurst et al. (1999).

Growth rates of the silage-fed animals were initially poor at 0.3 kg/d associated with a low dry matter content. To increase live weight gain it was essential to modify the grass silage without significantly changing its fatty acid composition. Hence, molassed sugarbeet pulp shreds (SBPS) (also present in the concentrate diet) was added at approximately 15% of the total DM intake, in January when the animals were 9 months old, with the aim of increasing silage DM and providing rapidly available energy to increase the efficiency of utilisation of metabolisable protein (MP) by rumen microbes and thereby improve animal performance. Following the inclusion of SBPS, growth rates increased to an acceptable level of around 0.9 kg/d.

2.3. Transport of animals, slaughter protocol, sampling and analysis

The 32 steers in each age group, were selected for slaughter on a live weight basis over a 4-week period, the heavier animals being slaughtered first, with equal numbers of each breed and diet on each occasion. Carcasses were subjected to electrical stimulation using a low voltage electrical stimulation unit (MIRINZ, Hamilton, New Zealand) delivering 90 v [125–500 mA, pulse width 5–10 ms, pulse period 57–80 ms (14.3 Hz)] for 60 s, 30 s after bleeding began. After dressing, the carcasses were transferred to a chiller at 2 °C. At 48 h after slaughter, carcasses were classified and samples removed for analysis. Cold carcass weight excluded kidney knob and channel fat (KKCF). External fatness and conformation scores were assessed by the same individual using the EEC carcass classification scheme as described by Kempster, Cook, and Grantley-Smith (1986). There are five main fatness and conformation classes to which numerical values are assigned.

Complete cross-sections of the *M. longissimus* from one side of the carcass at the 10–11th rib level, 20 mm thick, were taken for fatty acid analysis as described in detail by Scollan et al. (2001). Briefly, lipids were extracted using chloroform:methanol (2:1). Neutral lipid and phospholipid were separated using silicic acid chromatography. These were hydrolysed with 2 M KOH in water:methanol (1:1) and the fatty acids extracted into petroleum spirit. The fatty acids were methylated using diazomethane and analysed by gas liquid chromatography. Muscle fatty acid results are given as mg of fatty acid per 100 g wet tissue

quantified by reference to the internal standard (21:0) (useful for calculating nutritional value) or as proportion times 100 (the normal method of expression). Total lipid is the sum of the neutral lipid and phospholipid fractions. Only the major fatty acids and minor components readily identified and relevant to the study are reported, representing over 90% of the total fatty acids present. The fatty acid reported as 16:1*cis* consists of both the *n*-9 and *n*-7 isomers and contaminating branched 17-carbon fatty acids. The 18:1*trans* isomers are incompletely resolved by this procedure and are reported as one value. In view of the complexity of the chromatogram in this area, as a result of the wide range of 18:1 isomers in ruminant tissues (Hay & Morrison, 1972), some minor cross-contamination of the listed 18:1 isomers may be present.

2.4. Statistical analysis

Data for each age group were analysed using general linear models (GLM), with breed and diet as factors and including the interaction term (Minitab Release 14). Values in the Tables are the breed × diet interaction means. Paired comparisons between means in the event of a breed × diet interaction were assessed post hoc using either the Tukey test (balanced case) or the Tukey–Kramer test (unbalanced case). Live weight, live weight gains and carcass weights were corrected for differences in initial age and live weight by fitting covariates for these parameters. Data for the fatty acid composition of diets was analysed by ANOVA (Genstat 6, Lawes Agricultural Trust, 2002) using sampling time and feed type as factors.

3. Results

3.1. Diets

Average values for the chemical composition of the complete grass silage (including SBPS) and the concentrate diets are given in Table 2. Ether extract (EE) and total nitrogen (TN) contents were similar in the concentrate and silage. The coefficients of variation (CV) for the silage following inclusion of the SBPS were 0.07, 0.03, 0.08, 0.23, 0.16, 0.05 and 0.22 for DM, pH, TN, ammonia nitrogen, lactate, EE and WSC contents, respectively. The CV for the concentrate DM, organic matter, TN, WSC, NDF, ADF and EE were 0.01, 0.005, 0.08, 0.06, 0.13, 0.13 and 0.07, respectively.

The fatty acid composition of the concentrate and grass silage diets is given in Table 3. Total fatty acid levels in the concentrate were over twice those in the silage diet. The dominant fatty acids were 16:0, 18:2*n*-6 and 18:3*n*-3 in both the concentrate and silage. The CVs for 16:0, 18:2*n*-6 and 18:3*n*-3 for the concentrate were 0.08, 0.13 and 0.17, respectively. The CVs for the same FA for the silage were 0.07, 0.11 and 0.14, respectively. The silage had lower concentrations of 16:0 and 18:0 than the concentrate and considerably lower concentrations of oleic acid (18:1*cis*-9) and

Table 2
Chemical composition (g/kg DM unless otherwise stated) of the complete experimental diets

	Concentrates	Silage
Dry matter (g/kg fresh matter)	883.7	258.5
Organic matter	906.8	907.6
Total nitrogen (TN)	23.4	25.5
Water-soluble carbohydrates (WSC)	107.5	51.7
Neutral detergent fibre (NDF)	171.9	490.6
Acid detergent fibre (ADF)	80.4	318.3
Ether extract (EE)	42.4	40.7
Ammonia nitrogen (g/kg total nitrogen)	–	101.2
pH	–	3.3
Lactate	–	114.4
Acetate	–	19.6
Propionate	–	0.3
<i>n</i> -Butyric	–	0.0

Table 3
Concentrations (g/kg DM) of total and selected fatty acids in experimental diets

Fatty acid	Concentrate	Silage	SED ^a	Significance
Total	45.2	20.4	0.75	***
C12:0	0.5	0.1	0.11	***
C14:0	0.3	0.2	0.04	ns
C16:0	7.5	4.0	0.13	***
C16:1	0.06	0.05	0.002	***
C18:0	1.2	0.4	0.02	***
C18:1 <i>cis</i> -9	7.5	0.6	0.15	***
C18:1 <i>cis</i> -11	0.5	0.1	0.01	***
C18:2 <i>n</i> -6	24.7	3.3	0.39	***
C18:3 <i>n</i> -3	2.8	11.4	0.30	***
C20:0	0.13	0.13	0.003	ns

^a Standard error of the difference of the mean.

linoleic acid (18:2*n*-6). In contrast, the silage was high in α -linolenic acid (18:3*n*-3) compared with the concentrate, the diets averaging 56% and 6%, respectively.

3.2. Animal performance and carcass classification

Animal performance and carcass classification results are in Table 4. The intake of grass silage (kg DM/day) was higher than that of concentrate in all age groups, reflecting its lower energy value. Average daily gain differed slightly between the diets in all age groups, although the intention was to keep the growth rate the same for the two diets within each breed. HF were slightly younger at slaughter than AA in all the age groups. AA tended to be heavier than HF in the 14 months group although the difference was only significant on the grass silage diet. There were no differences between breeds or diets for live weight in the 19 month group. In the 24 month group, AA were heavier than HF on both diets. The carcass conformation score tended to be higher in AA than HF in the 14 month group, although the breed difference was only significant on the grass silage diet (similar result for final live weight) and was higher in AA in the 19 and 24 month groups. In the 24 month group, there was an effect of diet,

conformation score being lower in the steers fed concentrate. In the 14 month group, AA were fatter than HF and grass silage-fed steers were fatter than those fed concentrate. These same effects of breed and diet occurred in the 19 month and 24 month groups. In the 19 month steers fed grass silage (for example) these numerical values for conformation and fatness translate to Meat and Livestock Commission classification scores of R4H and O+3 in AA and HF, respectively. In the 24 month steers fed grass silage, the MLC scores would have been similar.

