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Effect of level of linseed on fatty acid composition of muscles and adipose tissues of lambs with emphasis on *trans* fatty acids

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Abstract

The effects of linseed content in concentrates on the fatty acid (FA) composition of adipose tissues and muscles of lambs were studied in a 2×4 design: males (M) vs. females (F) and linseed content (0%, L0, 3%, L3, 6%, L6, 9%, L9). FA proportions were determined both on a DB-wax and on a CP-Sil column in perirenal (PR), dorsal subcutaneous (SC) adipose tissue and in *longissusmus dorsi* muscle (IM). No effects of linseed contents in the diet on growth performances either in male or female lambs were observed. Linseed supplementation tended to decrease the fatness score. The proportion of linolenic acid increased linearly with the linseed content in the diet, from: 0.6, 0.5, and 0.5% for L0 to 1.9, 1.6, and 1.3% for L9, in PR, SC and IM, respectively. The increase in $n-3$ PUFA and in total PUFA was similar to that of linolenic acid. The $n-6$:$n-3$ ratio decreased from 5.7, 5.3 and 5.8 for L0 to 1.8, 1.7 and 2.7 for L9, in PR, SC and IM, respectively. There was no change in the proportion of docosahexaenoic acid with linseed supplementation. The proportions of C18:1*trans*-10 and C18:1*trans*-11 did not vary in PR, SC and IM with linseed supplementation. The total proportion of *trans*-octadecenoic acid was high in each tissue type and group of lambs. C18:1*trans*-10 represented about half of the total *trans*-octadecenoic isomers. With an increase in linolenic acid, most *cis*- and *trans*-octadecenoic isomers also increased, but *trans*-10 and *trans*-11 isomers did not and *cis*-9 and *cis*-11 isomers decreased. With linseed supplementation there was a decrease in the Δ9 desaturase indices in SC.

Keywords: Lamb; Adipose tissue; Muscle; Linseed; Fatty acids; *trans*-Fatty acids

1. Introduction

Ruminant meat consumption is declining in Europe and North America, mainly due to health concerns. Concerns relate to sanitary problems and that this meat contains too many saturated fatty acids (SFA). For human health the target for ruminant meat production towards leaner meat with lower saturated fat and higher monounsaturated (MUFA) and polyunsaturated fatty acid (PUFA) contents, because of the effects of fatty acids (FA) on numerous cancers, atherosclerosis and coronary heart disease (Scollan et al., 2006; Simopoulos, 2004). For human health ruminant meat studies are now focused on increasing the $n-3$ PUFA content, decreasing the $n-6$ PUFA: $n-3$ PUFA ratio and increasing the content of conjugated linoleic fatty acids (CLA). CLA contents in ruminant meat are increased when the animals are fed concentrates supplemented with unsaturated fat, rich in linoleic acid (Bauman, Corl, & Grinarii, 2000) or rich in $n-3$ PUFA and with pasture-based diets (Daniel, Wynn, Salter, & Buttery, 2004; Dannenberger et al., 2005). Due to the hydrogenation of PUFA in the rumen, modifications in the composition of tissue FA is limited in ruminants. Meat from forage fed-ruminants has higher n-3 PUFA contents than that from ruminants raised on concentrate-based diets (Bas & Morand-Fehr, 2000; Nuernberg et al., 2005). In European

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intensive rearing systems, lambs are often reared on a low forage diet comprising between 5% and 20% and slaughtered before 4 months of age. Strategies for enrichment of lamb meat in $n-3$ PUFA have included diets enriched with fish products or with linseed (Ponnampalam, Sinclair, Hosking, & Egan, 2002; Wachira et al., 2002).

The objective of the current study was to investigate the effects of increasing linseed diet supplementation, during the finishing period in male and female lambs fed high concentrate diets, on growth rate and the fate of linolenic acid in muscle and adipose tissues. Special attention was paid to alteration in the proportions of long-chain polyunsaturated fatty acids and monoene isomers.

