Animal (2011), **5:1**, pp 134–147 © The Animal Consortium 2010
doi:10.1017/S1751731110001485

animal

The fatty acid profile of muscle and adipose tissue of lambs fed camelina or linseed as oil or seeds

F. Noci[1,2], F. J. Monahan[2] and A. P. Moloney[1†]

[1]*Teagasc, Animal and Grassland Research and Innovation Centre, Grange, Dunsany Co., Meath, Ireland;* [2]*School of Agriculture, Food Science and Veterinary Medicine, College of Life Sciences, University College Dublin, Dublin 4, Ireland*

(Received 29 January 2010; Accepted 18 May 2010; First published online 22 July 2010)

The objective of this study was to evaluate the impact of diets enriched with plant oils or seeds, high in polyunsaturated fatty acids (PUFA), on the fatty acid profile of sheep intramuscular and subcutaneous adipose tissue (SAT). Sixty-six lambs were blocked according to initial body weight and randomly assigned to six concentrate-based rations containing 60 g fat/kg dry matter from different sources: (1) Megalac (MG; ruminally protected saturated fat), (2) camelina oil (CO), (3) linseed oil (LO), (4) NaOH-treated camelina seed (CS), (5) NaOH-treated linseed (LS) or (6) CO protected from ruminal saturation by reaction with ethanolamine; camelina oil amides (CA). The animals were offered the experimental diets for 100 days, after which samples of m. longissimus dorsi *and SAT were collected and the fatty acid profile determined by GLC. The data were analyzed using ANOVA with '*a priori*' contrasts including camelina* v. *linseed, oil* v. *NaOH-treated seeds and CS* v. *CA. Average daily gain and total fatty acids in intramuscular adipose tissue were similar across treatments. The NaOH-treatment of seeds was more effective in enhancing* cis-*9,* trans-*11 conjugated linoleic acid (CLA) incorporation than the corresponding oil, but the latter resulted in a higher content of* trans-*11 18:1 in both muscle neutral and polar lipids (*$P < 0.01$, $P < 0.001$, *respectively). Inclusion of LS resulted in the highest PUFA : saturated fatty acid (SFA) ratio in total intramuscular fat (0.22). The NaOH-treatment of seeds resulted in a higher PUFA/SFA ratio (0.21* v. *0.18,* $P < 0.001$) *than oils and on average, linseed resulted in a higher PUFA/SFA ratio than camelina (*$P < 0.01$). *Lambs offered LS had the highest concentration of n-3 PUFA in the muscle, while those offered MG had the lowest (*$P < 0.001$). *This was reflected in the lowest (*$P < 0.001$) *n-6: n-3 PUFA ratio for LS-fed lambs (1.15) than any other treatment, which ranged from 2.14 to 1.72, and the control (5.28). The trends found in intramuscular fat were confirmed by the data for SAT. This study demonstrated the potential advantage from a human nutrition perspective of feeding NaOH-treated seeds rich in PUFA when compared to the corresponding oil. The use of camelina amides achieved a greater degree of protection of dietary PUFA, but decreased the incorporation of biohydrogenation intermediates such as* cis-*9,* trans-*11 CLA and* trans-*11 18:1 compared to NaOH-treated seeds.*

Keywords: conjugated linoleic acid, biohydrogenation, polyunsaturated fatty acids, linseed, camelina

Implications

An increase in the n-3 polyunsaturated fatty acid and conjugated linoleic acid concentration in lamb meat is desirable from a consumer health perspective. This experiment demonstrates that providing a source of linolenic acid, such as linseed or the novel alternative, *Camelina sativa* as sodium hydroxide-treated seeds, which could be prepared on-farm, is effective in this regard. While the increases in beneficial fatty acids in lamb are small relative to dietary requirement for humans, they can contribute to marketing strategies to enhance the image of lean lamb as a healthy food.

† E-mail: aidan.moloney@teagasc.ie

Introduction

Consumption of fat, and in particular saturated fat, is regarded as one of the contributing factors to the incidence of coronary heart disease in humans (World Health Organization (WHO), 2003). Enser *et al.* (1996) showed that lean steaks from lamb loin had a fatty acid content of around 50 mg/g muscle or less and therefore they could be considered a low-fat food. However, because of biohydrogenation of dietary polyunsaturated fatty acids (PUFA) by ruminal microorganisms (Doreau and Ferlay, 1994), beef and lamb fat tends to contain more saturated fatty acids (SFA) than non-ruminant fat.

Feeding PUFA-rich plant oils or physically processed oilseeds to ruminants has been shown to increase the PUFA

concentration in muscle (e.g. Bolte *et al*., 2002), but an effect comparable to that achievable with non-ruminants would require protection of dietary PUFA from ruminal biohydrogenation. Feeding intact oilseeds has been shown to offer some degree of protection against ruminal biohydrogenation (Ekeren *et al*., 1992) and the use of seeds rather than oils has practical advantages in terms of handling of feed ingredients and ration manufacture. However, without some disruption of the seed coat, intact seeds may escape digestion completely as is the case with cereal grains (Drennan *et al*., 1995). Chemical treatment of canola seeds with an NaOH solution increased digestibility compared to untreated whole seeds but decreased ruminal biohydrogenation of PUFA compared to crushed canola seeds (Aldrich *et al*., 1997). Chemical protection of PUFA by direct reaction with amines also afforded some protection of fatty acids from ruminal biohydrogenation (Jenkins and Thies, 1997). However, efficient protection of dietary PUFA while enhancing the deposition of PUFA in tissue would likely decrease PUFA availability to ruminal bacteria and consequently the formation of biohydrogenation intermediates such as *trans*-11 18:1 and conjugated linoleic acid (CLA), in particular the cis-9, *trans*-11 isomer which has been shown to possess a variety of health benefits in animal models (Pariza *et al*., 2001).

Among plant oilseeds, linseed represents a rich source of 18:3n-3 and effects of inclusion of linseed or linseed oil (LO) as a means of increasing the n-3 PUFA content of ruminant muscle have been reviewed (Woods and Fearon, 2009). *Camelina sativa* is the second richest oilseed in 18:3n-3 (ranging between 30% and 40% of total fatty acids) having a high relative proportion of 18:2n-6 to 18:3n-3 (Budin *et al*., 1995; Givens *et al*., 2000). Biohydrogenation of 18:2n-6 leads to the formation of *cis*-9, *trans*-11 CLA and *trans*-11 18:1, whereas biohydrogenation of 18:3n-3 leads to the formation of *trans*-11 18:1 without involving *cis*-9, *trans*-11 CLA as an intermediate (Harfoot and Hazelwood, 1997). Little information is available on the effect of camelina *per se* or the form of camelina oil (CO) on the fatty acid composition of ruminant muscle.

The objective of this study was to compare the effects of addition of camelina or linseed *per se* as fat sources in sheep diets, the effect of feeding the fat sources as unprotected oils or caustic treated seeds and the effect of chemically protecting CO on the fatty acid composition of intramuscular and subcutaneous adipose tissue.

Material and methods

Feed preparation and animal management

The fat sources examined were Megalac® (MG, Volac Feeds Ltd, Co. Cavan, Ireland), CO (*Camelina sativa* grown at Teagasc, Oak Park Research Centre, Carlow, Ireland and extracted as described by Crowley and Fröhlich, 1998), LO (Flood Horse Feeds, Newbridge, Ireland), camelina seed treated with NaOH (CS; *Camelina sativa* grown at Teagasc, Oak Park Research Centre, Carlow, Ireland and seeds harvested as described by Crowley and Fröhlich, 1998), while linseeds treated with NaOH (LS, seeds supplied by Wholefoods Wholesale, Ltd, Dublin, Ireland) and CO amides (CA). The NaOH treatment was as follows: NaOH was added to the seeds (in batches of 25 kg; 10% w/w when treating camelina seeds and 5% w/w when treating linseeds, to compensate for the different surface area of the seeds), dry-mixed and then 6 l of water were added in the mixer. The seeds were mixed in a Little Benford Tip-up tumbling mixer 60 l (Terex Corporation, Westport, CT, USA) rotating at 27 rpm for 15 min. After removal from the tumbling mixer, treated seeds were spread on a concrete floor. The temperature was monitored and the seeds mixed by hand at regular intervals. After reaching ambient temperature the seeds were transferred to boxes for storage before preparation of the ration. Fatty acyl amides of CO were prepared by reacting CO and ethanolamine (1.38 g oil/g ethanolamine) at 70°C for at least 48 h according to the method described by Feairheller *et al*. (1994).

Table 1 *Formulation of experimental rations*

	Treatment					
	MG	CO	LO	CS	LS	CA
Ingredients (g/kg)						
Barley	350	285	285	282	328	303
Beet pulp	350	430	430	370	339	363
Soybean	103	100	100	30	29	112
Molasses	100	100	100	100	100	100
Mineral and vitamin mix[1]	25	25	25	25	25	25
Megalac	72	–	–	–	–	–
Camelina oil	–	60	–	–	–	–
Linseed oil	–	–	60	–	–	–
Camelina seed/NaOH	–	–	–	193	–	–
Linseed/NaOH	–	–	–	–	179	–
Camelina oil amide	–	–	–	–	–	97

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseeds; CA = camelina oil amides.
[1]The mineral and vitamin mix contained Ca (48%), Na (12%), ammonium chloride (12%), vitamin A (480 000 IU/kg), vitamin D_3 (96 000 IU/kg), vitamin E (20 000 IU/kg), cobalt carbonate (40 mg/kg), calcium iodate (80 mg/kg), iron sulfate (1000 mg/kg), manganese oxide (1600 mg/kg), sodium selente (8 mg/kg) and zinc oxide (2000 mg/kg).

Six experimental rations were prepared that differed in the source of fat used (Table 1). All rations were formulated to be isoenergetic and a mineral and vitamin mix was added to the rations with a target vitamin E concentration of 500 IU/kg concentrate. In the CA diet, CO amides were included at a level calculated to provide the same amount of fatty acids as did the CO diet. Individual fat sources were added to the other ingredients in batches of approximately 500 kg using an Abbey Gearbox drive Diet Feeder 100 (Abbey, Nenagh, Co. Tipperary, Ireland), and mixed at 1700 rpm for 15 min. Fatty acyl amides were melted at 70°C immediately before inclusion in the diet mix to facilitate the mixing. Three batches of each ration were prepared during the course of the study.

Sixty-six Suffolk crossbred wether lambs (average weight 40.0 kg (s.d. 4.69) and approximately 10 months of age) were used. Prior to the commencement of the study, the

animals were offered grass hay *ad libitum* and 0.5 kg whole barley/animal daily for 4 months. The animals were blocked by initial body weight (BW) and, within block, assigned at random to one of six rations. They were housed in individual pens and fed once daily in the morning and had free access to clean drinking water. The concentrate allowance was 25 g/kg BW and was increased every 4 weeks based on animal weight. Animals also received 100 g of chopped hay/day. Refusals, which were rare, were removed and weighed daily and the weight of the animals was monitored bi-weekly. Samples of the concentrates and hay offered were collected twice weekly and stored at −20°C for subsequent chemical analyses. After 8 weeks of treatment, animals in the first two blocks (i.e. no. = 2 per treatment) were transferred after weighing to metabolism crates that allowed the separate collection of urine and feces and offered the same dietary allowances. After a 1-day adjustment to the crates, all feces produced in the subsequent 8-day period were collected, the quantity recorded and representative subsamples stored at −20°C for subsequent chemical analyses. Upon completion of the above collections, the animals were returned to the regular sheep facility, replaced in the crates by animals from blocks three and four and the collection procedure repeated.