3.3. Fatty acid content and composition

Values for total lipid, total neutral lipid, (NL) and total phospholipid (PL) fatty acids and the major fatty acid classes of muscle are given in Table 5 and include all the fatty acids in these fractions. In the 14 month group, diet affected fatty acid amounts and proportions more than breed. The amounts (mg/100 g muscle) of total lipid, NL, saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and *n*-3 PUFA and the proportions of these in total lipid were all significantly higher in the animals fed grass silage. On the other hand, the amounts and proportions of PUFA and *n*-6 PUFA were higher in the steers fed concentrate. The only significant breed difference was in the proportion of *n*-6 PUFA which was higher in HF ($P < 0.05$). The amount of PL was not affected by diet or breed. The same trends were apparent in the 19 month group, although very high values for amounts of total lipid, NL, SFA and MUFA and the proportion of SFA in AA fed grass silage resulted in significant ($P < 0.05$) breed \times diet interactions for these components. In the same way, a bigger response to diet by HF caused a breed \times diet interaction for the proportion of *n*-3 PUFA. Amounts and proportions of PUFA and *n*-6 PUFA were higher in the steers fed concentrate and the amount of *n*-3 PUFA was higher in those fed grass silage. In the 24 month group, both breed and diet had significant effects on lipid fractions and fatty acid classes. Total lipid, NL, SFA and MUFA amounts were higher in AA and so was the proportion of SFA. The proportions of PUFA, *n*-6 PUFA and *n*-3 PUFA were higher in HF although the big difference between diets for *n*-3 PUFA in HF caused a breed \times diet interaction similar to that in the 19 month group. The effects of diet observed in the earlier age groups were again apparent; the grass silage diet produced high amounts of total lipid, NL, SFA, MUFA and *n*-3 PUFA and higher proportions of MUFA and *n*-3 PUFA, especially in HF. The amounts and proportions of PUFA and *n*-6 PUFA were higher in the concentrate diet. As with the other age groups, the amount of PL was not affected by breed or diet. PL was approximately 0.25 of total lipid at 14 months of age and 0.12 at 24 months.

The relationships between the percentages of SFA and PUFA and the amount of total lipid are shown in Fig. 1 for concentrate and silage-fed animals in all 3 age groups

Table 4
Animal performance and carcass classification of steers of different breeds fed concentrate or grass silage and slaughtered at 14, 19 or 24 months of age. All parameters except carcass conformation and fatness corrected for differences in initial live weight and age

	14 months						19 months						24 months					
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a	
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet
Total intake ^c	5.4	6.6	5.4	6.3	ns	***	5.7	7.7	5.6	7.5	ns	***	5.9	7.9	5.6	7.4	ns	***
Concentrate intake	3.0	–	3.0	–	ns	–	3.5	–	3.3	–	***	–	3.7	–	3.4	–	***	–
Forage intake	2.4	6.6	2.4	6.3	ns	***	2.3	7.7	2.3	7.5	ns	***	2.2	7.9	2.2	7.4	ns	***
Live weight gain (kg/d)	0.74 ^j	0.82 ^k	0.82 ^k	0.74 ^j	b	b	0.82 ^{pq}	0.87 ^q	0.88 ^q	0.77 ^p	b	b	0.84 ^{tu}	0.89 ^u	0.85 ^{tu}	0.77 ^t	b	b
Age at slaughter (d)	450	450	426	432	***	ns	569	581	553	561	**	ns	756	755	743	741	*	ns
Final live weight (kg)	389.9 ^{jk}	408.1 ^k	377.2 ^{jk}	363.6 ^j	b	b	518.8	514.1	510.9	489.7	ns	ns	659.4	686.3	593.6	614.3	***	ns
Half carcass wt (kg)	96.7 ^{jk}	101.9 ^k	92.0 ^j	88.7 ^j	b	b	134.1 ^{pq}	143.4 ^q	128.1 ^p	125.2 ^p	b	b	174.1	199.4	161.6	180.9	**	***
Conformation ^d	44.9 ^j	77.5 ^k	39.5 ^j	37.1 ^j	b	b	77.7	87.7	41.8	55.6	***	ns	71.0	85.2	38.3	64.0	***	**
Fatness ^d	54.9	63.0	24.5	42.7	***	**	69.6	114.1	26.7	74.1	***	***	85.9	107.1	42.1	67.0	***	***

AA – Aberdeen Angus, HF = Holstein–Friesian.

^a Significance of the main effects of breed and diet. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; ns not significant.

^b Significant Breed \times Diet interaction. Means with the same letter within age group (^{jk} 14 months, ^{pq} 19 months, ^{tu} 24 months) do not differ significantly, Tukey–Kramer test, post hoc ($P \leq 0.05$).

^c Intakes expressed as kg DM/day.

^d Based on EEC beef carcass classification scheme as amended by Kempster et al. (1986).

combined. This shows the clear decline in PUFA percentage as muscle lipid increased.

3.4. Muscle neutral lipid

The neutral lipid fatty acids, expressed as mg/100 g muscle and as proportions of total NL fatty acids $\times 100$ are presented in Tables 6 and 7, respectively. Muscle NL was dominated by 16:0, 18:0 and 18:1*cis*-9, which accounted for 28%, 13% and 37% of NL fatty acids, respectively.

In the 14 month group there were no significant breed effects on the amounts of individual NL fatty acids (Table 6), but all fatty acids were affected by diet. The grass silage diet produced more 14:0, 16:0, 16:1, 18:0, 18:1*cis*-9, 18:1*cis*-11, 20:1 and 18:3*n*-3. The concentrate-fed animals were higher in 18:1*trans*, 18:2*n*-6 and CLA. The same effects were observed in the 19 month group but, as was observed for the lipid classes and fatty acids fractions in Table 5, there were important breed \times diet interactions, all caused by an extreme response of AA to the grass silage diet. Thus, 14:0, 16:0, 16:1, 18:0, 18:1*cis*-9, 18:1*cis*-11, 20:1, 18:3*n*-3 and total NL fatty acids were higher in the animals fed grass silage but particularly so in AA. The concentrate diet produced higher amounts of 18:1*trans*, 18:2*n*-6 and CLA. All the same patterns were observed in the 24 month group but there was only one breed \times diet interaction (in this case for 18:3*n*-3). Again, the effect of diet (more 18:3 in the grass silage diet) was more pronounced in AA than HF. AA were higher than HF in 14:0, 16:0, 16:1, 18:0, 18:1*cis*-9, 18:1*cis*-11, 20:1 and CLA. The grass silage diet produced higher levels of all these fatty acids except CLA which was higher on the concentrate diet ($P < 0.01$). The amount of 18:3*n*-3 was higher in the animals fed grass silage and animals

fed concentrate were higher in 18:1*trans* and 18:2*n*-6 (as well as CLA).

There were few effects of breed on fatty acid proportions in the 14 month group (Table 7), although HF were higher in 18:3*n*-3. The grass silage diet produced higher proportions of 16:0, 16:1, 18:1*cis*-9 and 18:3*n*-3. The concentrate diet produced higher proportions of 18:1*trans*, 18:2*n*-6 (note interaction) and CLA. In the 19 month group, the proportions of 14:0 and 16:0 were higher in AA than HF whereas proportions of 18:1*cis*-9, 18:1*cis*-11 and 18:3*n*-3 were higher in HF. The grass silage diet produced higher proportions of 14:0, 16:0, 16:1, 18:1*cis*-9, 18:1*cis*-11 and 18:3*n*-3. The concentrate diet produced higher proportions of 18:0, 18:1*trans*, 18:2*n*-6 and CLA. In the 24 month group the proportion of 16:0 was higher in AA than HF and proportions of 18:1*trans*, 18:3*n*-3 and CLA are higher in HF. The significant breed \times diet interaction for 18:2*n*-6 was explained by a very high value in HF given the concentrate diet.