2. Materials and methods

2.1. Animals, diets and tissue sampling

Twenty male and twenty female lambs of the Mouton Vendeen breed were suckled by their mother up to eleven weeks of age. After weaning, lambs were offered wheat straw and concentrate *ad libitum* until slaughter. Lambs from each sex were randomly allocated to four treatment groups according to the linseed content in the concentrate. The concentrate compositions are presented in Table 1. Linseed, supplied from Croquelin® (Valorex, Combourtouillé, France), contained (50% extruded linseed, 20% wheat bran, and 20% sunflower meal). The experiment was designed to give carcasses weighing about 18 kg for M and about 16 kg for F lambs, in about 7 weeks. Lambs were weighed at the beginning of the experiment and every fortnight until the day before slaughter. Immediately after slaughter, fat status was determined according to the 12-point scale of Ofival, (Normand, Thériez, Bas, Aurousseau, & Sauvant, 1999). The weights of the cold carcasses were measured after 18 h cooling and drying at 3 °C. Immediately after slaughter, two adipose tissue samples were removed from the perirenal fat (near the kidney on its long curve, PR), and from subcutaneous fat (from the back between the 10th and the 13th ribs, SC). Samples of muscle were removed from the *longissimus dorsi* muscle (posterior to the 13th rib; IM), and were frozen at −30 °C until analysis.

Table 1
Chemical composition of concentrates

Ingredients	Type of concentrate			
	L0	L3	L6	L9
Concentrate composition, % of DM				
Wheat	23.3	19.6	11.9	0.0
Barley	10.0	8.4	5.1	0.0
Triticale	20.0	20.0	20.0	19.4
Rapeseed meal	7.0	7.0	7.0	0.7
Soybean meal	8.8	3.7	1.5	9.0
Sunflower meal	3.4	9.2	10.0	10.0
Sugar beet pulp	21.3	20.0	20.0	30.0
Molasses, cane	3.0	3.0	3.0	3.0
Wheat bran	0.0	0.0	5.0	5.0
Croquelin®[a]	0.0	6.0	12.0	18.0
Sodium Carbonate	1.6	1.6	3.0	2.4
Mineral and vitamin mixture	1.7	1.5	1.5	2.5
Chemical composition, % of DM				
Organic matter	92.7	92.5	91.2	90.8
Crude protein	18.5	18.9	19.8	20.8
Crude fibre	9.3	10.4	12.0	13.9
Starch	37.3	35.4	28.5	21.8
Total fatty acids	1.8	2.7	4.1	5.2
Fatty acids, g/kg DM				
C16:0	2.6	2.7	3.6	4.0
C18:0	0.3	0.6	1.1	1.5
C18:1*cis*-9	4.1	6.1	9.2	11.3
C18:2$n-6$	9.0	9.9	11.9	12.9
C18:3$n-3$	1.2	7.1	14.0	21.9

[a] Croquelin® = 50% extruded linseed, 30% wheat bran, 20% sunflower meal.