Post-slaughter measurements and sampling procedure
The animals were slaughtered after 100 days on the experimental rations. After slaughter, the weight of the carcass, kidneys, liver, and perirenal fat depot were recorded. Carcasses were then chilled for 24 h and the loin and associated muscles were removed by dissection. Two steaks approximately 25 mm thick were cut from the region of the 7th rib of the *m. longissimus dorsi* for fatty acid analysis. A sample of subcutaneous adipose tissue (SAT) was also taken from the region of the 9th rib. This was dissected free of muscle and connective tissue associated with the sample was not removed before analysis. Samples for fatty acid analysis and meat composition were vacuum-packed and stored frozen at −30°C.

General feed composition
The dry matter (DM) concentration of concentrates and feces was determined by drying at 98°C (15 h) as described by Moloney *et al*. (1996). Concentrates and dried feces (40°C for 48 h) were also analyzed for CP (Association of Official Analytical Chemists (AOAC), 1990), ash (Moloney *et al*., 1996), oil (ether extract following acid hydrolysis, European Communities (EC), 1984) and NDF (Van Soest *et al*., 1991).

Fatty acid analysis of intramuscular fat, SAT, feeds and feces
The procedures used for fatty acid extraction, separation of lipid classes, methylation and determination of the profile both for the intramuscular and SAT were described by Noci *et al*. (2005). This extraction and methylation procedure was also used for determination of fatty acids in dried feces. The fatty acid profile of the freeze-dried rations and the fat sources was determined as described by Sukhija and Palmquist (1988).

Statistical analysis
Data were subjected to analysis of variance in GenStat (12th edition, VSN International Ltd, Hemel Hempstead, UK) using a model that had block and ration as the main effects. Animals were considered the experimental unit and the following '*a priori*' contrasts were carried out:

(i) PUFA-rich rations *v.* control (MG).
(ii) Method of oil supplementation (oil *v.* seed; CO + LO *v.* CS + LS).
(iii) Source of oil (camelina *v.* linseed; CO + CS *v.* LO + LS).
(iv) Interaction of method of feeding and source of oil.
(v) Method of protection of CO (CS *v.* CA).

Results

Feed chemical and fatty acid composition
The fatty acid composition of the individual fat sources before mixing with other ingredients is summarized in Table 2. The trend in the data was for NaOH-treatment to increase the proportion of individual and total SFA and to decrease the proportion of 18:3n-3 and total PUFA in total fatty acids, the latter being particularly pronounced for LS. All sources of CO had 3% 22:1 approximately, in contrast to either MG or sources of LO. Compared to CO, treatment with ethanolamine tended to increase the SFA proportion and to decrease the proportion of monounsaturated fatty acid (MUFA), PUFA and unidentified fatty acids. The data relating to the chemical composition and fatty acid profile of the rations are summarized in Table 3. Camelina-based rations had similar fatty acid profiles with regard to 18:0, 18:1, 18:2n-6, 18:3n-3 and 20:1, while linseed-based rations had higher 18:1 and 18:3n-3 than camelina-based rations. The LS ration had the highest content of 18:2n-6 and was lower than the LO ration in 18:3n-3. Overall, linseed-based rations had a higher content of PUFA, while camelina-based rations were higher in MUFA and the MG ration was highest in SFA content.

Intake, diet digestibility and components of BW
Compared to the MG ration, feed intake tended ($P < 0.1$) to be higher for lambs offered the PUFA-rich rations. Intake was higher ($P < 0.05$) for lambs offered the oil-based rations than for the NaOH-treated oilseed-based rations while camelina-based rations resulted in a lower ($P < 0.05$) intake compared to linseed-based rations. There was no difference in intake between lambs offered the two protected camelina treatments (Table 4).

Compared to the MG ration, the digestibility of dietary DM, organic matter, NDF, oil and the digestible OM in the DM (DOMD) was similar, the digestibility of ash was higher ($P < 0.05$) and the digestibility of CP was lower ($P < 0.05$) for the PUFA-rich rations. The digestibility of DM, OM and CP and DOMD were higher ($P < 0.05$) for oil-based rations than for NaOH-treated oilseed-based rations. The digestibility of DM and OM was higher ($P < 0.05$) for camelina-based rations than for linseed-based rations. There was an interaction for the digestibility of oil such that it was lower

Table 2 *Fatty acid composition (mean (s.d.)) of fat sources*

	Fat source							
	MG	CO	LO	C	CS	L	LS	CA
Number of samples	6	6	6	4	6	4	4	6
Fatty acids (g/100 g FAME)								
14:0	1.0 (0.01)	0.0 (0.00)	0.0 (0.01)	0.0 (0.01)	0.2 (0.04)	0.0 (0.00)	0.5 (0.18)	0.1 (0.00)
16:0	44.2 (0.19)	4.1 (0.23)	4.4 (0.34)	4.6 (0.35)	9.5 (2.02)	4.7 (0.09)	12.1 (3.32)	4.5 (0.35)
16:1	0.2 (0.08)	0.1 (0.01)	0.1 (0.00)	0.1 (0.01)	0.3 (0.10)	0.0 (0.00)	0.1 (0.04)	0.1 (0.01)
18:0	4.7 (0.10)	2.5 (0.05)	3.3 (0.15)	2.2 (0.01)	4.1 (0.54)	2.7 (0.01)	6.1 (1.69)	1.5 (1.50)
18:1	38.3 (0.36)	14.0 (0.16)	18.5 (0.13)	12.8 (0.36)	12.8 (0.45)	12.1 (0.01)	18.9 (4.27)	11.9 (2.22)
18:2n-6	9.4 (0.62)	13.6 (0.26)	15.4 (0.51)	15.8 (0.27)	21.1 (1.12)	15.8 (0.02)	16.9 (2.42)	11.7 (1.48)
18:3n-3	0.3 (0.02)	32.1 (3.29)	56.6 (0.48)	39.5 (0.73)	28.6 (2.89)	63.1 (0.14)	37.4 (10.70)	29.9 (6.21)
20:0	0.2 (0.02)	1.6 (0.16)	0.1 (0.01)	0.9 (0.12)	1.0 (0.05)	0.1 (0.01)	0.2 (0.15)	2.5 (0.91)
20:1	0.1 (0.00)	21.2 (3.34)	0.2 (0.17)	15.4 (0.98)	12.4 (1.13)	0.2 (0.01)	0.7 (0.120	15.5 (3.47)
22:1	0.2 (0.06)	4.0 (0.20)	0.1 (0.01)	3.3 (0.21)	2.7 (0.22)	0.0 (0.00)	0.1 (0.03)	3.6 (0.95)
SFA[1]	50.4 (0.31)	9.0 (0.23)	8.1 (0.43)	8.3 (0.21)	15.7 (2.95)	7.8 (0.31)	19.6 (5.30)	13.6 (5.54)
MUFA[2]	38.8 (0.24)	39.9 (3.18)	18.9 (0.30)	32.3 (1.12)	29.0 (1.61)	12.5 (0.14)	20.4 (4.67)	31.9 (6.46)
PUFA[3]	9.8 (0.62)	50.2 (3.33)	72.5 (0.19)	57.8 (0.91)	53.7 (2.10)	79.2 (0.35)	55.0 (12.80)	45.4 (7.58)
n-6 PUFA[4]	9.4 (0.62)	16.0 (0.13)	15.8 (0.60)	18.4 (0.17)	23.4 (1.02)	16.0 (0.07)	17.6 (2.14)	14.7 (2.54)
n-3 PUFA[5]	0.4 (0.01)	34.2 (3.29)	56.6 (0.47)	39.5 (0.73)	30.3 (3.06)	63.2 (0.34)	37.4 (10.70)	30.6 (5.31)

MG = megalac; CO = camelina oil; LO = linseed oil; C = camelina seeds; CS = NaOH-treated camelina seed; L = linseed; LS = NaOH-treated Linseed; CA = Camelina oil amide; FAME = fatty acid methyl esters; SFA = saturated fatty acids; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid.
[1]SFA = sum of all even chain fatty acid up to 22:0.
[2]MUFA = sum of 14:1, 16:1, 18:1, 20:1 and 22:1.
[3]PUFA = sum of 18:2, 18:3, 20:2, 20:3, 20:4, 20:5, 22:4 and 22:6.
[4]n-6 PUFA = sum of 18:2, 18:3n-6, 20:2, 20:3n-6, 20:4 and 22:2.
[5]n-3 PUFA = sum of 18:3n-3, 20:3n-3, 20:5, 22:5 and 22:6.

Table 3 *Chemical and fatty acid composition of the concentrates (s.d.)*

	Treatment					
	MG	CO	LO	CS	LS	CA
Number of samples	6	6	6	6	6	6
Dry matter (DM, g/kg)	884 (4.4)	902 (3.3)	906 (7.7)	886 (5.3)	890 (6.4)	897 (10.8)
CP (g/kg)	140 (8.9)	135 (7.0)	128 (3.3)	121 (4.4)	119 (3.9)	190 (5.1)
Ash (g/kg)	85.2 (7.1)	80.2 (7.7)	77.2 (4.1)	90.6 (3.4)	80.5 (3.3)	72.1 (2.3)
Oil (g/kg)	67 (6.2)	81 (3.1)	77 (4.8)	58 (8.0)	61 (8.1)	63 (4.8)
Neutral detergent fiber (g/kg)	159 (12.1)	160 (12.6)	158 (11.2)	175 (7.0)	175 (13.8)	161 (12.1)
Fatty acids (g/100 g FAME)						
16:0	39.7 (1.00)	8.0 (1.20)	7.9 (0.47)	9.5 (2.02)	12.1 (3.23)	7.6 (0.19)
18:0	5.1 (0.09)	4.3 (1.14)	4.2 (0.26)	4.1 (0.53)	6.1 (1.70)	3.8 (0.46)
18:1	34.7 (0.62)	14.0 (0.45)	17.4 (0.74)	12.6 (0.38)	18.9 (4.27)	13.0 (0.28)
18:2n-6	14.9 (2.14)	20.1 (0.40)	21.7 (0.33)	21.1 (1.10)	16.9 (2.42)	20.3 (0.50)
18:3n-3	0 (0)	29.6 (2.09)	46.1 (0.47)	28.6 (2.89)	37.4 (10.66)	27.1 (0.82)
20:1	1.6 (0.39)	13.4 (2.77)	0.5 (0.19)	12.5 (1.13)	0.7 (0.12)	13.3 (0.12)
SFA[1]	46.7 (1.23)	14.3 (2.19)	12.8 (0.64)	15.7 (2.95)	19.6 (5.03)	13.8 (0.62)
MUFA[2]	37.3 (0.27)	31.3 (3.57)	18.3 (0.86)	29.0 (1.61)	20.4 (4.67)	30.0 (0.19)
PUFA[3]	15.3 (2.04)	53.3 (1.34)	68.2 (0.69)	53.7 (2.10)	55.0 (12.55)	51.8 (0.56)
n-6: n-3 PUFA ratio	–	0.71 (0.059)	0.48 (0.010)	0.76 (0.110)	0.47 (0.068)	0.75 (0.040)

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; FAME = fatty acid methyl esters; SFA = saturated fatty acids; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid.
[1]SFA = sum of all even chain fatty acid up to 22:0.
[2]MUFA = sum of 14:1, 16:1, 18:1, 20:1.
[3]PUFA = sum of 18:2, 18:3, 20:2, 20:3,20:4, 20:5, 22:4 and 22:6.
n-6 PUFA = sum of 18:2, 18:3n-6, 20:2, 20:3n-6, 20:4 and 22:2, n-3 PUFA = sum of 18:3n-3, 20:3n-3, 20:5, 22:5 and 22:6.

($P < 0.05$) for the LS ration than for the LO ration but the corresponding camelina-based rations did not differ. The digestibility of CP and the DOMD were higher ($P < 0.05$) for the CA ration compared to the CS ration.