The relationships between the percentages of 18:2*n*-6, 18:3*n*-3 and total NL in concentrate and grass silage-fed animals for all 3 age groups combined are illustrated in Fig. 2. As total NL increased, so the percentages of 18:2*n*-6 and 18:3*n*-3 were reduced by dilution with SFA and MUFA. The relationship between the percentages of CLA and 18:1*trans* (mainly *trans*-11, *trans* vaccenic acid, TVA) in the NL, the fraction containing most of this fatty acid, is shown in Fig. 3. There was a clear separation between the two diets, with silage-fed steers clustered in the low CLA/low TVA part of the graph. Assuming a linear relationship between CLA and TVA (Enser et al. (1999) the overall equation was: CLA = 0.15 \times TVA + 0.075, $R^2 = 0.9$), indicating 1 molecule of CLA produced for every 6 molecules of TVA.

Table 5

Total lipid, total neutral lipid (NL) and total phospholipid (PL) levels in *M. longissimus* (mg/100 g) and proportions (times 100) of fatty acid classes in total fatty acids from steers of different breeds fed concentrate or grass silage to 14, 19 or 24 months of age

	14 months						19 months						24 months					
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a	
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet
Total lipid	1822	2668	1600	2518	ns	***	3129 ^P	6173 ^Q	2838 ^P	3667 ^P	b	b	5477	9616	4055	5100	**	*
Total NL	1276	2112	1109	1934	ns	***	2447 ^P	5485 ^Q	2243 ^P	3066 ^P	b	b	4802	8925	3353	4339	**	*
Total PL	546	556	491	584	ns	ns	683	688	595	601	ns	ns	675	692	702	761	ns	ns
SFA ^c	720	1128	614	1043	ns	***	1288 ^P	2768 ^Q	1143 ^P	1501 ^P	b	b	2282	4260	1602	2053	**	*
MUFA ^d	665	1090	569	1006	ns	***	1237 ^P	2679 ^Q	1131 ^P	1629 ^P	b	b	2461	4362	1744	2341	**	*
PUFA ^e	248.7	187.3	246.1	205.6	ns	**	330.5	229.8	311.8	210.4	ns	***	322.5	238.8	360.1	262.4	ns	***
Sum <i>n</i> -6 ^f	223.2	102.8	222.7	116.9	ns	***	310.0	123.7	291.5	113.2	ns	***	301.9	123.9	338.4	133.7	ns	***
Sum <i>n</i> -3 ^g	25.5	85.5	23.4	88.7	ns	***	20.5	106.1	20.3	97.2	ns	***	20.6	114.9	21.7	128.8	ns	***
<i>Proportions × 100</i>																		
SFA	39.6	42.0	38.3	41.0	ns	**	41.1 ^P	44.9 ^Q	40.3 ^P	40.7 ^P	b	b	41.5	43.3	39.4	40.0	***	ns
MUFA	36.2	40.8	35.2	39.8	ns	***	39.0	43.1	39.6	44.4	ns	***	44.4	45.7	42.8	45.4	ns	*
PUFA	13.8	7.2	15.7	8.7	ns	***	11.0	4.0	11.2	5.9	ns	***	6.5	3.0	9.2	5.7	***	***
Sum <i>n</i> -6	12.4	4.0	14.2	5.0	*	***	10.3	2.1	10.4	3.2	ns	***	6.1	1.5	8.7	2.9	***	***
Sum <i>n</i> -3	1.4	3.3	1.5	3.7	ns	***	0.7 ^P	1.9 ^Q	0.7 ^P	2.7 ^F	b	b	0.4 ^T	1.4 ^U	0.5 ^T	2.8 ^V	b	b

^a Significance of the main effects of breed and diet. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; ns not significant.

^b Significant Breed × Diet interaction. Means with the same letter within age group (^{PQ}19 months, ^{UV}24 months) do not differ significantly, Tukey–Kramer test, post hoc ($P \leq 0.05$).

^c SFA, saturated fatty acids (14:0 + 16:0 + 18:0).

^d MUFA, monounsaturated fatty acids (16:1 + 18:1_{cis}-9 + 18:1_{cis}-11 + 18:1_{trans}-11 + 20:1).

^e PUFA, polyunsaturated fatty acids (18:2_n-6 + 20:3_n-6 + 20:4_n-6 + 22:4_n-6 + 18:3_n-3 + 20:4_n-3 + 20:5_n-3 + 22:5_n-3 + 22:6_n-3).

^f Sum *n*-6 PUFA (18:2_n-6 + 20:3_n-6 + 20:4_n-6 + 22:4_n-6).

^g Sum *n*-3 PUFA (18:3_n-3 + 20:4_n-3 + 20:5_n-3 + 22:5_n-3 + 22:6_n-3).

3.5. Muscle phospholipid

The PL fatty acids expressed as mg/100 g muscle and as proportions of total PL fatty acids $\times 100$ are presented in Tables 8 and 9, respectively. The dominant fatty acids in the phospholipid fraction mirrored those in neutral lipid 16:0, 18:0 and 18:1*cis*-9 accounting for 15%, 11% and 20% of total PL, respectively. 18:2*n*-6 had an overall proportion of 14% of total PL compared with 1.5% of NL. Longer chain (C20–22) *n*-6 and *n*-3 PUFA constituted about 100 mg/100 g muscle in PL but were undetectable in NL.

There were no breed effects on the amounts of PL fatty acids in the 14 month group (Table 8), but most fatty acids were affected by diet. The grass silage diet produced higher

amounts of 14:0, 16:1, 18:1*cis*-9, 18:1*cis*-11, 18:3*n*-3, 20:4*n*-3, 20:5*n*-3, 22:5*n*-3 and 22:6*n*-3. The concentrate diet produced higher amounts of 18:1*trans*, 18:2*n*-6, 20:3*n*-6, 20:4*n*-6 and 22:4*n*-6. Similar results were observed in the 19 month group. There were breed effects for three fatty acids, 16:0, 16:1 and 18:1*cis*-9, all of which were higher in AA. Silage-fed steers had higher amounts of 16:1, 18:1*cis*-9, 18:3*n*-3, 20:4*n*-3, 20:5*n*-3, 22:5*n*-3 and 22:6*n*-3. Concentrate-fed animals had higher amounts of 18:1*trans*, 18:2*n*-6, CLA, 20:3*n*-6, 20:4*n*-6 and 22:4*n*-6. At 24 months, three fatty acids were significantly affected by breed and for two there were breed \times diet interactions: HF had higher amounts of 18:2*n*-6, 18:3*n*-3 and 20:4*n*-6 and the interactions indicated particularly high amounts of 20:5*n*-3 and 22:6*n*-3 in HF on the grass silage diet.