2.2. Chemical analysis

Sample dry matter was determined after 48-h freeze–drying. Extraction of total fat was carried out according to the Rule method (1997), but using heneicosanoic acid as an internal standard in the extraction solvent mixture for PR and SC, but tricosanoic acid for IM because of possible interferences with PUFA on the DB-wax column and with linoleic acid isomers on the CP-SIL column. This solvent mixture contained 26 ppm of BHT. To avoid isomerization during esterification of FA, a two-step method, adapted from Christie, Sébédio, and Juanéda (2001) was used for free and esterified lipids. Briefly, esterified lipids (10–20 mg) dissolved in toluene (50 μL) were transmethylated, in 16 × 125 mm screw-cap borosilicate tubes with Teflon-lined caps, with 2N sodium methoxide in anhydrous methanol (100 μL). After mixing, the solution was left at room temperature for 20 min. and then esterification was continued by addition of 500 μL of boron-trifluoride in methanol (14%, wt/vol). The solution was mixed and again left at room temperature for 20 min. Then, 2 mL of $n-$ hexane and 5 mL of saturated sodium bicarbonate were added to the solution. After mixing, the two phases were separated by centrifugation at 2000*g* for 3 min. The upper $n-$ hexane phase was then transferred to a vial for GLC analysis. Samples were injected twice with an auto sampler CP-8410 into a Varian CP-3900 gas–liquid chromatograph (Varian, Les Ulis, France) either on a DB-wax fused silica capillary column (60-mL × 0.25-mm i.d. × 0.25-μm film thickness: JW, Folsom, CA), or a CP-SIL 88 fused silica capillary column (100-mL × 0.25-mm i.d. × 0.20-μm film thickness: Varian 3900, Les Ulis, France). Two different columns were used because of the differences in their characteristics (Kramer, Blackadar, & Zhou, 2002). For the two GLC procedures, the split/splitless injector, type 1177, and the flame ionisation detector were held at 250 °C and 280 °C, respectively. In the first run performed on the DB-wax column, the oven temperature was programmed to increase from 120 to 195 °C at 4 °C/min, and then held for 60 min at constant

temperature. The injector was in splitless mode for 1.0 min and then in split mode until the end of the run with a split ratio of 30:1. The column flow rate was 1.2 mL/min of He. In the second run, performed on the CP-SIL column, the oven temperature was programmed to increase from 80 to 140 °C at 20 °C/min, from 140 °C to 170 °C at 1.2 °C/min, 60 min at constant temperature, then from 170 to 220 °C at 5 °C/min, and then held at 220 °C for 50 min. The inlet column pressure was 172 kPa of He. The injector was in splitless mode for 0.10 min and in split mode until the end of the run. The shorter period in splitless mode with the CP-SIL run meant there was less fat on the column than with the DB-wax run, and minor fatty acids could not be reliably determined with the CP-SIL run. Fatty acids were further identified from equivalent chain-length (ECL) (Miwa, Mikolajzack, Earle, & Wolff, 1960) determined by interpolation between two consecutive even straight-chain saturated fatty acids and compared to reference standards (Sigma, St. Louis, MO; Interchim, Montluçon, France) analyzed under similar conditions. Identification of *trans*-C18:1 isomer peaks was carried out on a CP-Sil chromatogram with C18:1*trans*-5 to C18:1*trans*-15 standards kindly supplied by Ledoux M. (AFSSA, Maisons-Alfort, France) and based on published isomeric profiles (Griinari et al., 1998; Wolff & Bayard, 1995). Under these chromatographic conditions, C18:1*trans*-6 to C18:1*trans*-8 were unresolved and were thus combined in the Tables 3–6. C18:1*trans*-13 and C18:1*trans*-14 were badly resolved and partly overlapped the oleic acid peak. Their amounts were thus not determined very accurately, especially in IM because of oleic acid loading. Moreover, C18:1*cis*-6 to C18:1*cis*-10 co-eluted with C18:1*trans*-13 and C18:1*trans*-14 and C18:1*cis*-9 (Kramer et al., 2002). Percentages of C18:1 isomers separated on the CP-SIL column were determined in relation to the percentage of heptadecanoic acid obtained on the DB-wax column. The FA were summed by families according to their structure of the DB-wax run (even straight-chain saturated FA), ESFA = C10:0 + C12:0 + C14:0 + C16:0 + C18:0 + C20:0; even straight-chain monounsaturated FA, EMUFA = C14:1 + $\sum$C16:1 + $\sum$C18:1; oddMUFA = C17:1 + C19:1; PUFA = C18:2$n-6$ + C18:3$n-6$ + C18:3$n-3$ + C20:4$n-6$ + C18:2*cis*-9, *trans*-11 + other $\sum$ isomers of linoleic acid (from ECL = 18.67 to ECL = 18.90; i.e. 18.67, 18.72, 18.76, 18.80 for PR; 18.67, 18.72, 18.76, 18.80, 18.87, and 18.92 for SC, and 18.67 and 18.80 for IM) and + C20:2$n-6$, C20:3$n-6$, C22:4$n-6$, C20:3$n-3$, C20:5$n-3$, C22:5$n-3$ and C22:6$n-3$, for IM; oddFA = C13:0 + C15:0 + C17:0 + C17:1 + C19:0 + C19:1. Indices (ID14, ID16, ID18 and IDCLA) of the Δ9-desaturase activity were calculated according to Malau-Aduli, Siebert, Bottema, and Pitchford (1997). ID14 = C14:1*cis*-9 × 100/(C14:0 + C14:1*cis*-9); ID16 = C16:1*cis*-9 × 100/(C16:0 + C16:1*cis*-9); ID18 = C18:1*cis*-9 × 100/(C18:0 + C18:1*cis*-9); IDCLA = C18:2*cis*-9,*trans*-11 × 100/(C18:1*trans*-11 + C18:2*cis*-9,*trans*-11).