Growth rate averaged 169 g/day and did not differ between treatments. Compared to the MG ration, the animal production characteristics measured were similar for the PUFA-rich rations. Carcass weight was higher ($P < 0.05$) and

Table 4 *Feed intake, ration digestibility* in vivo *and animal production characteristics*

	Treatment							Contrasts				
	MG	CO	LO	CS	LS	CA	s.e.d.	PUFA	O *v.* S	C *v.* L	M × F	CS *v.* CA
Intake (g dry matter/day)	976	997	1018	981	1001	993	11.2	+	*	*	ns	ns
Digestibility (g/kg)												
Dry matter	794	825	807	805	765	822	13.7	ns	**	**	ns	ns
Ash	402	566	501	610	513	572	28.7	***	ns	***	ns	ns
Organic matter	836	850	836	827	791	844	13.1	ns	**	*	ns	ns
CP	768	768	719	677	679	802	19.9	*	***	ns	ns	*
Neutral detergent fiber	609	612	586	618	592	648	36.9	ns	ns	ns	ns	ns
Oil	717	815[a]	752[a]	775[a]	404[b]	749	59.5	ns	***	***	**	ns
DOMD	755	775	764	742	719	776	12.0	ns	***	ns	ns	*
Preslaughter weight (kg)	56.7	57.1	57.3	57.0	56.0	58.2	1.09	ns	ns	ns	ns	ns
Carcass weight (kg)	29.2	29.7	29.8	28.7	28.9	29.3	0.66	ns	*	ns	ns	ns
Killout (%)	51.5	52.0	51.8	50.3	51.5	50.4	0.79	ns	ns	ns	ns	ns
Kidney channel fat (g)	489	553	629	460	471	415	92.4	ns	+	ns	ns	ns
Kidneys weight (g)	124.7	122.4	141.2	125.5	123.6	142.0	7.28	ns	ns	ns	ns	*
Liver weight (g)	742	693[a]	782[b]	698[a]	673[a]	872	30.4	ns	*	ns	*	*

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; O = oil; S = seed; C = camelina; L = linseed; M = method of feeding (oil or seed); F = fat source (camelina or linseed); DOMD = digestible organic matter in the dry matter; ns = non-significant, $P > 0.05$; +, *, ** and *** refer to significance levels $P < 0.1$, $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. For a significant M × F interaction, means with a common superscript do not differ ($P < 0.05$).

the weight of perirenal fat tended ($P < 0.1$) to be higher for lambs offered the oil-based rations than for the NaOH-treated oilseed-based rations. There was an interaction for liver weight such that it was lower ($P < 0.05$) for lambs offered the LS ration than for the LO ration but the corresponding camelina-based rations did not differ. The weight of the kidneys and liver were higher ($P < 0.05$) for lambs offered the CA ration compared to the CS ration.

Fatty acid composition of feces

Compared to the MG ration, for the major fatty acids detected, feces from animals offered the PUFA-rich rations had on average a lower ($P < 0.05$) proportion of 16:0 and total SFA and a higher ($P < 0.05$) proportion of 18:0, *trans*-9 18:1 *trans*-11, 18:1, 20:0, 20:1, 22:0, 24:0, 24:1 and MUFA. Feces from lambs offered the oil-based rations had a lower ($P < 0.05$) proportion of 18:2n-6, 18:3n-3 and total PUFA and a higher ($P < 0.05$) proportion of 20:0 compared to that from the NaOH-treated oilseed-based rations. Feces from lambs offered the camelina-based rations had a higher ($P < 0.05$) proportion of 15:0, 18:3n-6, 20:0, 20:2, 22:0, 22:1, 24:1 and total PUFA and a lower ($P < 0.05$) proportion of *trans* 11 18:1 than that from the linseed-based rations. There was an interaction for 18:0 and total SFA such that the proportions were lower ($P < 0.05$) for feces from lambs offered the CS ration compared to the CO ration but were similar for the linseed-based rations. In contrast, the interaction for 20:1 and 24:0 indicated that the proportions were higher ($P < 0.05$) for feces from lambs offered the CS ration compared to the CO ration but were lower ($P < 0.05$; 24:0 only) for the LS ration compared to the LO ration. The proportions of 18:2n-6, 18:3n-3, 20:1, 24:0 and total PUFA were lower ($P < 0.05$) in feces from lambs fed the CA ration compared to the CS ration (Table 5).

Fatty acid composition of total lipids in intramuscular fat

The fatty acid concentration in the total lipid fraction did not differ between treatments. Compared to the MG ration, total lipid from lambs fed the PUFA-rich rations had a lower ($P < 0.05$) proportion of 14:1, 16:0, 16:1, *cis*-9 18:1, *cis*-11 18:1, 18:2n-6, 20:3n-6, 20:4n-6, total SFA, n-6 PUFA and n-6: n-3 PUFA ratio and a higher ($P < 0.05$) proportion of *trans*-9 18:1, *trans*-11 18:1, *cis*-9, *trans*-11 CLA, 18:3n-3, 20:0, 20:1, 20:2n-6, 20:5n-3, 22:5n-3, PUFA, n-3 PUFA and PUFA/SFA ratio (Table 6).

Total lipid from lambs fed the oil-based rations had a lower ($P < 0.05$) proportion of 18:0, *cis*-9, *trans*-11 CLA, 20:2n-6, 20:4n-6, PUFA and PUFA/SFA ratio and a higher ($P < 0.05$) proportion of *trans*-9 18:1, *trans*-11 18:1 and n-6: n-3 PUFA ratio compared to that from lambs fed the NaOH-treated oilseeds-based rations.

Total lipid from lambs fed the camelina-based rations had a higher ($P < 0.05$) proportion of 18:3n-6, 20:2n-6, 20:3n-3, 22:1, MUFA and n-6: n-3 PUFA ratio and a lower ($P < 0.05$) proportion of PUFA and PUFA/SFA ratio compared to that from lambs fed the linseed-based rations. There was an interaction ($P < 0.05$) for the proportion of *cis*-9 18:1 (which was lower in LO than in CO, but not different between CS and LS) for the proportions of 18:3n-3 and n-3 PUFA (whereby the difference was greater between CS and LS than between CO and LO), for the proportion of 20:1 (whereby the difference was greater between CO and LO than between CS and LS), for the proportions of 20:5n-3 and 22:5n-3 (which were higher in LS than in CS, but not different between CO

Table 5 *Fatty acid proportion of fecal fat*

	Treatment							Contrasts				
	MG	CO	LO	CS	LS	CA	s.e.d.	PUFA	O *v.* S	C *v.* L	M × F	CS *v.* CA
Fatty acids (g/100 g FAME)												
14:0	0.88	0.78[a]	0.65[a]	0.82[a]	0.28[b]	0.96	0.131	ns	ns	**	*	ns
14:1	0.61	0.16	0.01	0.10	0.01	0.13	0.374	ns	ns	ns	ns	ns
15:0	1.39	1.60	1.26	1.48	0.77	1.89	0.335	ns	ns	*	ns	ns
16:0	42.83	9.82	9.08	9.83	9.22	10.41	1.422	***	ns	ns	ns	ns
17:0	1.42	1.94	1.81	1.83	1.00	1.94	0.352	ns	ns	ns	ns	ns
18:0	30.50	44.90[a]	49.60[a]	33.90[b]	54.40[a]	35.30	5.330	*	ns	**	*	ns
18:1 *cis*-9	3.54	1.87	2.61	2.66	2.82	2.67	0.678	ns	ns	ns	ns	ns
18:1 *trans*-9	3.57	8.87	10.79	7.56	11.61	8.89	2.681	*	ns	ns	ns	ns
18:2n-6	0.23	0.18	0.22	0.46	0.29	0.28	0.080	ns	**	ns	ns	*
18:3n-3	0.04	0.06	0.04	0.28	0.15	0.07	0.083	ns	*	ns	ns	*
18:3n-6	0.20	0.59	0.07	0.49	0.06	0.45	0.084	ns	ns	***	ns	ns
20:0	0.90	6.79	1.52	5.23	0.56	4.91	0.742	***	*	***	ns	ns
20:1	0.07	1.96[a]	0.75[b]	4.64[c]	0.21[b]	2.76	0.620	***	*	***	**	*
20:2	0.08	0.25	0.11	0.32	0.07	0.18	0.107	ns	ns	*	ns	ns
22:0	0.46	0.86	0.51	0.87	0.36	0.78	0.106	*	ns	*	ns	ns
22:1	0.09	0.66	0.22	0.78	0.03	0.94	0.293	*	ns	*	ns	ns
24:0	0.43	0.97[a]	0.76[a]	1.32[b]	0.35[c]	0.92	0.168	*	ns	***	**	*
24:1	0.02	0.61	0.43	0.66	0.20	0.92	0.151	***	ns	**	ns	+
18:1 *trans*-11	0.80	3.65	5.03	3.58	4.50	4.72	0.729	***	ns	*	ns	ns
Unidentified	11.24	12.80[a]	13.83[a]	20.88[b]	12.30[a]	19.63	2.224	*	ns	*	**	ns
SFA[1]	79.00	67.80[a]	65.30[a]	55.70[b]	67.00[a]	57.30	4.770	**	ns	ns	*	ns
MUFA[2]	9.10	18.10	20.10	20.50	19.60	21.50	4.210	*	ns	ns	ns	ns
PUFA[3]	0.73	1.32	0.71	2.92	1.08	1.53	0.486	ns	*	**	ns	*

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; O = oil; S = seed; C = camelina; L = linseed; M = method of feeding (oil or seed); F = fat source (camelina or linseed); FAME = fatty acid methyl esters; SFA = saturated fatty acids; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid; ns = non-significant, $P > 0.05$; +, *, ** and *** refer to significance levels $P < 0.1$, $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. For a significant M × F interaction, means with a common superscript do not differ ($P < 0.05$).
[1]SFA = sum of all even chain fatty acid up to 22:0.
[2]MUFA = sum of 14:1, 16:1, 18:1 and 20:1.
[3]PUFA = sum of 18:2, 18:3, 20:2, 20:3, 20:4, 20:5, 22:4 and 22:6.

and LO) and for the proportion of 22:6n-3 (which was lower in LO compared to CO but higher in LS compared to CS).

The proportions of *trans*-11 18:1, *trans* 18:2n-6, *cis*-9, *trans*-11 CLA, 18:3n-6, 20:0, 20:2n-6, 20:4n-6 ($P < 0.1$), 20:5n-3 and 22:1n-9 were lower ($P < 0.05$) and the proportions of *trans*-10, *cis*-12 CLA, 18:3n-3 ($P < 0.1$) and total SFA ($P < 0.1$) were higher in total lipid from lambs fed the CA ration compared to the CS ration.

Fatty acid composition of neutral lipids (NL) in intramuscular fat

The total fatty acid concentration in NL did not differ between treatments. Compared to the MG ration, NL from animals fed the PUFA-rich rations had a lower ($P < 0.05$) proportion of 14:1, 16:0, 16:1, 18:0, 18:1n-9, 20:4n-6, SFA and n-6: n-3 PUFA ratio and a higher ($P < 0.05$) PUFA/SFA ratio (Table 7).

The NL from lambs offered the oil-based rations had a lower ($P < 0.05$) proportion of 18:0, *cis*-9, *trans*-11 CLA, 20:2n-6 ($P < 0.01$), PUFA and PUFA/SFA ratio and a higher ($P < 0.05$) proportion of *trans*-9 18:1 and *trans*-11 18:1 compared to lambs fed the NaOH-treated oilseeds-based rations. The NL from lambs fed the camelina-based rations had a higher ($P < 0.05$) proportion of 20:2n-6, 20:3n-3, 22:1n-9 and n-6: n-3 PUFA ratio and a lower ($P < 0.05$) proportion of 14:1 ($P < 0.1$) and PUFA compared to lambs fed the linseed-based rations. There was an interaction ($P < 0.05$) for the proportions of 18:1n-9, 20:4n-6, 20:5n-3, 22:5n-3 and 22:6n-3 (whereby LO tended to be lower than CO, but LS tended to be higher than CS) for 18:3n-3 and n-3 PUFA (such that the increase caused by feeding linseed was higher when it was fed as NaOH-treated seed than when it was fed as oil), for the proportion of 20:1 (whereby the decrease caused by feeding linseed was greater when it was fed as oil rather than as NaOH-treated seed) and for total MUFA (whereby LO was lower ($P < 0.05$) than CO, but LS and CS did not differ).