Proportions of four fatty acids in the PL fraction were affected by breed in the 14 month group (Table 9). AA were higher in 16:1 and 18:1*cis*-9 and HF higher in 18:2*n*-6 and 20:4*n*-6. All fatty acids were affected by diet, the grass silage diet producing higher proportions of 14:0, 16:0, 16:1, 18:1*cis*-9, 18:1*cis*-11, 18:3*n*-3, 20:4*n*-3, 20:5*n*-3, 22:5*n*-3 and 22:6*n*-3. The concentrate diet produced higher proportions of 18:0, TVA, 18:2*n*-6, CLA, 20:3*n*-6, 20:4*n*-6 and 22:4*n*-6. Similar results were observed in the 19 month group although there were significant breed \times diet interactions for five fatty acids due to breeds responding more extremely to diets (but in the same direction). AA had higher proportions of 14:0 and 16:0 (particularly on the silage diet) and there were bigger diet differences for HF for 18:1*cis*-11, 20:5*n*-3 and 22:6*n*-3. Breed affected proportions of 16:1 and 18:1*cis*-9 (higher in AA) and 20:4*n*-6 (higher in HF). The grass silage diet produced higher proportions of 16:1, 18:1*cis*-9, 18:3*n*-3 and 22:5*n*-3 and the concentrate diet produced higher proportions of

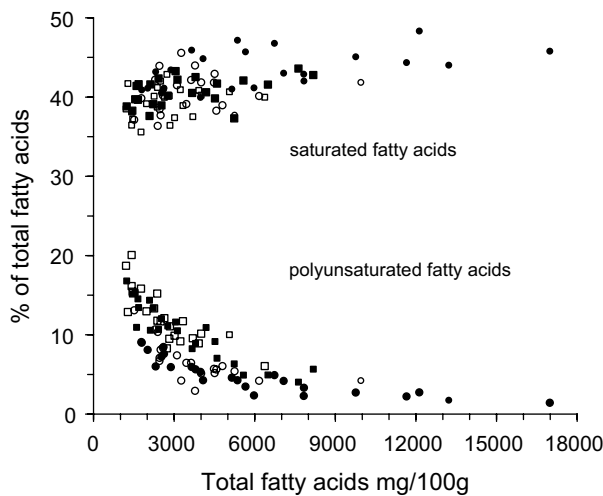


Fig. 1. Relationship between muscle total fatty acids (intramuscular fat) and the percentages of PUFA and SFA (■, □ concentrate ●, ○ silage; closed symbols AA, open symbols HF).

Table 6

Fatty acid concentrations (mg/100 g muscle) in *M. longissimus* neutral lipid from steers of different breeds fed concentrate or grass silage to 14, 19 or 24 months of age

	14 months						19 months						24 months					
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a	
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet
14:0	34.1	64.1	30.7	54.3	ns	***	74.8 ^P	211.1 ^Q	64.9 ^P	92.2 ^P	b	b	140.8	305.2	90.7	129.4	*	*
16:0	346	625	291	562	ns	***	710 ^P	1703 ^Q	624 ^P	879 ^P	b	b	1382	2674	903	1215	**	*
16:1	43.9	94.3	39.5	74.2	ns	***	101.0 ^P	285.2 ^Q	99.1 ^P	159.4 ^P	b	b	220.7	424.6	157.2	227.9	*	*
18:0	199.3	289.8	165.0	277.1	ns	***	331.4 ^P	645.3 ^Q	304.9 ^P	364.8 ^P	b	b	584.5	1074.2	429.1	497.5	**	*
18:1 <i>trans</i>	45.2	22.9	39.2	25.0	ns	***	82.1	56.6	68.9	34.7	*	***	138.5	86.1	108.2	45.4	*	***
18:1 <i>cis</i> -9	452	782	395	722	ns	***	876 ^P	2023 ^Q	821 ^P	1196 ^P	b	b	1835	3453	1265	1752	**	*
18:1 <i>cis</i> -11	16.9	32.7	15.3	27.5	ns	***	36.4	91.4	37.2	56.4	ns	***	94.8	155.1	66.0	86.3	**	*
18:2 <i>n</i> -6	29.3	14.7	31.6	16.5	ns	***	52.5	37.1	48.9	24.5	ns	***	81.4	50.3	76.3	28.9	ns	***
20:1	1.5	2.4	1.3	2.0	ns	**	2.7	6.0	2.5	3.8	ns	**	6.4	11.0	4.0	5.7	*	*
18:3 <i>n</i> -3	3.4	10.6	3.2	11.4	ns	***	4.1 ^P	24.9 ^F	4.1 ^P	16.1 ^Q	b	b	5.6 ^t	36.5 ^v	4.8 ^t	20.0 ^u	b	b
CLA ^c	7.1	4.6	6.6	4.5	ns	**	13.5	11.7	12.6	7.7	ns	*	27.3	18.6	21.0	10.3	*	**
Total	1276	2112	1109	1934	ns	***	2447 ^P	5485 ^Q	2243 ^P	3066 ^P	b	b	4802	8925	3353	4339	**	*

^a Significance of the main effects of breed and diet. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; ns not significant.

^b Significant Breed \times Diet interaction. Means with the same letter within age group (^{PQ}19 months, ^{uv}24 months) do not differ significantly, Tukey–Kramer test, post hoc ($P \leq 0.05$).

^c Conjugated linoleic acid, 18:2*cis*-9, *trans*-11.

Table 7

Fatty acid proportions ($\times 100$) in *M. longissimus* neutral lipid from steers of different breeds fed concentrate or grass silage to 14, 19 or 24 months of age

	14 months						19 months						24 months					
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a	
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet
14:0	2.7	3.0	2.8	2.8	ns	ns	3.0	3.9	2.9	2.9	*	*	2.9	3.2	2.6	2.9	ns	ns
16:0	27.4	29.5	26.1	28.8	ns	***	28.6	31.3	27.7	28.4	**	*	28.8	29.3	26.5	27.9	**	ns
16:1	3.5	4.4	3.5	3.8	ns	*	4.0	5.3	4.4	5.2	ns	***	4.5	4.8	4.5	5.1	ns	*
18:0	15.5	13.7	15.2	14.4	ns	ns	14.0	11.8	13.8	12.0	ns	***	12.4	12.1	13.3	11.8	ns	ns
18:1 $trans$	3.5	1.2	3.6	1.3	ns	***	3.3	1.0	3.1	1.1	ns	***	2.9	1.0	3.3	1.1	*	***
18:1 cis -9	35.2	37.1	35.3	37.4	ns	*	35.7	36.6	36.5	39.2	*	*	38.2	39.3	37.9	40.3	ns	ns
18:1 cis -11	1.3	1.6	1.4	1.5	ns	ns	1.5	1.6	1.6	1.9	*	*	2.0	1.8	2.0	2.0	ns	ns
18:2 n -6	2.30 ^k	0.71 ^j	2.85 ^l	0.91 ^j	b	b	2.24	0.68	2.45	0.81	ns	***	1.71 ^u	0.59 ^t	2.38 ^v	0.71 ^t	b	b
20:1	0.12	0.11	0.11	0.10	ns	ns	0.11	0.10	0.11	0.13	ns	ns	0.13	0.13	0.12	0.12	ns	ns
18:3 n -3	0.26	0.52	0.29	0.60	*	***	0.17	0.46	0.19	0.54	**	***	0.12	0.43	0.15	0.49	*	***
CLA ^c	0.55	0.22	0.58	0.24	ns	***	0.54	0.21	0.56	0.25	ns	***	0.56	0.22	0.62	0.24	*	***

^a Significance of the main effects of breed and diet. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; ns not significant.

^b Significant Breed \times Diet interaction. Means with the same letter within age group (^{ijkl}14 months, ^{tuv}24 months) do not differ significantly, Tukey–Kramer test, post hoc ($P \leq 0.05$).

^c Conjugated linoleic acid, 18:2 cis -9, $trans$ -11.

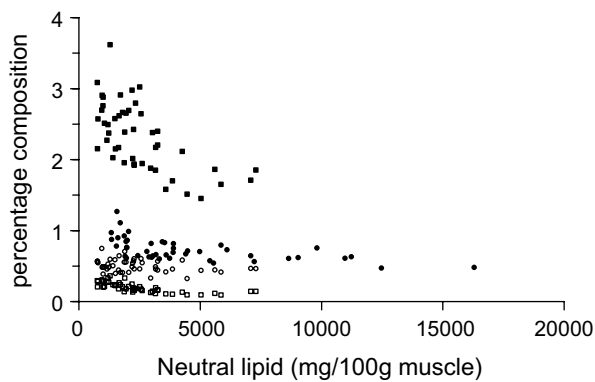


Fig. 2. Relationship between percentages of 18:2 n -6, 18:3 n -3 and total amount of neutral lipid (mg/100 g muscle) (■, □ concentrate ●, ○ silage; closed symbols 18:2, open symbols 18:3).