2.3. Statistical analysis

Statistical analysis of experimental data was performed using the GLM procedure of (SAS, 1987). Effects of concentrate type (C) and sex (S) were tested in a two-way balanced factorial data arrangement, (3 degrees of freedom (df) for C, 1 df for S and 3 df for C × S). Initial live weight (ILW) and duration of the experimental period were used as covariables for testing variations in long-chain fatty acid contents in muscle.

3. Results

3.1. Growth performance and carcass composition

There were no effects of concentrate type on growth performance, in both male and female lambs (Table 2). Males and females were both slaughtered at 4 months of age so that the expected carcass weights of 18 and 16 kg, i.e. for 38 ± 0.55 kg and 32.5 ± 0.305 kg of live weight, respectively, were reached. The duration of the experiment was about a week longer for M than for F (44.4 ± 3.3 vs. 37.7 ± 2.9 days, for M and F, respectively). The higher the ILW the shorter the duration of the experiment ($r = 0.86, n = 40$). ILW explained two-thirds of the variance in the duration of the experiment and the age at slaughter. Lambs fed linseed supplements tended to be thinner ($P = 0.08$) than control lambs.

Table 2
Growth performance and carcass composition of lambs

Type of concentrate	L0		L3		L6		L9		SEM	Effect, *P*-value		
Sex	M	F	M	F	M	F	M	F		C[a]	Sex	C × sex
Initial liveweight, kg	24.0	21.5	23.5	23.5	23.9	22.6	24.8	21.4	0.574	0.979	0.119	0.743
Live weight at slaughter, kg	39.2	32.1	36.7	32.5	38.0	33.0	38.2	32.6	0.323	0.681	0.001	0.462
Cold carcass weight, kg	18.7	15.5	18.2	15.9	17.8	16.1	18.5	15.6	0.172	0.996	0.001	0.422
Age at slaughter, d	126	122	122	116	120	112	121	118	2.58	0.794	0.307	0.986
Duration of the experiment, d	48	44	44	37	43	36	43	41	2.50	0.777	0.338	0.975
ADG[b], g/d	326	243	309	254	340	292	309	280	6.50	0.248	0.001	0.537
Fat score[c]	9.0	9.4	8.2	10.6	8.2	9.0	8.6	9.0	0.116	0.079	0.001	0.012

[a] C = effect of type of concentrate.
[b] ADG = average daily gain during the experiment.
[c] Fat score = 12-point scale according to Ofival.

3.2. DM and lipid composition of adipose tissue and muscles

DM contents of PR, SC and IM (Tables 3–5) did not differ with concentrate type, but were higher in M than in F (+7.5, +1.4 and +1.3 points, for SC, PR and IM, respectively). However, muscle FA content did not significantly differ with concentrate type and sex.