The proportions of *trans*-11 18:1, *trans* C18:2n-6, *cis*-9, *trans*-11 CLA, 20:0, 20:2n-6 and 22:1n-9 were lower ($P < 0.05$) in NL from lambs fed the CA ration compared to the CS ration.

Fatty acid composition of polar lipids (PL) in intramuscular fat

The total fatty acid concentration in PL did not differ between treatments. Compared to the MG ration, PL from animals fed the PUFA-rich rations had on average, a lower

Table 6 *Fatty acid proportion of total intramuscular fat from* m. longissimus dorsi

	Treatment							Contrasts				
	MG	CO	LO	CS	LS	CA	s.e.d.	PUFA	O *v.* S	C *v.* L	M × F	CS *v.* CA
Total fatty acids (mg/100g fresh muscle) (g/100 g FAME)	3524	4659	4177	4056	3980	4171	376.0	ns	ns	ns	ns	ns
10:0	0.06	0.05	0.07	0.05	0.06	0.05	0.008	ns	ns	*	ns	ns
11:0	–	–	–	–	–	–	–	–	–	–	–	ns
12:0	0.06	0.06	0.05	0.05	0.06	0.05	0.006	ns	ns	ns	*	ns
13:0	0.01	0.01	0.01	0.01	0.01	0.01	0.001	ns	ns	ns	*	ns
14:0	1.81	1.98	1.76	1.68	1.77	1.76	0.128	ns	ns	ns	ns	ns
14:1	0.10	0.08	0.08	0.07	0.08	0.08	0.008	*	ns	ns	ns	ns
15:0	0.30	0.32	0.29	0.29	0.31	0.28	0.018	ns	ns	ns	ns	ns
16:0	24.14	21.51	21.16	20.72	20.83	21.70	0.538	***	ns	ns	ns	ns
16:1	1.69	1.20	1.12	1.05	1.11	1.02	0.084	***	ns	ns	ns	ns
17:0	1.16	1.23	1.23	1.25	1.36	1.16	0.056	ns	ns	ns	ns	ns
17:1	0.53	0.51	0.47	0.46	0.49	0.43	0.034	ns	ns	ns	ns	ns
18:0	15.65	13.10	14.66	15.44	15.65	16.28	0.826	ns	**	ns	ns	ns
18:1 *cis*-9	39.01	36.68^{a}	34.58^{b}	36.23^{a,b}	37.05^{a,c}	36.44	0.981	*	ns	ns	*	ns
18:1 *trans*-9	0.86	1.74	1.75	1.39	1.44	1.18	0.156	***	**	ns	ns	ns
18:1 *cis*-11	0.53	0.43	0.38	0.38	0.36	0.33	0.056	*	ns	ns	ns	ns
18:1 *trans*-11	2.85	4.61	5.28	4.13	3.87	3.32	0.337	***	***	ns	ns	*
18:2n-6 *cis*	3.45	2.86	3.01	3.01	3.03	3.32	0.187	*	ns	ns	ns	ns
18:2n-6 *trans*	0.05	0.11^{a}	0.17^{b}	0.10^{a}	0.08^{a}	0.06	0.018	***	***	ns	**	*
CLA *cis*-9, *trans*-11	0.82	0.95	0.98	1.24	1.41	0.80	0.092	***	***	ns	ns	*
CLA *trans*-10, *cis*-12	0.01	0.01^{b}	0.03^{c}	0.01^{a,b}	0.00^{a}	0.03	0.005	ns	***	ns	*	*
18:3n-6	0.06	0.12	0.06	0.12	0.05	0.08	0.010	***	ns	***	ns	*
18:3n-3	0.50	1.27^{b}	1.74^{c}	1.66^{c}	2.56^{d}	1.90	0.132	***	***	***	*	+
20:0	0.06	0.15^{b}	0.05^{a}	0.21^{c}	0.06^{a}	0.16	0.015	***	**	***	**	*
20:1	0.19	1.62^{c}	0.13^{a}	1.22^{b}	0.11^{a}	1.20	0.087	***	***	***	**	ns
20:2n-6	0.07	0.22	0.11	0.24	0.12	0.20	0.011	***	*	***	ns	*
20:3n-3	0.06	0.12^{b}	0.07^{a}	0.12^{b}	0.07^{a}	0.11	0.016	ns	ns	***	ns	ns
20:3n-6	0.07	0.04^{a}	0.04^{a}	0.05^{a}	0.06^{b}	0.04	0.005	***	**	ns	*	ns
20:4n-6	0.60	0.33	0.31	0.36	0.42	0.29	0.036	***	**	ns	ns	+
20:5n-3	0.07	0.11^{a}	0.12^{a}	0.16^{b}	0.30^{c}	0.12	0.016	***	***	***	***	*
22:1n-9	0.01	0.08	0.01	0.08	0.01	0.06	0.007	***	ns	***	ns	*
22:2n-6	0.01	0.02	0.02	0.02	0.03	0.02	0.004	**	*	ns	ns	ns
22:5n-3	0.20	0.20^{a}	0.21^{a}	0.22^{a}	0.32^{b}	0.20	0.015	***	***	***	***	ns
22:6n-3	0.04	0.05^{a}	0.03^{b}	0.04^{a,b}	0.08^{c}	0.03	0.006	ns	***	***	***	ns
24:0	0.00	0.01	0.01	0.00	0.01	0.01	0.003	ns	ns	*	ns	ns
SFA[1]	43.26	38.43	39.29	39.71^{a}	40.10	41.48	0.919	***	ns	ns	ns	+
MUFA[2]	45.78	46.95	43.81	45.01	44.53	44.06	0.965	ns	ns	*	ns	ns
PUFA[3]	6.02	6.41	6.91	7.35	8.54	7.20	0.319	***	***	***	ns	ns
n-6 PUFA[4]	4.31	3.70	3.72	3.90	3.80	4.00	0.212	*	ns	ns	ns	ns
n-3 PUFA[5]	0.87	1.75^{b}	2.18^{c}	2.21^{c}	3.33^{d}	2.36	0.150	***	***	***	**	ns
PUFA/SFA ratio	0.15	0.17^{b}	0.18^{b}	0.19^{b}	0.22^{c}	0.18	0.010	***	***	**	ns	ns
n-6:n-3 PUFA ratio	5.28	2.14^{b}	1.75^{b}	1.83^{b}	1.15^{a}	1.72	0.248	***	*	**	ns	ns

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; O = oil; S = seed; C = camelina; L = linseed; M = method of feeding (oil or seed); F = fat source (camelina or linseed); FAME = fatty acid methyl esters; CLA = conjugated linoleic acid; SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids; ns = non-significant, $P > 0.05$; +, *, ** and *** refer to significance levels $P < 0.1$, $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. For a significant M × F interaction, means with a common superscript do not differ ($P < 0.05$).
[1]SFA = sum of all even chain fatty acid up to 24:0 + 13:0, 15:0 and 17:0.
[2]MUFA = sum of 14:1, 16:1, 17:1, all 18:1, 20:1, 22:1 and 24:1.
[3]PUFA = sum of total n-6, total n-3, total CLA.
[4]n-6 PUFA = sum of 18:2n-6, 18:3n-6, 20:2, 20:3n-6, 20:4 and 22:2.
[5]n-3 PUFA = sum of 18:3n-3, 20:3n-3, 20:5, 22:5 and 22:6.

($P < 0.05$) proportion of 16:0, 16:1, *cis*-9 18:1, *cis*-11 18:1, 20:3n-6, 20:4n-6, SFA, MUFA, n-6 PUFA and n-6: n-3 PUFA ratio and a higher ($P < 0.05$) proportion of 17:0, C18:0, *trans*-9 18:1, *trans*-11 18:1, *cis*-9, *trans*-11 CLA, 18:3n-3, 20:1, 20:2, 20:3n-3, 20:5n-3, 22:2n-6, 22:5n-3, PUFA, n-3 PUFA and PUFA/SFA ratio (Table 8).

Table 7 *Fatty acid proportion of the neutral lipid fraction of intramuscular fat from* m. longissimus dorsi

	Treatment							Contrasts				
	MG	CO	LO	CS	LS	CA	s.e.d.	PUFA	O *v.* S	C *v.* L	M × F	CS *v.* CA
Total fatty acids (mg/100 g fresh muscle) (g/100 g FAME)	3196	4225	3788	3678	3609	3783	341.0	ns	ns	ns	ns	ns
10:0	0.06	0.06	0.07	0.05	0.06	0.05	0.009	ns	ns	*	ns	ns
12:0	0.07	0.06	0.05	0.05	0.06	0.06	0.005	*	ns	ns	*	ns
13:0	0.01	0.01	0.01	0.01	0.01	0.01	0.001	ns	ns	ns	*	ns
14:0	1.89	2.06	1.83	1.75	1.84	1.83	0.133	ns	ns	ns	ns	ns
14:1	0.11	0.08	0.09	0.07	0.09	0.08	0.009	*	ns	+	ns	ns
15:0	0.31	0.33	0.29	0.30	0.31	0.29	0.018	ns	ns	ns	ns	ns
16:0	24.30	21.70	21.39	20.92	21.06	21.84	0.566	***	ns	ns	ns	ns
16:1	1.77	1.24	1.16	1.09	1.16	1.05	0.086	***	ns	ns	ns	ns
17:0	1.03	1.10	1.09	1.07	1.16	1.02	0.062	ns	ns	ns	ns	ns
17:1	0.54	0.51	0.48	0.47	0.50	0.43	0.035	ns	ns	ns	ns	ns
18:0	16.39	13.46	15.14	15.95	16.19	16.84	0.901	ns	**	ns	ns	ns
18:1 *cis*-9	39.91	37.27^{ab}	35.50^{a}	37.05^{ab}	38.40^{b}	37.31	1.002	**	ns	ns	*	ns
18:1 *trans*-9	0.91	1.81	1.81	1.45	1.51	1.23	0.161	***	**	ns	ns	ns
18:1 *cis*-11	0.43	0.39	0.31	0.33	0.29	0.28	0.057	ns	ns	ns	ns	ns
18:1 *trans*-11	3.01	4.76	5.45	4.29	4.03	3.43	0.350	***	***	ns	ns	*
18:2n-6 *cis*	2.47	2.20	2.26	2.34	2.32	2.54	0.148	ns	ns	ns	ns	ns
18:2n-6 *trans*	0.05	0.11^{a}	0.18^{b}	0.10^{a}	0.08^{a}	0.06	0.019	***	***	ns	**	*
CLA *cis*-9, *trans*-11	0.86	0.98	1.01	1.28	1.46	0.83	0.095	***	***	ns	ns	*
CLA *trans*-10, *cis*-12	0.01	0.01^{a}	0.03^{b}	0.01^{a}	0.00^{a}	0.03	0.005	ns	***	ns	*	*
18:3n-6	0.05	0.11	0.05	0.12	0.04	0.07	0.011	***	ns	ns	ns	*
18:3n-3	0.47	1.13^{a}	1.46^{b}	1.44^{b}	2.15^{c}	1.64	0.126	***	***	***	*	ns
20:0	0.06	0.15^{b}	0.05^{a}	0.22^{c}	0.06^{a}	0.16	0.016	***	**	***	**	*
20:1	0.19	1.64^{c}	0.13^{a}	1.23^{b}	0.11^{a}	1.22	0.090	***	**	***	**	ns
20:2n-6	0.07	0.20	0.11	0.22	0.12	0.19	0.010	***	*	***	ns	*
20:3n-3	0.06	0.12	0.07	0.11	0.06	0.11	0.017	**	ns	***	ns	ns
20:3n-6	0.03	0.03	0.02	0.02	0.03	0.02	0.003	*	ns	ns	*	ns
20:4-n6	0.15	0.14^{a,c}	0.09^{b}	0.11^{b}	0.13^{a}	0.10	0.013	***	ns	ns	**	ns
20:5-n3	0.02	0.05^{a}	0.04^{b}	0.05^{a}	0.09^{c}	0.04	0.005	***	***	***	***	ns
22:1n-9	0.01	0.08	0.01	0.08	0.02	0.06	0.008	***	ns	***	ns	*
22:2n-6	0.01	0.02	0.01	0.01	0.02	0.01	0.004	ns	ns	ns	ns	ns
22:5n-3	0.10	0.13^{a}	0.11^{a}	0.12^{a}	0.16^{a,b}	0.11	0.013	***	*	ns	**	ns
22:6n-3	0.02	0.03^{a}	0.02^{b}	0.02^{b}	0.04^{c}	0.02	0.005	ns	*	ns	***	ns
24:0	0.00	0.00	0.01	0.00	0.01	0.01	0.002	ns	ns	*	ns	ns
SFA[1]	44.13	38.95	39.95	40.33	40.76	42.13	1.001	***	ns	ns	ns	ns
MUFA[2]	46.88	47.79^{a}	44.94^{b}	46.08^{ab}	46.10^{ab}	45.10	0.956	ns	ns	*	*	ns
PUFA[3]	4.36	5.27^{b}	5.46^{bc}	5.97^{c}	6.71^{d}	5.79	0.290	***	***	*	ns	ns
n-6 PUFA[4]	2.82	2.81	2.72	2.94	2.73	3.00	0.162	ns	ns	ns	ns	ns
n-3 PUFA[5]	0.67	1.46^{a}	1.70^{a,b}	1.74^{b}	2.51^{c}	1.92	0.138	***	***	***	*	ns
PUFA/SFA ratio	0.100	0.136	0.137	0.149	0.166	0.138	0.009	***	**	ns	ns	ns
n-6: n-3 PUFA ratio	4.50	1.93	1.64	1.80	1.10	1.57	0.246	***	ns	**	ns	ns