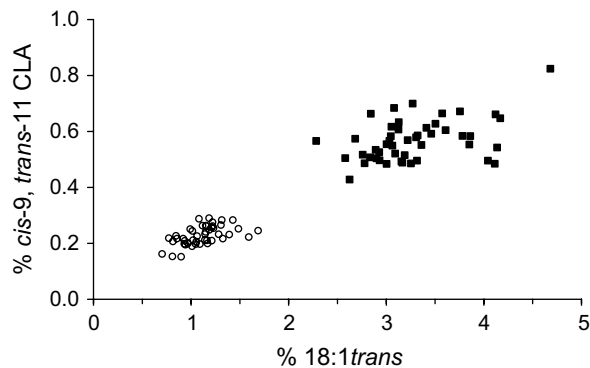


Fig. 3. Relationship between CLA and 18:1 $trans$ in neutral lipid for the two diets (■ concentrate, ○ silage).

TVA, 18:2 n -6, CLA, 20:3 n -6, 20:4 n -6 and 22:4 n -6. In the 24 month group, five fatty acids showed significant breed \times diet interactions. AA showed a bigger increase in 16:1 on the grass silage diet, 18:1 cis -11 was higher on the grass silage diet only in HF and higher values for 18:3 n -3, 20:5 n -3

and 22:6 n -3 in the grass silage diet were particularly obvious in HF compared with AA. Breed effects were present for 14:0, 16:0, 18:1 cis -9 and CLA (higher in AA) and 18:0, 18:2 n -6, 20:3 n -6 and 20:4 n -6 (higher in HF). Diet affected proportions of 14:0, 16:0, 18:1 cis -9, 20:4 n -3 and 22:5 n -3 (higher in grass silage) and TVA, 18:2 n -6, CLA, 20:3 n -6, 20:4 n -6 and 22:4 n -6 (higher in concentrate).

3.6. Nutritional indices

Fatty acid ratios important for human nutrition (P:S and n -6: n -3 in total lipid) and ratios between some n -3 PUFA in PL, indicating conversion between them, are shown in Table 10. In the 14 month group, the P:S ratio was significantly higher in HF than AA ($P < 0.05$) and higher in the concentrate than the grass silage diet ($P < 0.001$). The n -6: n -3 ratio was not affected by breed but was much lower in the steers on the grass silage diet ($P < 0.001$). Of the ratios between n -3 PUFA, only DHA/18:3 was affected by breed, being higher in HF ($P < 0.05$). EPA/18:3, DHA/18:3 and DPA/18:3 were all higher in the steers fed concentrate. In the 19 month group, breed did not affect P:S or n -6: n -3 but diet had highly significant effects ($P < 0.001$), P:S and n -6: n -3 being lower on the grass silage diet. As in the 14 month group, the ratio of DHA/18:3 was higher in HF than AA ($P < 0.05$) and so was the ratio of DHA/EPA ($P < 0.05$). The ratio of EPA/18:3 was higher in the steers fed grass silage ($P < 0.05$) whereas DPA/18:3 was higher in those fed concentrate ($P < 0.001$). In the 24 month group, P:S was higher in HF than AA and in steers fed concentrate compared with grass silage ($P < 0.001$). The ratio of n -6: n -3 PUFA was much lower in the steers fed grass silage compared with concentrate ($P < 0.001$). A significant breed \times diet interaction for DHA/18:3 was due to a big increase in the ratio in HF steers fed grass silage. DPA/18:3 was

Table 8
Fatty acid concentrations (mg/100 g muscle) in *M. longissimus* phospholipid from steers of different breeds fed concentrate or grass silage to 14, 19 or 24 months of age

	14 months						19 months						24 months					
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a	
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet
14:0	1.0	2.0	0.9	1.5	ns	***	1.9 ^p	6.6 ^q	1.3 ^p	3.0 ^p	b	b	2.6	6.8	2.2	4.1	ns	**
16:0	79.4	87.9	71.8	86.8	ns	ns	97.7	126.5	82.0	95.7	*	ns	100.0	125.8	98.6	123.9	ns	*
16:1	4.6	9.1	3.0	8.1	ns	***	6.9	17.4	4.7	12.0	**	***	10.4	20.4	9.8	17.0	ns	***
18:0	59.9	59.1	55.1	61.4	ns	ns	73.1	75.6	66.0	66.6	ns	ns	72.2	73.9	78.8	82.8	ns	ns
18:1 ^{trans}	4.5	1.8	3.6	2.2	ns	***	6.3	3.1	5.2	2.7	ns	***	6.1	2.7	7.0	2.9	ns	***
18:1 ^{cis-9}	87.1	131.9	62.8	133.4	ns	***	111.0	180.5	80.0	149.5	*	***	131.4	192.8	111.8	184.3	ns	***
18:1 ^{cis-11}	9.3	10.8	8.6	12.2	ns	**	14.9	15.7	12.4	15.2	ns	ns	17.0	16.7	14.9	19.7	ns	ns
18:2 ⁿ⁻⁶	119.0	46.6	117.5	52.6	ns	***	157.6	46.9	144.2	49.2	ns	***	125.3	40.9	150.3	58.6	*	***
18:3 ⁿ⁻³	4.0	20.6	3.6	21.0	ns	***	4.0	23.4	3.6	22.9	ns	***	3.1	22.7	3.5	30.1	*	***
CLA ^c	1.0	0.7	0.8	0.7	ns	ns	1.4	1.0	1.1	0.9	ns	*	1.6	1.2	1.5	1.2	ns	*
20:3 ⁿ⁻⁶	14.3	6.1	13.8	6.9	ns	***	18.4	5.9	16.3	5.8	ns	***	18.0	5.4	20.4	7.6	ns	***
20:4 ⁿ⁻³	0.8	4.4	0.7	4.4	ns	***	0.9	5.9	0.7	5.0	ns	***	1.1	5.8	1.1	6.8	ns	***
20:4 ⁿ⁻⁶	54.2	33.2	53.3	38.5	ns	***	70.9	31.8	67.8	31.9	ns	***	69.9	25.7	83.2	36.8	*	***
20:5 ⁿ⁻³	4.8	18.6	4.1	19.9	ns	***	2.6	19.7	2.6	20.5	ns	***	3.1 ^t	19.1 ^u	4.3 ^t	30.9 ^v	b	b
22:4 ⁿ⁻⁶	6.3	2.2	6.5	2.5	ns	***	10.7	1.9	9.0	1.8	ns	***	10.7	1.6	8.1	1.7	ns	***
22:5 ⁿ⁻³	11.2	25.7	10.5	26.1	ns	***	8.6	27.2	8.5	25.8	ns	***	7.3	27.6	7.4	33.4	ns	***
22:6 ⁿ⁻³	1.2	4.7	1.4	5.9	ns	***	0.6	5.1	0.8	6.9	ns	***	0.5 ^t	3.3 ^u	0.6 ^t	7.5 ^v	b	b
Total	546	556	491	584	ns	ns	683	688	595	601	ns	ns	675	692	702	761	ns	ns

^a Significance of the main effects of breed and diet. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; ns not significant.

^b Significant Breed \times Diet interaction. Means with the same letter within age group (^{p,q,r}19 months, ^{u,v,w}24 months) do not differ significantly, Tukey–Kramer test, post hoc ($P \leq 0.05$).

^c Conjugated linoleic acid, 18:2^{cis-9}, ^{trans-11}.