3.3. Changes in adipose tissue and muscle fatty acid proportions with diet

With linseed supplementation, the principal change in adipose tissue and muscle FA composition was, as expected, a marked increased in C18:3$n-3$, a decrease in oddFA and a change in the proportions of nearly all the C18:1 isomers (Tables 3–5). The increase in the proportion of C18:3$n-3$ was highest in PR and lowest in IM (+1.3, +1.2 and +0.9 points, in PR, SC and IM, respectively). For each group of lambs, the variation coefficients of the proportions of C18:3$n-3$ in PR, SC and IM were high, between 15% and 40%. The relationships between the proportions of C18:3$n-3$ in tissues and C18:3$n-3$ content in the concentrates gave regression coefficients of about 0.05, the highest in PR and the lowest in IM (C18:3$n-3$ (% in tissue) $= 0.059 \times$ C18:3$n-3$ (g/kg diet DM) $+ 0.62$; $= 0.055 \times$ C18:3$n-3 + 0.0.49$; $= 0.042 \times$ C18:3$n-3 + 0.46$, in PR, SC and IM, respectively). In contrast, the proportions of C18:2$n-6$, C18:2*cis*-9,*trans*-11 and C16:0 did

Table 3
Effects of types of concentrate on fatty acid composition of perirenal adipose tissue of lambs

Type of concentrate	L0		L3		L6		L9		SEM	Effect, *P*-value		
Sex	M	F	M	F	M	F	M	F		C[a]	Sex	C × sex
DM, %	89.7	91.9	90.3	91.4	91.1	92.0	90.6	91.9	0.279	0.689	0.019	0.844
FA composition, g/100 g of FA												
C14:0	2.8	3.7	3.0	3.2	3.2	3.0	2.5	3.1	0.164	0.830	0.255	0.623
C15:0	0.51	0.56	0.54	0.42	0.52	0.42	0.45	0.49	0.017	0.507	0.400	0.159
C16:0	20.7	23.1	20.5	20.1	20.0	20.1	17.7	20.8	0.441	0.215	0.160	0.424
C17:0	2.2	2.1	2.2	1.9	1.9	1.9	1.9	1.8	0.039	0.035	0.203	0.453
C18:0	24.9	24.1	22.4	23.2	23.1	24.8	23.0	23.5	0.412	0.490	0.526	0.733
C16:1*cis*-9	1.13	1.18	1.21	1.12	1.09	0.97	0.99	1.08	0.024	0.084	0.705	0.327
C17:1*cis*-9	0.67	0.65	0.68	0.63	0.61	0.50	0.51	0.53	0.015	0.003	0.185	0.440
C18:1*cis*-9	28.6	28.2	28.2	31.9	31.1	26.8	26.4	27.4	0.483	0.157	0.965	0.048