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; O = oil; S = seed; C = camelina; L = linseed; M = method of feeding (oil or seed); F = fat source (camelina or linseed); FAME = fatty acid methyl esters; CLA = conjugated linoleic acid; SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids; ns = non-significant; $P > 0.05$; +, *, ** and *** refer to significance levels $P < 0.1$, < 0.05, $P < 0.01$ and $P < 0.001$, respectively. For a significant M × F interaction, means with a common superscript do not differ ($P < 0.05$).
[1]SFA = sum of all even chain fatty acid up to 24:0+13:0, 15:0 and 17:0.
[2]MUFA = sum of 14:1, 16:1, 17:1, all 18:1, 20:1, 22:1 and 24:1.
[3]PUFA = sum of total n-6, total n-3, total CLA.
[4]n-6 PUFA = sum of 18:2n-6, 18:3n-6, 20:2, 20:3n-6, 20:4 and 22:2.
[5]n-3 PUFA = sum of 18:3n-3, 20:3n-3, 20:5, 22:5 and 22:6.

The PL from lambs offered the oil-based rations had a lower (<0.05) proportion of 18:0, 18:3n-3, 20:0, 20:2n-6, 20:3n-3, 20:4n-6, SFA, PUFA and n-3 PUFA and a higher ($P < 0.05$) proportion of *cis*-9 18:1, 18:2n-6, 20:1, MUFA and n-6: n-3 PUFA compared to lambs fed the NaOH-treated oilseeds-based rations.

The PL from lambs fed the camelina-based rations had a higher ($P < 0.05$) proportion of *cis*-9 18:1, 20:0, 20:1, 20:2n-6,

Table 8 *Fatty acid proportion of the polar lipid fraction of intramuscular fat from* m. longissimus dorsi

	Treatment							Contrasts				
	MG	CO	LO	CS	LS	CA	s.e.d.	PUFA	O *v.* S	C *v.* L	M × F	CS *v.* CA
Total fatty acids (mg/100 g fresh muscle) (g/100 g FAME)	328.1	433.8	388.9	377.6	370.5	388.3	35.01	ns	ns	ns	ns	ns
10:0	0.02	0.01	0.02	0.01	0.02	0.01	0.005	ns	ns	ns	ns	ns
12:0	0.01	0.01	0.01	0.00	0.00	0.00	0.003	ns	*	ns	ns	ns
14:0	0.64	0.46	0.56	0.62	0.59	0.52	0.105	ns	ns	ns	ns	ns
15:0	0.18	0.19	0.21	0.19	0.21	0.22	0.020	ns	ns	ns	ns	ns
16:0	22.14	17.96	17.65	17.57	17.48	19.15	0.613	*	ns	ns	ns	*
16:1	0.65	0.46	0.48	0.42	0.41	0.42	0.049	*	ns	ns	ns	ns
17:0	2.96	3.55	3.49	3.94	4.39	3.64	0.188	*	***	ns	ns	ns
17:1	0.38	0.41	0.40	0.35	0.34	0.33	0.029	ns	**	ns	ns	ns
18:0	6.07	6.87	7.10	7.61	8.00	6.79	0.387	*	**	ns	ns	*
18:1 *cis*-9	27.25	25.88	19.81	23.26	16.77	21.82	1.537	*	*	***	ns	ns
18:1 *trans*-9	0.18	0.43[a]	0.63[b]	0.43[a]	0.31[c]	0.33	0.038	*	***	ns	***	*
18:1 *cis*-11	1.84	1.22	1.52	1.21	1.32	1.15	0.128	*	ns	ns	ns	ns
18:1 *trans*-11	0.80	1.85[a]	2.56[b]	1.60[a]	1.55[a]	1.35	0.174	*	***	**	**	ns
18:2n-6 *cis*	16.17	14.79	15.03	13.45	13.56	16.54	0.935	ns	*	ns	ns	*
18:2n-6 *trans*	0.04	0.02	0.06	0.04	0.07	0.02	0.016	ns	ns	**	ns	ns
CLA *cis*-9, *trans*-11	0.29	0.33	0.46	0.53	0.56	0.29	0.042	*	***	*	ns	*
CLA *trans*-10, *cis*-12	0.02	0.01	0.03	0.01	0.01	0.01	0.008	ns	*	ns	ns	ns
18:3n-6	0.20	0.18	0.21	0.18	0.23	0.16	0.014	ns	ns	***	ns	ns
18:3n-3	0.90	3.84	6.21	5.10	8.57	6.26	0.442	*	***	***	ns	*
20:0	0.09	0.09	0.06	0.12	0.08	0.09	0.009	ns	**	***	ns	*
20:1	0.18	1.30[a]	0.24[b]	1.01[c]	0.13[b]	0.91	0.062	*	***	***	*	ns
20:2n-6	0.15	0.47	0.17	0.56	0.19	0.42	0.033	*	*	***	ns	*
20:3n-3	0.04	0.19	0.09	0.20	0.13	0.18	0.020	*	*	***	ns	ns
20:3n-6	0.64	0.34[a,b]	0.32[a]	0.39[b]	0.50[c]	0.30	0.027	*	***	*	**	*
20:4n-6	6.53	3.83	3.70	4.28	4.79	3.54	0.350	*	**	ns	ns	*
20:5n-3	0.69	1.29[a]	1.48[a]	1.91[b]	3.41[c]	1.53	0.161	*	***	***	***	*
22:1n-9	0.00	0.04	0.00	0.03	0.00	0.02	0.007	*	*	***	ns	ns
22:2n-6	0.01	0.05[a]	0.07[a]	0.09[a]	0.21[b]	0.06	0.030	*	***	**	*	ns
22:5n-3	1.52	1.41[a]	1.75[b]	1.86[b]	2.65[c]	1.61	0.104	*	***	***	**	*
22:6n-3	0.32	0.33[a]	0.31[a]	0.36[a]	0.72[b]	0.27	0.049	ns	***	***	***	ns
24:0	0.01	0.02	0.02	0.01	0.08	0.01	0.028	ns	ns	ns	ns	ns
SFA[1]	32.12	29.16	29.13	30.08	30.84	30.43[b]	0.702	*	*	ns	ns	ns
MUFA[2]	31.27	31.59	25.64	28.30	20.82	26.34	1.472	*	***	***	ns	ns
PUFA[3]	27.53	27.11	29.89	28.96	35.59	31.21	1.522	*	***	***	ns	ns
n-6 PUFA[4]	23.74	19.69	19.56	18.99	19.53	21.0[a]	1.121	*	ns	ns	ns	*
n-3 PUFA[5]	3.47	7.07	9.84	9.44	15.49	9.85	0.598	*	***	***	ns	ns
PUFA/SFA ratio	0.86	0.94	1.03	0.97	1.16	1.03	0.063	*	ns	**	ns	ns
n-6: n-3 PUFA ratio	6.96	2.78	2.01	2.03	1.27	2.15	0.248	*	**	**	ns	ns

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; O = oil; S = seed; C = camelina; L = linseed; M = method of feeding (oil or seed); F = fat source (camelina or linseed); FAME = fatty acid methyl esters; CLA = conjugated linoleic acid; SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids; ns = non-significant, $P > 0.05$; +, *, ** and *** refer to significance levels $P < 0.1$, < 0.05, $P < 0.01$ and $P < 0.001$, respectively. For a significant M × F interaction, means with a common superscript do not differ ($P < 0.05$).
[1]SFA = sum of all even chain fatty acid up to 24:0+13:0, 15:0 and 17:0.
[2]MUFA = sum of 14:1, 16:1, 17:1, all 18:1, 20:1, 22:1 and 24:1.
[3]PUFA = sum of total n-6, total n-3, total CLA.
[4]n-6 PUFA = sum of 18:2n-6, 18:3n-6, 20:2, 20:3n-6, 20:4 and 22:2.
[5]n-3 PUFA = sum of 18:3n-3, 20:3n-3, 20:5, 22:5 and 22:6.

20:3n-3, 22:1, MUFA and n-6: n-3 PUFA and a lower ($P < 0.05$) proportion of 18:3n-6, 18:3n-3, PUFA, n-3 PUFA and PUFA/SFA ratio compared to lambs fed the linseed-based rations. There was an interaction for the proportion of *trans*-9 18:1 (whereby LO was higher than CO but LS was lower than CS), for *trans*-11 18:1 (whereby LO was higher than CO but LS was similar to CS), for 20:1 (whereby CO was higher than LO but this difference was greater than that between LS and CS), for 20:3n-6, 20:5n-3, 22:2n-6 and 22:6n-6 (whereby there was no difference between CO and LO but LS was higher than CS)

and for 22:5n-3 (whereby LO was higher than CO but this difference was greater between CS and LS).

The proportions of 18:0, *trans*-9 18:1, *cis*-9, *trans*-11 CLA, 20:0, 20:2n-6, 20:3n-6, 20:4n-6, 20:5n-3 and 22:5n-3 were lower ($P < 0.05$) and the proportions of 16:0, 18:2n-6, 18:3n-3 and n-6 PUFA were higher ($P < 0.05$) in PL from lambs fed the CA ration compared to the CS ration.