Table 9
Fatty acid proportions ($\times 100$) in *M. longissimus* phospholipid from steers of different breeds fed concentrate or grass silage to 14, 19 or 24 months of age

	14 months						19 months						24 months					
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a	
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet
14:0	0.18	0.35	0.19	0.26	ns	***	0.26 ^p	0.96 ^q	0.21 ^p	0.49 ^p	b	b	0.39	0.96	0.30	0.47	**	***
16:0	14.6	15.7	14.6	14.9	ns	*	14.2 ^p	18.3 ^r	13.8 ^p	16.0 ^q	b	b	14.9	18.1	14.1	16.0	**	***
16:1	0.8	1.6	0.6	1.4	*	***	1.0	2.5	0.8	2.0	**	***	1.5 ^t	2.9 ^v	1.4 ^t	2.1 ^u	b	b
18:0	11.0	10.6	11.2	10.6	ns	**	10.8	11.0	11.1	11.1	ns	ns	10.7	10.7	11.2	10.9	**	ns
18:1 ^{trans}	0.8	0.3	0.7	0.4	ns	***	0.9	0.4	0.9	0.5	ns	***	0.9	0.4	1.0	0.4	ns	***
18:1 ^{cis-9}	15.8	23.6	12.9	23.0	**	***	15.9	26.3	13.5	24.9	*	***	19.4	28.0	15.8	23.9	***	***
18:1 ^{cis-11}	1.7	2.0	1.8	2.0	ns	**	2.2 ^p	2.3 ^{p,q}	2.1 ^p	2.5 ^q	b	b	2.5 ^u	2.4 ^u	2.1 ^t	2.6 ^u	b	b
18:2 ⁿ⁻⁶	22.0	8.4	23.8	8.9	*	***	23.2	6.8	24.2	8.2	ns	***	18.6	5.9	21.7	7.9	***	***
18:3 ⁿ⁻³	0.7	3.7	0.7	3.6	ns	***	0.6	3.4	0.6	3.8	ns	***	0.5 ^t	3.3 ^u	0.5 ^t	4.0 ^v	b	b
CLA ^c	0.18	0.13	0.17	0.12	ns	***	0.20	0.15	0.18	0.15	ns	***	0.24	0.17	0.21	0.15	*	***
20:3 ⁿ⁻⁶	2.6	1.1	2.8	1.2	ns	***	2.7	0.8	2.8	1.0	ns	***	2.7	0.8	2.9	1.0	**	***
20:4 ⁿ⁻³	0.15	0.79	0.15	0.76	ns	***	0.13	0.86	0.13	0.88	ns	***	0.17	0.85	0.16	0.92	ns	***
20:4 ⁿ⁻⁶	10.0	6.1	10.9	6.6	**	***	10.4	4.5	11.4	5.3	**	***	10.4	3.7	11.8	4.9	***	***
20:5 ⁿ⁻³	0.85	3.37	0.84	3.42	ns	***	0.39 ^p	2.86 ^q	0.44 ^p	3.41 ^r	b	b	0.51 ^t	2.77 ^u	0.58 ^t	4.15 ^v	b	b
22:4 ⁿ⁻⁶	1.2	0.4	1.3	0.4	ns	***	1.5	0.3	1.5	0.3	ns	***	1.6	0.2	1.2	0.2	ns	***
22:5 ⁿ⁻³	2.1	4.6	2.2	4.5	ns	***	1.3	4.0	1.4	4.3	ns	***	1.1	4.0	1.1	4.4	ns	***
22:6 ⁿ⁻³	0.22	0.85	0.28	1.00	ns	***	0.10 ^p	0.72 ^q	0.13 ^p	1.13 ^r	b	b	0.07 ^t	0.47 ^u	0.09 ^t	1.02 ^v	b	b

^a Significance of the main effects of breed and diet. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; ns not significant.

^b Significant Breed \times Diet interaction. Means with the same letter within age group (^{p,q,r}19 months, ^{u,v,w}24 months) do not differ significantly, Tukey–Kramer test, post hoc ($P \leq 0.05$).

^c Conjugated linoleic acid, 18:2^{cis-9}, ^{trans-11}.

much higher in steers fed the concentrate than the grass silage diet ($P < 0.001$).

The relationships between the P:S ratio and 1/total muscle lipid for each treatment group (all ages pooled) were investigated using linear regression analysis. Untrans-

formed relationships with total lipid were curvilinear. Tests for parallel slopes and equal intercepts indicated that the data for both breeds on the concentrate diet and similarly for both breeds on the silage diet could be combined ($P > 0.05$). Fig. 4 shows the regression lines for concentrate

Table 10
Nutritional indices of total fatty acids in *M. longissimus* from steers of different breeds fed concentrate or grass silage to 14, 19 or 24 months of age and relationship between 18:3 and long-chain PUFA in phospholipid

	14 months						19 months						24 months						
	AA		HF		Significance ^a		AA		HF		Significance ^a		AA		HF		Significance ^a		
	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	Conc.	Silage	Conc.	Silage	Breed	Diet	
P:S ^c	0.22	0.09	0.26	0.11	*	***	0.18	0.05	0.19	0.08	ns	***	0.10	0.04	0.15	0.07	***	***	
<i>n</i> -6: <i>n</i> -3 ^d	9.0	1.2	9.5	1.3	ns	***	15.1	1.2	14.3	1.2	ns	***	14.9	1.1	16.2	1.0	ns	***	
Ratios in phospholipid																			
EPA ^e /18:3	1.15	0.92	1.17	0.96	ns	**	0.73	0.83	0.72	0.90	ns	*	1.07	0.85	1.19	1.03	ns	ns	
DPA ^e /18:3	2.79	1.26	3.03	1.27	ns	***	2.34	1.17	2.35	1.13	ns	***	2.39	1.23	2.09	1.11	*	***	
DHA ^e /18:3	0.30	0.23	0.39	0.28	*	**	0.19	0.21	0.22	0.30	*	ns	0.16 ^f	0.14 ^f	0.17 ^f	0.25 ^u	b	b	
DHA/EPA	0.27	0.25	0.35	0.29	ns	ns	0.24	0.25	0.31	0.33	*	ns	0.26	0.17	0.24	0.25	ns	ns	

^a Significance of the main effects of breed and diet. ****P* ≤ 0.001; ***P* ≤ 0.01; **P* ≤ 0.05; ns not significant.
^b Significant Breed × Diet interaction. Means with the same letter within age group (^u24 months) do not differ significantly, Tukey–Kramer test, post hoc.
^c P:S, (18:2*n*-6 + 18:3*n*-3)/(14:0 + 16:0 + 18:0).
^d *n*-6:*n*-3, (18:2*n*-6 + 20:3*n*-6 + 20:4*n*-6)/(18:3*n*-3 + 20:4*n*-3 + 20:5*n*-3 + 22:5*n*-3 + 22:6*n*-3).
^e EPA, 20:5*n*-3, DPA, 22:5*n*-3, DHA, 22:6*n*-3.

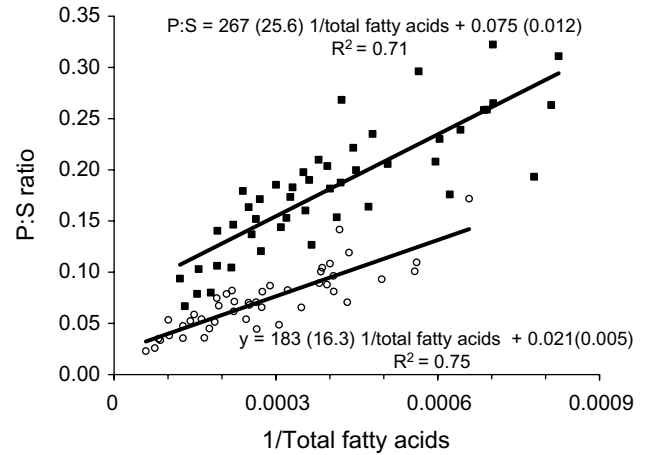


Fig. 4. The relationship between the reciprocal of the total fatty acid concentration in muscle (mg/100 g) and P:S ratio for the two diets (■ concentrate, ○ silage).

and silage fed animals, each having significantly different slopes and intercepts (*P* < 0.05), hence, as total lipid increased, the P:S ratio declined but was always higher in the animals fed concentrate.