C18:1*cis*-11	1.38	1.30	1.19	1.05	1.22	1.14	1.12	0.95	0.040	0.073	0.255	0.845
C18:1*cis*-12	0.16	0.17	0.14	0.15	0.23	0.22	0.36	0.28	0.013	0.001	0.510	0.695
C18:1*cis*-13	0.12	0.09	0.12	0.11	0.14	0.16	0.15	0.16	0.005	0.008	0.863	0.391
C18:1*cis*-15	0.27	0.29	0.36	0.28	0.41	0.48	0.75	0.59	0.029	0.002	0.522	0.533
C18:1*trans*-6,7,8[b]	0.42	0.37	0.68	0.31	0.51	0.47	0.80	0.54	0.024	0.003	0.001	0.056
C18:1*trans*-9	0.33	0.29	0.50	0.26	0.41	0.27	0.57	0.40	0.017	0.004	0.001	0.192
C18:1*trans*-10	4.2	3.9	6.9	4.6	3.3	5.9	6.7	4.5	0.332	0.245	0.449	0.048
C18:1*trans*-11	1.9	0.9	0.9	0.9	1.3	1.4	2.4	2.2	0.260	0.291	0.606	0.866
C18:1*trans*-12	0.27	0.27	0.35	0.26	0.40	0.40	0.44	0.53	0.023	0.007	0.969	0.615
C18:1*trans*-13,14[c]	0.16	0.24	0.37	0.29	0.42	0.27	0.88	0.29	0.054	0.095	0.091	0.169
C18:1*trans*-15	0.17	0.18	0.27	0.16	0.33	0.35	0.53	0.48	0.022	0.001	0.477	0.736
C18:1*trans*-16	0.18	0.17	0.20	0.18	0.29	0.29	0.34	0.41	0.015	0.001	0.807	0.766
C18:2$n-6$	3.5	2.8	3.5	3.1	3.0	3.2	3.5	2.4	0.104	0.766	0.026	0.163
C18:2*cis*-9,*trans*-11	0.44	0.34	0.35	0.42	0.47	0.43	0.49	0.44	0.035	0.794	0.681	0.835
C18:3$n-3$	0.6	0.6	1.3	1.1	1.5	1.5	2.2	1.5	0.066	0.001	0.127	0.231
oddFA	3.5	3.5	3.6	3.1	3.2	3.0	3.0	3.0	0.058	0.016	0.132	0.396
ESFA[d]	48.9	51.9	46.5	47.1	46.9	48.4	43.7	48.0	0.474	0.012	0.019	0.525
MUFA[e]	40.6	38.7	42.3	42.6	41.8	40.0	42.6	40.8	0.428	0.083	0.089	0.690
PUFA[f]	4.8	4.0	5.3	4.9	5.2	5.5	6.5	4.6	0.164	0.070	0.036	0.158
$n-6$	3.6	2.9	3.6	3.2	3.2	3.4	3.7	2.6	0.692	0.800	0.036	0.170
$n-3$	0.6	0.6	1.3	1.1	1.5	1.5	2.2	1.5	0.416	0.001	0.127	0.231
$n-6/n-3$	6.1	5.2	2.9	2.9	2.2	2.3	1.8	1.8	0.080	0.001	0.236	0.144
ID14[g]	1.9	1.9	1.8	2.0	1.9	1.5	1.9	1.7	0.065	0.804	0.353	0.487
ID16[g]	5.2	4.9	5.6	5.3	5.2	4.6	5.4	4.9	0.091	0.242	0.036	0.897
ID18[g]	53.5	54.1	55.7	58.0	57.2	51.9	53.2	53.7	0.618	0.219	0.695	0.171
IDCLA[g]	24.4	23.2	27.7	34.7	27.0	25.7	23.9	22.0	1.072	0.045	0.765	0.421