Fatty acid composition of SAT

The total fatty acid concentration in SAT did not differ between treatments. Compared to the MG ration, animals fed the PUFA-rich rations had a lower ($P < 0.05$) proportion of 16:0, 16:1, *cis*-9 18:1, 20:4n-6, SFA and n-6: n-3 PUFA ratio and a higher ($P < 0.05$) proportion of *trans*-11 18:1, *cis*-9, *trans*-11 CLA, 18:3n-6, 18:3n-3, 20:0, 20:1, 20:2n-6, 20:3n-3, 20:5n-3, 22:1, 22:5n-3, PUFA, n-6 PUFA and PUFA/SFA ratio (Table 9).

The SAT from lambs offered the oil-based rations had a lower ($P < 0.05$) proportion of 18:0, *cis*-9 18:1, *cis*-9, *trans*-11 CLA, 18:3n-3, 20:4n-6, SFA and n-3 PUFA and a higher ($P < 0.05$) proportion of 14:0, 15:0, *trans*-11, 18:1 *trans* 18:2n-6, 20:3n-6 and MUFA compared to lambs fed the NaOH-treated oilseeds-based rations.

The SAT from lambs fed the camelina-based rations had a lower ($P < 0.05$) proportion of 18:0, *cis*-9, *trans*-11 CLA, 18:3n-3, SFA, PUFA ($P < 0.1$) and n-3 PUFA and a higher ($P < 0.05$) proportion of 20:2n-6, 22:1, 22:2 and MUFA compared to lambs fed the linseed-based rations. There was an interaction for the proportion of 18:2n-6 (whereby LO was higher than CO but there was no difference between CS and LS), for 18:3n-6 and 20:0 (whereby CS tended to be higher than CO but LS tended to be lower than LO), for 20:1 and 20:3n-3 (whereby the difference was greater for the oil-based rations), for 20:5n-3, 22:5n-3 and 22:6n-3 (whereby there was no difference between CO and LO but LS was higher than CS) and for n-6 PUFA (whereby there was no difference between CO and LO but LS was lower than CS).

The proportions of 14:1, 18:2n-6, 18:3n-3, 20:3n-6 and n-3 PUFA were higher ($P < 0.05$) and the proportions of *cis*-9, *trans*-11 CLA, 18:3n-6 and 22:1n-9 were lower ($P < 0.05$) in SAT from lambs fed the CA ration compared to the CS ration.

Discussion

Camelina sativa is a summer annual oilseed plant of the genus Cruciferae that grows well in temperate climates and has lower costs of production than other oilseed plants such as rapeseed (Crowley and Fröhlich, 1998). Averaged across several varieties, CO contained approximately 16.5% linoleic acid and 39% linolenic acid (Crowley and Fröhlich, 1998), making CO an attractive alternative source of n-3 PUFA to LO in both human and animal nutrition. Moreover, as there is increasing interest in CO as a feedstock for biodiesel production, an increase in the availability of both the oil and co-products is likely to occur (Fröhlich and Rice, 2005). As there are no reports on the effects of CO on the fatty acid composition of ruminant tissue, the main objective of this study was to compare camelina and LS in both oil and seed form relative to a non-PUFA-rich (isolipid) control ration. To avoid passage through the gastrointestinal tract, undamaged seeds were treated with NaOH since this is a procedure that can be used readily on the farm and Kirkland *et al*. (1998) showed that NaOH treatment of LSs could increase the C18:3n-3 proportion of milk. The efficacy of amides of camelina fatty acids as a ruminal protection strategy was also examined as the potential of this strategy has been demonstrated for soybean (Jenkins and Bridges, 2007). The oil from the camelina seeds had a similar fatty acid composition to that reported by Crowley and Fröhlich (1998), which was expected, as the camelina was grown under similar environmental and agronomic conditions. The CO as used, was cold-pressed approximately 9 months before the commencement of the experiment and stored in a sealed opaque container at ambient temperature. Previous studies had shown that little oxidation occurs under these storage conditions (Crowley and Fröhlich, 1998). Nevertheless, there was a small loss of 18:3n-3 due to storage of the oil as described above (32.1 *v.* 39.5 g/100 g fatty acid methyl esters for oil and seeds, respectively). The LSs and LO were from different suppliers but had a similar fatty acid composition. The apparent increase in SFA due to NaOH treatment of whole seeds can be also inferred in the data of Aldrich *et al*. (1997) in which total fatty acid consumption from rations based on crushed canola oil- and NaOH-treated seeds was similar, but SFA consumption tended to be higher from the latter ration. The intention was to formulate rations to the same oil concentration. While this was successful for MG, CS, LS and CA, the oil concentration in CO and LO was similar but higher than intended despite measuring the oil concentration in the seeds in advance of ration manufacture. The comparison of oil- and NaOH-treated seeds may be confounded to some extent by this difference. The CP concentration of MG, CO, LO, CS and LS was similar as intended. Owing to the uncertainty about the ruminal degradability and tissue metabolism of the nitrogen in the camelina amides, it was decided not to make the other rations isonitrogenous with CA. Comparison of CS and CA therefore incorporates differences in CP as part of the method of protection.

Apparent total tract digestibility was measured to determine the effectiveness of the chemical treatments. The digestibility of organic matter from the NaOH-treated oilseed rations was close to that of the corresponding oil-based rations (97% and 95% of that observed for CO and LO, respectively), indicating that the NaOH treatment was moderately effective. Nevertheless, this difference was reflected in higher carcass weights for the oil-based rations. In contrast, the lower oil digestibility of the LS ration (54% that of LO) suggests that the NaOH treatment as used in this study was not sufficient to ensure complete digestion. The higher CP digestibility in the CA ration may reflect the higher CP consumption due to the addition of the amide bond and/or differences in ruminal degradability. Similarly, the higher DOMD may reflect the higher consumption of digestible organic matter and lower consumption of NDF by animals

Table 9 *Fatty acid proportion in the subcutaneous adipose tissue*

	Treatment							Contrasts				
	MG	CO	LO	CS	LS	CA	s.e.d.	PUFA	O *v.* S	C *v.* L	M × F	CS *v.* CA
Total fatty acids (mg/g tissue) (g/100 g FAME)	581.7	597.0	594.5	562.5	575.5	581.7	24.55	ns	ns	ns	ns	ns
10:0	0.14	0.15	0.15	0.16	0.14	0.15	0.013	ns	ns	ns	ns	ns
12:0	0.08	0.08	0.07	0.07	0.07	0.07	0.006	ns	ns	ns	ns	ns
13:0	0.01	0.02	0.02	0.01	0.01	0.01	0.001	ns	**	ns	ns	ns
14:0	3.35	3.57	3.55	3.25	3.25	3.31	0.196	ns	*	ns	ns	ns
14:1	0.17	0.20	0.20	0.17	0.20	0.22	0.016	ns	ns	ns	ns	*
15:0	0.47	0.57	0.59	0.47	0.53	0.50	0.033	*	**	ns	ns	ns
15:1	0.01	0.01	0.01	0.01	0.01	0.01	0.003	ns	ns	ns	ns	ns
16:0	26.36	18.44	19.47	18.57	19.05	18.48	0.609	*	ns	ns	ns	ns
16:1	2.00	1.02	1.06	0.99	1.08	0.99	0.080	*	ns	ns	ns	ns
17:0	1.35	1.48	1.67	1.32	1.64	1.39	0.100	ns	ns	***	ns	ns
17:1	0.52	0.52	0.56	0.46	0.56	0.46	0.044	ns	ns	*	ns	ns
18:0	18.22	16.05	16.89	18.70	20.34	19.12	0.842	ns	***	*	ns	ns
18:1 *cis*-9	32.95	27.03	28.02	30.87	29.97	30.87	1.212	*	**	ns	ns	ns
18:1 *trans*-9	0.40	1.27	0.80	0.65	0.62	0.55	0.390	ns	ns	ns	ns	ns
18:1 *cis*-11	0.96	0.78	1.00	0.38	0.93	0.72	0.286	ns	ns	ns	ns	ns
18:1 *trans*-11	4.76	10.77	10.91	7.39	7.57	6.43	1.325	*	***	ns	ns	ns
18:2n-6 *cis*	2.05	2.24^{a}	2.90^{b}	1.95^{a}	1.98^{a}	2.46	0.186	ns	***	*	*	*
18:2n-6 *trans*	0.03	0.16	0.28	0.09	0.07	0.12	0.072	ns	*	ns	ns	ns
CLA *cis*-9, *trans*-11	0.59	0.82	1.04	1.33	1.53	0.79	0.090	*	***	**	ns	*
CLA *trans*-10, *cis*-12	0.04	0.09	0.12	0.08	0.08	0.06	0.034	ns	ns	ns	ns	ns
18:3n-6	0.04	0.38^{b}	0.10^{a}	0.43^{b}	0.05^{a}	0.27	0.030	*	ns	***	*	*
18:3n-3	0.22	1.09	1.55	1.48	2.09	1.84	0.146	*	***	***	ns	*
20:0	0.06	0.43^{c}	0.23^{b}	0.73^{d}	0.06^{a}	0.40	0.069	*	ns	***	***	*
20:1	0.16	4.19^{c}	0.31^{a}	3.09^{b}	0.14^{a}	3.11	0.172	*	***	***	***	ns
20:2n-6	0.04	0.43^{d}	0.15^{b}	0.37^{cd}	0.14^{b}	0.33	0.047	*	ns	***	ns	ns
20:3n-3	0.00	0.20^{c}	0.03^{a}	0.16^{b}	0.02^{a}	0.17	0.009	*	**	***	*	ns
20:3n-6	0.02	0.03	0.04	0.03	0.01	0.05	0.008	ns	**	ns	ns	*
20:4n-6	0.14	0.09	0.08	0.10	0.10	0.10	0.008	*	*	ns	ns	ns
20:5n-3	0.01	0.03^{a}	0.03^{a}	0.03^{a}	0.07^{b}	0.03	0.004	*	***	***	***	ns
22:0	0.01	0.02^{b}	0.01^{a}	0.02^{b}	0.01^{a}	0.02	0.002	*	ns	***	*	ns
22:1n-9	0.00	0.32	0.03	0.34	0.01	0.25	0.019	*	ns	***	ns	*
22:2n-6	0.01	0.02	0.01	0.02	0.01	0.02	0.003	ns	ns	***	ns	ns
22:5n-3	0.08	0.11^{a}	0.11^{a}	0.12^{a}	0.19^{b}	0.12	0.010	*	***	***	***	ns
22:6n-3	0.01	0.02^{a}	0.01^{a}	0.02^{a}	0.05^{b}	0.01	0.006	ns	***	**	***	ns
24:1	0.00	0.01^{a}	0.00^{b}	0.01^{a}	0.00^{b}	0.01	0.002	ns	ns	***	**	ns
SFA[1]	50.07	40.81	42.67	43.31	45.10	43.48	1.053	*	**	*	ns	ns
MUFA[2]	41.94	46.12	42.91	44.37	41.08	43.61	1.084	ns	*	***	ns	ns
PUFA[3]	3.29	5.72	6.43	6.23	6.41	6.38	0.341	*	ns	+	ns	ns
n-6 PUFA[4]	2.33	3.37^{a}	3.54^{a}	2.99^{b}	2.37^{c}	3.35	0.221	*	***	ns	*	ns
n-3 PUFA[5]	0.33	1.44^{b}	1.73^{bc}	1.82^{c}	2.43^{d}	2.18	0.157	*	***	***	ns	ns
PUFA/SFA ratio	0.07	0.14^{b}	0.15	0.14	0.14	0.15	0.009	*	ns	ns	ns	ns
n-6: n-3 PUFA ratio	7.63	2.41	2.09	1.68	0.99	1.55	0.420	*	**	ns	ns	ns

MG = megalac; CO = camelina oil; LO = linseed oil; CS = NaOH-treated camelina seeds; LS = NaOH-treated linseed; CA = camelina oil amide; O = oil; S = seed; C = camelina; L = linseed; M = method of feeding (oil or seed); F = fat source (camelina or linseed); FAME = fatty acid methyl esters; CLA = conjugated linoleic acid; SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids; ns = non-significant, $P > 0.05$; +, *, ** and *** refer to significance levels $P < 0.1$, < 0.05, $P < 0.01$ and $P < 0.001$, respectively. For a significant M × F interaction, means with a common superscript do not differ ($P < 0.05$).
[1]SFA = sum of all even chain fatty acid up to 24:0+13:0, 15:0 and 17:0.
[2]MUFA = sum of 14:1, 16:1, 17:1, all 18:1, 20:1, 22:1 and 24:1.
[3]PUFA = sum of total n-6, total n-3, total CLA.
[4]n-6 PUFA = sum of 18:2n-6, 18:3n-6, 20:2, 20:3n-6, 20:4 and 22:2.
[5]n-3 PUFA = sum of 18:3n-3, 20:3n-3, 20:5, 22:5 and 22:6.

offered the CA ration compared to those offered the CS ration. The lack of effect of the ethanolamine treatment on DM and NDF digestibility contrasts with the decreases reported by Jenkins (1997) due to similar treatment of soybean oil.