4. Discussion

4.1. Animal performance and carcass characteristics

A major aim of the experiment was to compare tissue composition and meat quality in concentrate-fed and grass-fed cattle growing at the same rate to the slaughter end point. This has not been achieved in most previous work, where results have been affected by low carcass weights and fat levels in cattle fed forage-based diets associated with low growth rates (Bowling et al., 1978, Harrison et al., 1978). French, O’Riordan, Monahan, Caffrey, and Moloney (2003) clearly showed that increasing the concentrate intake of grazing animals in a 100 d finishing period increased both the final carcass weight and the intramuscular fat content. By restricting feed intake in the concentrate-fed steers in this work, similar growth rates were obtained between the diets within each breed.

Despite similar growth rates and final live weights, the steers fed grass silage were fatter than those fed concentrate, progressively so as age increased. Again, these results are contrary to previous studies, where forage-fed cattle have usually been leaner than those fed grain-based diets (Bowling et al., 1977; Hedrick et al., 1983) due to a low feed energy intake, but are similar to those of French et al. (2000) when autumn grazed animals were compared with those fed concentrates and slaughtered at a similar weight. The results suggest a nutritional imbalance in the grass silage diet, which included sugarbeet pulp, compared with the concentrate diet (e.g. a low ratio of good quality protein to energy).

Aberdeen Angus have a lower mature body weight than HF so are a relatively early maturing breed, explaining

their greater carcass fatness at each age. The AA steers reached particularly high levels of carcass fat on the grass silage diet. An average fat classification score of 4H, which translates into about 25% of separable fat in the carcass (Kempster et al., 1986), means that at 19 and 24 months these carcasses were too fat for the UK beef market. The HF on the silage diet at these ages were at fat class 3, which translates to 19% separable fat. Total muscle lipid (intramuscular fat) was also high in AA, especially those in the 19 and 24 month groups fed grass silage. The value of 9616 mg/100 g total lipid at 24 months contrasts with values between 3000 and 4000 mg/100 g in our previous research (Choi et al., 2000; Scollan et al., 2001). In the 14 month group, total lipid was similar in the 2 breeds although AA carcasses were considerably fatter. This is evidence of breed difference in the partitioning of body fat, with dairy breeds depositing relatively more fat in internal depots, including intramuscular fat (Choi et al., 2000).

4.2. Muscle fatty acid composition

The importance of total fat in explaining treatment differences in the proportions of lipid classes is seen by comparing the age groups. At 14 months, PL was 0.25 of total lipid and at 24 months it was 0.12. During this time NL increased greatly and PL only slightly. Changes in lipid classes and individual fatty acids are revealed in Figs. 1 and 2 when the 3 age groups were combined. As total lipid increased, there was a marked fall in PUFA% accounted for mainly by increases in SFA and MUFA percentages in NL. In NL itself, percentages of the 2 main dietary PUFA, 18:2 n -6 and 18:3 n -3 declined as NL increased, more rapidly for 18:2 n -6 in concentrate-fed animals than the other 3 groups. In PL, percentages of 18:2 n -6 and 18:3 n -3 remained high in all 3 age groups and changes with age in all fatty acids were small.

Differences between the breeds in fatty acid classes as a percentage of total lipid (Table 5) reflect differences in the amount of lipid and were more apparent in the fatter 24 month group. Thus AA, with more total lipid, had higher percentages of SFA and MUFA and a lower percentage of PUFA mainly due to absolute amounts of PUFA remaining similar whilst total fat increased more in AA than HF. Within NL, breed differences were relatively small but bigger at 24 months. AA had a higher percentage of 16:0 and HF higher percentages of 18:1 $trans$, CLA, 18:2 n -6 and 18:3 n -3. These differences again reflect the higher amount of NL in AA. Breed differences were also apparent in PL at 24 months, the differences following the same pattern as in NL and total lipid, although the amount of PL was not different between the breeds. Thus, AA had higher percentages of 14:0, 16:0, 16:1, 18:1 cis -9 and CLA and HF had higher percentages of most PUFA. The proportion of DHA was over 1% of phospholipid fatty acids in silage-fed HF in all three age groups in comparison with 0.4–0.8% in AA. Malau-Aduli, Siebert, Bottema, and Pitchford (1998) reported a higher proportion of EPA in Jersey than

Limousin cattle and Laborde, Mandell, Tosh, Wilton, and Buchanan-Smith (2001) also noted less n -3 fatty acids in total lipid of Simmental compared to Red Angus steers when both were slaughtered at the same level of finish.

The possibility of a genetic difference in fatty acid metabolism underlying these breed effects on PL fatty acid composition comes from the n -3 PUFA ratios (Table 10). HF in each age group had higher ratios of DHA/18:3, showing greater conversion of 18:3 n -3 to this long-chain product.

Diet had by far the biggest effects on fatty acid composition in all age groups and these occurred in both NL and PL. The grass silage diet produced higher proportions of SFA and MUFA (associated with its promotion of fat deposition) and particularly increased the proportions of all n -3, at the expense of n -6 PUFA. The concentrate diet produced higher proportions of total PUFA but these were dominated by the n -6 PUFA, particularly 18:2 n -6.

The concentrate diet also produced higher proportions of 18:1 $trans$ and CLA. Both these were higher in NL than PL and in NL the proportions in concentrate-fed animals were double those in the steers fed silage. The clear effect of the concentrate diet in raising CLA proportions is in contrast to other studies showing higher CLA proportions in grass-grazed cattle or sheep (French et al., 2000; Steen & Porter, 2003; Arousseau, Bauchart, Calichon, Micol, & Priolo, 2004). In these other studies, the forage diets were the major source of PUFA, whereas in this study the intake of total PUFA was similar in both diets. In this study, full fat soya was used in the concentrate with the result that relative to other studies involving concentrate feeding, the diet was higher in 18:2 n -6. In the rumen, 18:2 n -6 and 18:3 n -3 are rapidly biohydrogenated to 18:0 but key intermediates of this process include vaccenic acid (18:1 $trans$ -11) and CLA. The higher levels of muscle CLA and TVA are, therefore, probably partly related to greater production of TVA and CLA in the rumen on the n -6 rich concentrate relative to the n -3 rich grass silage. The fact that silage rather than fresh grass was used in this study is also important. The high concentration of readily fermentable sugars and soluble fibre in fresh grass compared with grass silage (Dhiman, Satter, & Pariza, 1996) creates a rumen environment promoting biohydrogenation, and hence TVA and CLA production or reduced utilisation, with the fibriolytic bacterium *Butyrivibrio fibrisolvens* predominant in this process (Kelly, Kolver, Bauman, Van Amburgh, & Muller, 1998; Kepler, Hiron, McNeill, & Tove, 1966). When a subset of the same animals examined here was grazed on fresh grass from 14 months and slaughtered at 19 months, CLA concentrations in adipose tissue were similar to those produced by the concentrate diet and higher than those produced by the grass silage diet (Wood, Warren, Stonehouse, Hallett, & Whittington, 2006), a similar result to that found by French et al. (2000). The close association between TVA and CLA found here when cattle of the 3 groups were pooled (Fig. 3) confirms the strong relationship between tissue CLA and TVA and supports the view

that most tissue CLA is synthesised from TVA by the enzyme delta-9 desaturase.