We have no explanation as to why the weight of liver was lower from animals offered the LS ration compared to the LO ration. The larger kidney and liver in animals offered the CA ration compared to the CS (or CO) ration may reflect the

greater detoxification of ammonia in these animals due to the greater CP consumption. Support for this suggestion is found in Smith *et al*. (1964) who observed heavier livers in lambs chronically fed urea in addition to soybean and merits further study.

In this experiment, total fatty acid concentration in muscle was similar across treatments, as planned. This result was desirable as an increase in intramuscular fat is generally accompanied by a decrease in the SFA and PUFA proportions and an increase in the MUFA proportion in intramuscular lipid (Moreno *et al*., 2008). Thus, differences in total fatness or total intramuscular fat confound the effects of dietary PUFA on the fatty acid profile of muscle.

The efficacy of linseed as oil or extruded/damaged seeds in modifying the fatty acid composition of ruminant fat has been examined in several studies in sheep. When compared with studies that included a non-PUFA supplemented (iso-lipid) control ration, the results of this study are broadly similar to the literature, that is, a 3-fold increase in the proportion of 18:3n-3 in muscle lipids (e.g. Wachira *et al*., 2002; Bas *et al*., 2007). Similarly, 18:3n-3 was found in greater proportions in the muscle PL fraction than in the NL fraction and at a level similar to that reported by Cooper *et al*. (2004) for lambs fed high concentrate rations. The effect of LO inclusion in this study on the 18:3n-3 proportion of the muscle PL fraction was greater than that observed by Demirel *et al*. (2004a), which reflected the high concentration of forage used in the latter study.

To our knowledge, the effect of camelina on the fatty acid composition of sheep tissue has not been reported. Muscle from lambs offered the camelina oil-based ration had a higher content of long chain MUFA, in particular 20:1, a similar proportion of 18:2n-6, and a lower proportion of 18:3n-3 and n-3 PUFA and a tendency toward a higher n-6: n-3 PUFA ratio than the LO-based treatment, which largely reflected the fatty acid composition of the rations. In general, a diet with a low n-6: n-3 PUFA ratio is reflected in a low n-6: n-3 PUFA ratio in intramuscular fat and SAT despite the rumen biohydrogenation of dietary fatty acids.

An increase in the MUFA of milk fatty acids was reported by Hurtaud and Peyraud (2007) due to the inclusion of camelina seeds or meal in the ration of dairy cows. However, 20:1 was not reported. Peiretti *et al*. (2007) also observed an increase in rabbit muscle perirenal adipose tissue 20:1 proportion due to dietary inclusion of pelleted camelina seeds. In this study, the proportion of 20:1 was higher in SAT, followed by muscle NL and PL fractions. This was unexpected given that long chain fatty acids tend to be associated more with the PL fraction than the triacylglycerol fractions (Noci *et al*., 2007). While the proportion of 20:0 was higher in the tissue of lambs offered the camelina-based rations compared to the linseed-based rations, the levels were smaller than 20:1, suggesting that a considerable proportion of dietary 20:1 escaped ruminal biohydrogenation. The presence of 20:1 in feces from lambs offered the camelina-based rations also suggests that a proportion of this fatty acid escaped absorption for the small intestine. In contrast to tissue, the higher proportion of 20:0 compared to 20:1 in feces of lambs offered the camelina-based rations suggests that biohydrogenation occured in the large intestine.

In this study, feeding seeds treated with NaOH was a more effective method than feeding unprotected oil in enhancing the incorporation of PUFA in the muscle NL, PL and SAT, indicating the protection of oil by the chemically disrupted seed coat. However, the scale of increase in muscle PL in 18:3n-3 (1.33 and 1.38-fold for camelina and linseed, respectively) and 18:2n-6 (0.91 and 0.90-fold for camelina and linseed, respectively) suggests that modest ruminal protection was achieved. For logistical reasons, amide formation using ethanolamine as a means of ruminal protection was evaluated only with camelina and this approach was more effective than the NaOH-treatment of seeds (an increase in 18:3n-3 of 1.63 and 1.33 in muscle PL for CA and CS, respectively, compared to CO with corresponding values of 1.12 and 0.91 for 18:2n-2). There are no comparable data available for lamb muscle but Jenkins and Thies (1997) observed a 1.24-fold increase in sheep plasma 18:2n-6 concentration when soybean oil was replaced with ethanolamine-treated soybean oil.

Of the protection approaches examined, the most effective seems to be the encapsulation of oil in a matrix of formaldehyde-treated protein (e.g. Kitessa *et al*., 2001). Kitessa *et al*. (2009) applied this technology to a ground soybean/LO mixture (70:30) and observed a 1.82-fold increase in lamb muscle 18:3n-3 proportion compared to a non-lipid-supplemented control ration. This compares to a 1.50-fold increase for CA compared to CO and 1.47-fold increase for LS compared to LO in total muscle in this study. However, compared to the control ration in this study, increases of 3.8-fold for CA and 5.1-fold for LS were observed. The differences between these studies likely reflect differences in 18:3n-3 intake among other confounding factors and the absence of a direct comparison made the drawing of definite conclusions on the different protection technologies impossible.

The lack of an increase in 18:2n-6 in muscle NL, PL or SAT due to NaOH-treatment of either linseeds or camelina seeds was unexpected considering the increase in 18:3n-3. Kirkland *et al*. (1998) similarly observed no increase in milk 18:2n-6 despite an increase in 18:3n-3 due to the consumption of NaOH-treated linseed. This may reflect a different structural arrangement of these fatty acids within the seeds but could be viewed as a positive effect contributing to the decrease in n-6: n-3 PUFA ratio observed due to NaOH-treated seed feeding. In contrast, treatment with ethanolamine also increased the proportion of 18:2n-6 in all tissues examined consistent with plasma data of Jenkins and Thies (1997) from sheep fed ethanolamine-treated soybean oil.

While linseed is considered the major plant source of 18:3n-3, these data demonstrate the potential of camelina as a means of enhancing the n-3 PUFA content of muscle. The observation of an increase in the proportion of longer carbon chain n-3 PUFA with an increase in 18:3n-3 supply (and absorption) is consistent with the literature (e.g. Wachira *et al*., 2002; Demirel *et al*., 2004a; Kitessa *et al*., 2009). Nevertheless, the proportion of longer chain n-3 PUFA

remains relatively low, particularly from a human consumption perspective. Thus, a 100 g serving of lamb from MG, CO, LO, CS, LS and CA would supply 13, 23, 18, 23, 31 and 19 mg long chain n-3 PUFA, respectively. The corresponding supply of 18:3n-3 would be 18, 59, 73, 67, 102 and 79 mg, respectively. These data can be viewed in the context of proposed labeling reference intake values for humans of 2 g and 250 mg/day for 18:3n-3 and EPA plus DHA (eicosapentaenoic acid and docosahexaenoic acid), respectively (European Food Safety Authority (EFSA), 2009).

Ruminant fat is the main dietary source of *cis*-9, *trans*-11 CLA (Chin *et al*., 1992), which has a number of beneficial health effects (Pariza *et al*., 2001). *Cis*-9, *trans*-11 CLA is produced in the rumen by incomplete biohydrogenation of dietary 18:2n-6 but is also synthesized in adipose tissue by desaturation of *trans*-11 18:1 produced during ruminal biohydrogenation of 18:2n-6 and 18:3n-3 (Griinari *et al*., 2000). Thus, Santora *et al*. (2000) reported 51% conversion of available *trans*-11 18:1 to *cis*-9, *trans*-11 CLA in mice. An increase in lamb muscle *cis*-9, *trans*-11 CLA concentration, with particular enrichment of the NL fraction, due to consumption of plant oils rich in PUFA is a consistent finding in the literature with oils rich in 18:2n-6 being more effective than those rich in 18:3n-3 (e.g. Mir *et al*., 2000; Bessa *et al*., 2007).

In this study, a similar amount of 18:2n-6 for direct ruminal synthesis of *cis*-9, *trans*-11 CLA, but smaller amounts of 18:3n-3 for indirect synthesis of *cis*-9, *trans*-11 CLA via tissue desaturation of ruminally derived *trans*-11 18:1 (Griinari *et al*., 2000) was supplied by camelina compared to linseed. We hypothesized, therefore, that the concentration of *cis*-9, *trans*-11 CLA would be higher in lambs fed the linseed-based rations and the results support the hypothesis that an increase in the availability of 18:3n-3 can enhance the proportion of *cis*-9, *trans*-11 CLA in muscle and adipose tissues. Raes *et al*. (2004) also observed an increase in bovine muscle *cis*-9, *trans*-11 CLA concentration due to linseed feeding at a constant 18:2n-6 consumption. Wachira *et al*. (2002) found a 1.55-fold increase in the concentration of *cis*-9, *trans*-11 CLA in NL of muscle from lambs fed an linseed-based diet compared to the control diet (3.5% MG), while Demirel *et al*. (2004b) observed a 1.68-fold increase in total intramuscular lipid, both findings being somewhat higher than that observed in this study.

If ruminal protection of dietary PUFA is efficient, a decrease in biohydrogenation intermediates would be expected as was seen by Scollan *et al*. (2003) who used the aldehyde/protein technology. This was the case with ethanolamine-treated CO, that is, a decrease in *cis*-9, *trans*-11 CLA and *trans*-11 18:1. A decrease in *cis*-9, *trans*-11 CLA was also observed by Lundy *et al*. (2004) in milk from cows due to feeding soybean oil amides rather than free oil. In contrast, the greater accumulation of *cis*-9, *trans*-11 CLA at the expense of *trans*-11 18:1 due to NaOH-treatment of seeds in this study indicates a decrease in the rate of biohydrogenation of 18:2n-6 and/or an increase in the extent of tissue desaturation. A possible explanation for the former hypothesis is likely the shorter time available to rumen microorganisms to hydrogenate 18:2n-6 as they must digest and penetrate the NaOH-treated seed coat before the seeds leave the rumen. If this occurred, an increase in tissue 18:2n-6 would be expected that was not observed. Alternatively, the NaOH-treatment of seeds as carried out in this study may cause an inhibition of the hydrogenation of *cis*-9, *trans*-11 CLA *per se*. Owing to the positive influence on tissue CLA, this issue merits further investigation.

Epidemiological associations between the risk of coronary heart disease and the consumption of *trans*-PUFA has focused attention on their concentration in food products. Under the analytical procedure used in this study, *trans*-9 18:1 and *trans*-11 18:1 were the main *trans* fatty acids detected. While the proportion of both was elevated due to oil supplementation, *trans*-11 18:1 represented on average 73% of total *trans*-PUFA and this proportion was not affected by treatment. Jakobsen *et al*. (2008) recently concluded that the consumption of ruminant *trans*-fatty acids does not pose a risk to human health most likely due to the high proportion of *trans*-11 18:1 in ruminant derived foods, as seen in this study.

Conclusions

The results of this experiment confirm the considerable influence of dietary fatty acid composition on the fatty acid composition of muscle and adipose tissue, despite extensive biohydrogenation in the rumen. Providing a fat source rich in 18:3n-3, such as linseed, caused a desirable increase in the proportion of cis-9, *trans*-11 CLA in muscle and SAT, while also contributing to a decrease in the n-6: n-3 PUFA ratio. The novel alternative source of 18:3n-3, *Camelina sativa* was also effective in this regard. Treatment of intact seeds with NaOH achieved some ruminal protection of PUFA and increased the incorporation of *cis*-9, *trans*-11 CLA in both intramuscular fat and SAT. Ethanolamine treatment of CO was a more effective protection strategy than NaOH-treatment of intact camelina seeds but consequently resulted in a lower proportion of *cis*-9, *trans*-11 CLA in tissue.

Acknowledgments

The assistance of the late Dr Jim Crowley (Oak Park Research Centre) in providing the CO and seeds is gratefully acknowledged. The technical assistance of V. McHugh and A. Marron (Grange Beef Research Centre) and E. Vesey (Ashtown Food Research Centre) is also acknowledged, as is the assistance of P. McGovern with the care of the animals.

References

Association of Official Analytical Chemists (AOAC) 1990. Official methods of analysis, 15th edition. AOAC, Washington, DC, USA.

Aldrich CG, Merchen NR, Drackley JK, Gonzalez SS, Fahey GC Jr and Berger LL 1997. The effects of chemical treatment of whole canola seed on lipid and protein digestion by steers. Journal of Animal Science 75, 502–511.

Bas P, Bertholet V, Pottier E and Normand J 2007. Effect of level of linseed on fatty acid composition of muscles and adipose tissues of lambs with emphasis on trans fatty acids. Meat Science 77, 678–688.

Bessa RJB, Alves SP, Jeronimo E, Alfaia CM, Prates JAM and Santos-Silva J 2007. Effect of lipid supplements on ruminal biohydrogenation intermediates and muscle fatty acids in lambs. European Journal of Lipid Science and Technology 109, 868–878.

Bolte MR, Hess BW, Means WJ, Moss GE and Rule DC 2002. Feeding lambs high-oleate or high-linoleate safflower seeds differentially influences carcass fatty acid composition. Journal of Animal Science 80, 609–616.

Budin JT, Breene WM and Putnam DH 1995. Some compositional properties of Camelina (*Camelina sativa* L. Crantz) seeds and oils. Journal of the American Oil Chemists' Society 72, 309–315.

Chin SF, Liu W, Storkson JM, Ha YL and Pariza WM 1992. Dietary sources of conjugated dienoic isomers of linoleic acid, a newly recognized class of anticarcinogens. Journal of Food Composition and Analysis 5, 185–197.

Cooper SL, Sinclair LA, Wilkinson RG, Hallett KG, Enser M and Wood JD 2004. Manipulation of the n-3 polyunsaturated fatty acid content of muscle and adipose tissue in lambs. Journal of Animal Science 82, 1461–1470.

Crowley JG and Fröhlich A 1998. Factors affecting the composition and use of camelina. End of Project Report. Teagasc, Carlow, Ireland.

Demirel G, Wachira AM, Sinclair LA, Wilkinson RG, Wood JD and Enser M 2004a. Effects of dietary n-3 polyunsaturated fatty acids, breed and dietary vitamin E on the fatty acids of lamb muscle, liver and adipose tissue. British Journal of Nutrition 91, 551–565.

Demirel G, Wood JD and Enser M 2004b. Conjugated linoleic acid content of the lamb muscle and liver fed different supplements. Small Ruminant Research 53, 23–28.

Doreau M and Ferlay A 1994. Digestion and utilisation of fatty acids by ruminants. Animal Feed Science and Technology 45, 379–396.

Drennan MJ, Almiladi AA and Moloney AP 1995. Digestibility of cereal grains, sugar-beet pulp and molasses in cattle. Irish Journal of Agricultural and Food Research 34, 1–11.

Ekeren PA, Smith DR, Lunt DK and Smith SB 1992. Ruminal biohydrogenation of fatty acids from high-oleate sunflower seeds. Journal of Animal Science 70, 2574–2580.

Enser M, Hallett K, Hewett B, Fursey GAJ and Wood JD 1996. Fatty acid content and composition of English beef, lamb and pork at retail. Meat Science 44, 443–458.

European Communities (EC) 1984. European communities (marketing of feedstuffs) regulation. Statutory instruments SI No. 200 of 1984. The Stationery Office, Dublin, Ireland.

European Food Safety Authority (EFSA) 2009. Scientific opinion: labeling reference intake values for n-3 and n-6 polyunsaturated fatty acids. The EFSA Journal 1176, 1–11.

Feairheller SH, Bistline RG Jr, Bilyk A, Dudley RL, Kozempel MF and Haas MJ 1994. A novel technique for the preparation of secondary fatty amides. III. Alkanolamides, diamides and aralkylamides. Journal of the American Oil Chemists' Society 71, 863–866.

Fröhlich A and Rice B 2005. Evaluation of camelina sativa oil as a feedstock for biodiesel production. Industrial Crops and Products 21, 25–31.

Givens DI, Cottrill BR, Davies M, Lee PA, Mansbridge RJ and Moss AR 2000. Sources of n-3 polyunsaturated fatty acids additional to fish oil for livestock diets – a review. Nutrition Abstracts and Reviews – Series B 70 (1), 1–19.

Griinari JM, Corl BA, Lacy SH, Chouinard PY, Nurmela KVV and Bauman DE 2000. Conjugated linoleic acid is synthesized endogenously in lactating dairy cows by delta 9-desaturase. Journal of Nutrition 130, 2285–2291.

Harfoot CG and Hazelwood GP 1997. Lipid metabolism in the rumen. In The rumen microbial ecosystem (ed. PN Hobson and CS Stewart), 2nd edition, p. 382. Blackie Academic and Professional, New York, USA.

Hurtaud C and Peyraud JL 2007. Effects of feeding camelina (seeds or meal) on milk fatty acid composition and butter spreadability. Journal of Dairy Science 90, 5134–5145.

Jakobsen MU, Overvad K, Dyerberg J and Heitmann BL 2008. Intake of ruminant *trans* fatty acids and risk of coronary heart disease. International Journal of Epidemiology 37, 173–182.

Jenkins TC 1997. Ruminal fermentation and nutrient digestion in sheep fed hydroxyethylsoyamide. Journal of Animal Science 75, 2277–2283.

Jenkins TC and Bridges WC Jr 2007. Protection of fatty acids against ruminal biohydrogenation in cattle. European Journal of Lipid Science and Technology 109, 778–789.

Jenkins TC and Thies E 1997. Plasma fatty acids in sheep fed hydroxyethylsoyamide, a fatty acyl amide that resists biohydrogenation. Lipids 32, 173–178.

Kirkland RM, Scaife JR and Goodwill M 1998. Effect of caustic-treated linseed on the composition of cow's milk. Proceedings of the British Society of Animal Science Meeting, March 1998, Scarborough, UK, p. 220.

Kitessa SM, Gulati SK, Ashes JR, Scott TW and Fleck E 2001. Effect of feeding tuna oil supplement protected against hydrogenation in the rumen on growth and n-3 fatty acid content of lamb fat and muscle. Australian Journal of Agricultural Research 52, 433–437.

Kitessa SM, Williams A, Gulati S, Boghossian V, Reynolds J and Pearce KL 2009. Influence of duration of supplementation with ruminally protected linseed oil on the fatty acid composition of feedlot lambs. Animal Feed Science and Technology 151, 228–239.

Lundy FP III, Block E, Bridges WC Jr, Bertrand JA and Jenkins TC 2004. Ruminal biohydrogenation in Holstein cows fed soyabean fatty acids as amides or calcium salts. Journal of Dairy Science 87, 1038–1046.

Mir Z, Rushfeldt ML, Mir PS, Paterson LJ and Weselake RJ 2000. Effect of dietary supplementation with either conjugated linoleic acid (CLA) or linoleic acid rich oil on the CLA content of lamb tissues. Small Ruminant Research 36, 25–31.

Moloney AP, Read MP and Keane MG 1996. Effects of ardacin supplementation on rumen fermentation and protein degradability in steers. Animal Feed Science and Technology 57, 97–110.

Moreno T, Keane MG, Noci F and Moloney AP 2008. Fatty acid composition of *M. Longissimus dorsi* from Holstein–Friesian steers of New Zealand and European/American descent and from Belgian Blue × Holstein–Friesian steers, slaughtered at two weights/ages. Meat Science 78, 157–169.

Noci F, Monahan FJ, French P and Moloney AP 2005. The fatty acid composition of muscle fat and subcutaneous adipose tissue of pasture-fed beef heifers: influence of the duration of grazing. Journal of Animal Science 83, 1167–1178.

Noci F, French P, Monahan FJ and Moloney AP 2007. The fatty acid composition of muscle fat and subcutaneous adipose tissue of grazing heifers supplemented with plant oil-enriched concentrates. Journal of Animal Science 85, 1062–1073.

Pariza MW, Park Y and Cook ME 2001. The biologically active isomers of conjugated linoleic acid. Progress in Lipid Research 40, 283–298.

Peiretti PG, Mussa PP, Prola L and Meinori G 2007. Use of different levels of false flax (*Camelina sativa* L) seed in diets for fattening rabbits. Livestock Science 107, 192–198.

Raes K, Haak L, Balcaen A, Claeys E, Demeyer D and De Smet S 2004. Effect of linseed feeding at similar linoleic acid levels on the fatty acid composition of double-muscled Belgian Blue young bulls. Meat Science 66, 307–315.

Santora JE, Palmquist DL and Roehrig KL 2000. *Trans*-vaccenic acid is desaturated to conjugated linoleic acid in mice. Journal of Nutrition 130, 208–215.

Scollan ND, Enser M, Gulati SK, Richardson I and Wood JD 2003. Effects of including a ruminally protected lipid supplement in the diet on the fatty acid composition of beef muscle. British Journal of Nutrition 90, 709–716.

Smith GS, Love SB, Durdle WM, Hatfield EE, Garrigus US and Neumann AL 1964. Influence of urea upon vitamin A nutrition of ruminants. Journal of Animal Science 23, 47–53.

Sukhija PS and Palmquist DL 1988. Rapid method for determination of total fatty acid content and composition of feedstuffs and faeces. Journal of Agricultural and Food Chemistry 36, 1202–1206.

Van Soest PJ, Robertson JB and Lewis BA 1991. Methods for dietary fibre, neutral detergent fibre, and non starch polysaccharides in relation to animal nutrition. Journal of Dairy Science 74, 3583–3597.

Wachira AM, Sinclair LA, Wilkinson RG, Enser M, Wood JD and Fisher AV 2002. Effects of dietary fat source and breed on the carcass composition, n-3 polyunsaturated fatty acid and conjugated linoleic acid content of sheep meat and adipose tissue. British Journal of Nutrition 88, 697–709.

World Health Organization (WHO) 2003. Diet, nutrition and the prevention of chronic diseases. Report of a Joint WHO/FAO Expert Consultation. WHO Technical Report Series 916. WHO, Geneva, Switzerland.

Woods VB and Fearon AM 2009. Dietary sources of unsaturated fatty acids for animals and their transfer into meat, milk and eggs: a review. Livestock Science 126, 1–20.