The levels and proportions of *n*-3 PUFA seen here in the grass silage-fed cattle compare with those found when feeding concentrate diets fortified with linseed and fish oil (Mandell, Buchanan-Smith, Holub, & Campbell, 1997; Scollan et al., 2001). The proportions of 18:3*n*-3 are similar to those obtained when feeding 21% bruised whole linseed for 120 days and the levels of longer-chain *n*-3 PUFA compare with those found when the diet contained 5% of fish oil (Scollan et al., 2001). These high levels of long-chain *n*-3 PUFA were synthesised from 18:3*n*-3 in the present study, rather than being obtained pre-formed from dietary fish oil.

Of particular interest here was the clear evidence that DHA was synthesised from 18:3*n*-3, which was apparent in both breeds at all ages, something we have not observed in cattle fed linseed (Choi et al., 2000; Scollan et al., 2001). Other studies have shown that grass or linseed feeding increases 18:3*n*-3 and 20:5*n*-3 proportions in ruminant muscle (Clinquart et al., 1991; Ponnampalam et al., 2002; Nuernberg et al., 2005; Raes, De Smet, Balcaen, Claeys, & Demeyer, 2003). Levels of these fatty acids are comparable between studies. However, the levels of DHA seen here are higher than reported previously in animals fed forage-based diets. The value of 1% DHA in phospholipid fatty acids of HF fed grass silage in all three age groups compares with 0.3% in the study of Marmer et al. (1984) and Raes et al. (2003) and 0.6% when whole linseed was fed in our own studies (Choi et al., 2000; Scollan et al., 2001).

A possible explanation for this greater production of DHA is the long feeding periods used here. Raes et al. (2003) have shown that the *n*-3 content of the feed in periods of growth prior to the finishing period are more important for increasing the long-chain *n*-3 PUFA in PL than when fed in the finishing period. Animals fed a diet high in linseed during early growth and then changed to a diet high in 18:2*n*-6 had just as much C22:6*n*-3 as those who remained on the high linseed diet, but their 18:3*n*-3 was content was reduced. However here, the ratio of DHA/18:3 was not different between the age groups and we have generally found that fatty acid composition changes in meat are achieved rather rapidly (Wood et al., 2003). The ratio was not consistently different between the diets, showing that it was not greater conversion of 18:3*n*-3 to DHA on the grass silage diet that was responsible for the high DHA levels, but rather the much higher level of 18:3*n*-3 in tissues. Equally the DHA% was linearly related to total PL in silage-fed animals and did not decrease, as a proportion of total PL, indicating that there was no competition between DHA and other PUFA for deposition.

4.3. Implications for human nutrition

The total lipid content of muscle increased with age as the cattle became fatter overall. In some groups, especially the AA fed grass silage to 24 months, the level would be

considered undesirably high. This increase in fat was also accompanied by increased SFA% and reduced PUFA%, so that the P:S ratio declined with age and was at its lowest in AA fed grass silage at 19 and 24 months. Values of around 0.1 for the silage-fed steers are similar to those for English beef at retail reported by Enser, Hallett, Hewett, Fursey, and Wood (1996). The UK Department of Health (1994) recommends a P:S ratio of 0.45 for the diet as a whole and this was only found here in animals with less than 1% total fat. Consumers would be able to achieve this in a diet containing normal levels of beef by balancing the diet with other foods containing high levels of PUFA, of which there is a large choice.

The *n*-6:*n*-3 fatty acid ratio should ideally be below 4.0, according to medical authorities such as Department of Health (1994). Whereas increases in dietary *n*-6 PUFA can readily be obtained from several foods, consumers have access to relatively few sources of *n*-3 PUFA (eggs, fish, ruminant meats). Thus beef, especially from grass-fed cattle, can make an important contribution to the diet. The *n*-6:*n*-3 ratio was consistently below 1.3 in silage-fed steers and from 9 to 16 in those fed concentrate.

It is apparently difficult in grass-fed cattle (particularly at high fat levels), to achieve a high P:S ratio whilst keeping *n*-6:*n*-3 low. This is due to a high degree of biohydrogenation of dietary PUFA, leading to production of SFA in the rumen and absorption in the small intestine. PUFA% was higher in the animals fed concentrate in all groups, partly because they were less fat overall. However, as Fig. 4 shows, the P:S ratio was higher in concentrate-fed cattle at the same value for total lipid. This ability of concentrate diets to raise muscle PUFA has been shown before (e.g. Scollan et al., 2006) and is related to a faster rate of passage of the less fibrous diet through the rumen, leading to reduced microbial action. The importance of biohydrogenation for muscle *n*-3 PUFA proportions was shown by Petit et al. (2002) who infused linseed oil directly into the duodenum of Holstein cows and thereby raised the P:S ratio of milk fat whilst keeping *n*-6:*n*-3 low. If the relationships shown in Fig. 4 are extrapolated to a desirable P:S ratio of 0.4, then it is suggested that this could be obtained at a total loin muscle fat content of 1% for concentrate-fed animals but only 0.5% for silage-fed animals. The latter value is approximately that for the total PL content of muscle. Another way to raise the P:S ratio in beef is to use protected lipid supplements (PLS), which cause lipids to pass through the rumen undegraded. Use of formaldehyde-treated proteins to encapsulate PUFA was developed in Australia by Scott, Cook, and Mills (1971) and has been used successfully in other studies (Ashes, Siebert, Gulati, Cuthbertson, & Scott, 1992; Cook, Scott, Faichney, & Lloyd Davies, 1972). Scollan, Enser, Gulati, Richardson, and Wood (2003) and Warren, Richardson, Wood, and Scollan (2004) achieved an increase in the muscle P:S from 0.1 to 0.25 whilst keeping *n*-6:*n*-3 low by feeding a PLS containing linseed and soya oil to steers and young bulls, respectively.

The recommended daily intake of long-chain *n*-3 PUFA for people is 100–200 mg/d (Department of Health, 1994). Levels in the silage-fed animals in this study were about 59 mg/100 g C20–22*n*-3 PUFA (24 mg as EPA and DHA), which shows that grass-fed beef can make an important contribution to a healthy diet. In addition, 43 mg/100 g was present as 18:3*n*-3, which may have nutritional benefits in its own right.

5. Implications

Beef producers in many countries are searching for ways to raise the nutritional value and quality of the meat they produce to make it more attractive to consumers. This research shows that the fatty acid composition of beef muscle lipid, which is an important factor in both nutritional value and quality, is affected by breed and diet. Age is another important factor and although results for the 3 ages were not directly compared in this work it is clear that as slaughter age progressed from 14 to 24 months, muscle fat levels greatly increased, especially in cattle fed grass silage compared with the concentrate diet. The ratio of polyunsaturated:saturated fatty acids declined with age and fatness and was lowest in the animals fed silage. These characteristics of a grass silage diet unbalanced with protein are undesirable. On the other hand, the grass silage diet produced beneficially low values for the ratio *n*-6:*n*-3 PUFA which ideally should be lower than 4.0 and was always higher than this in the steers fed concentrate. Intake of α -linolenic acid (18:3*n*-3) from the grass silage diet resulted in synthesis of long-chain C20–22*n*-3 PUFA, including DHA. Meat from grass-fed steers would make a significant contribution to *n*-3 PUFA intakes in people consuming beef. The concentrate diet increased levels and proportions of *n*-6 PUFA but also increased CLA (*cis*-9, *trans*-11 conjugated linoleic acid) in contrast to other work showing high levels of CLA in grass-fed beef. ‘Early maturing’ Aberdeen Angus crossbred steers had fatter carcasses and more muscle lipid than ‘late maturing’ Holstein–Friesians, the latter having higher concentrations of *n*-3 PUFA in muscle phospholipid.

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