[a] C = effect of type of concentrate.
[b] C18:1*trans*-6,7,8 = ∑C18:1*trans*-6 + C18:1*trans*-7 + C18:1*trans*-8.
[c] C18:1*trans*-13,14 = ∑C18:1*trans*-13 + C18:1*trans*-14.
[d] ESFA = even saturated fatty acids.
[e] MUFA = monounsaturated fatty acids.
[f] PUFA = polyunsaturated fatty acids.
[g] Indices of the Δ9-desaturase activity; ID14 = C14:1*cis*-9 × 100/(C14:0 + C14:1*cis*-9); ID16 = C16:1*cis*-9 × 100/(C16:0 + C16:1*cis*-9); ID18 = C18:1*cis*-9 × 100/(C18:0 + C18:1*cis*-9); IDCLA = C18:2*cis*-9,*trans*-11 × 100/(C18:1*trans*-11 + C18:2*cis*-9,*trans*-11).

Table 4
Effects of types of concentrate on fatty acid composition of subcutaneous adipose tissue of lambs

Type of concentrate	L0		L3		L6		L9		SEM	Effect, *P*-value		
Sex	M	F	M	F	M	F	M	F		C[1]	Sex	C × sex
DM, %	73.1	83.5	82.7	81.3	75.1	83.2	78.0	81.2	0.600	0.459	0.001	0.196
FA composition, g/100 g of FA												
C14:0	2.0	2.7	2.2	3.0	2.6	2.9	2.9	2.7	0.147	0.700	0.188	0.584
C15:0	1.7	0.9	1.5	0.8	1.1	0.7	1.1	0.7	0.053	0.029	0.001	0.266
C16:0	16.9	21.2	17.1	21.8	18.7	20.8	19.0	21.8	0.451	0.755	0.001	0.686
C17:0	4.2	3.8	4.0	2.9	2.5	2.9	2.9	2.7	0.164	0.103	0.095	0.827
C18:0	6.4	12.4	7.7	11.9	10.1	12.7	10.8	13.3	0.397	0.083	0.001	0.368
C16:1*cis*-9	2.1	1.7	1.9	1.7	1.8	1.6	1.6	1.6	0.050	0.166	0.061	0.626
C17:1*cis*-9	3.4	1.6	3.1	1.5	2.2	1.1	1.6	1.3	0.117	0.009	0.001	0.115
C18:1*cis*-9	32.0	35.1	32.7	36.0	34.9	34.2	30.9	32.3	0.409	0.063	0.039	0.282
C18:1*cis*-11	1.44	1.37	1.60	1.12	1.31	1.12	1.16	1.01	0.034	0.009	0.003	0.171
C18:1*cis*-12	0.14	0.15	0.18	0.14	0.22	0.25	0.31	0.28	0.010	0.001	0.739	0.592
C18:1*cis*-13	0.23	0.16	0.26	0.15	0.23	0.18	0.21	0.20	0.006	0.977	0.001	0.065
C18:1*cis*-15	0.20	0.26	0.26	0.25	0.34	0.46	0.56	0.56	0.028	0.001	0.437	0.830
C18:1*trans*-6,7,8[2]	0.20	0.24	0.42	0.26	0.32	0.35	0.54	0.42	0.022	0.003	0.248	0.257
C18:1*trans*-9	0.26	0.25	0.42	0.26	0.35	0.29	0.48	0.38	0.017	0.008	0.028	0.420
C18:1*trans*-10	2.5	3.7	4.3	4.2	2.6	4.4	5.2	4.0	0.276	0.256	0.468	0.284
C18:1*trans*-11	1.2	0.6	0.5	0.7	0.8	1.0	1.3	1.8	0.181	0.339	0.879	0.713
C18:1*trans*-12	0.15	0.19	0.21	0.22	0.27	0.32	0.38	0.44	0.016	0.001	0.225	0.941
C18:1*trans*-13,14[3]	0.24	0.29	0.32	0.15	0.37	0.36	0.37	0.50	0.027	0.043	0.988	0.272
C18:1*trans*-15	0.06	0.11	0.12	0.13	0.18	0.23	0.29	0.35	0.015	0.001	0.213	0.902
C18:1*trans*-16	0.11	0.13	0.16	0.14	0.21	0.24	0.24	0.31	0.013	0.001	0.450	0.578
C18:2$n-6$	2.3	2.4	2.5	2.7	2.5	2.6	3.0	2.0	0.099	0.824	0.528	0.152
C18:2*cis*-9,*trans*-11	0.70	0.35	0.50	0.49	0.55	0.52	0.71	0.49	0.061	0.938	0.215	0.725
C18:3$n-3$	0.4	0.5	0.9	1.0	1.2	1.4	1.9	1.4	0.063	0.001	0.743	0.297
C20:3$n-3$	0.01	0.01	0.03	0.02	0.03	0.02	0.04	0.02	0.002	0.013	0.015	0.681
oddFA	9.6	6.5	8.9	5.3	7.0	5.0	5.8	4.9	0.313	0.025	0.001	0.462
ESFA[4]	25.6	36.7	27.2	37.2	31.8	36.8	33.1	38.0	0.844	0.264	0.001	0.443
MUFA[5]	44.9	46.2	47.0	46.0	46.5	46.4	45.4	45.6	0.461	0.786	0.917	0.844
PUFA[6]	4.0	3.7	4.4	4.6	4.8	5.0	6.0	4.3	0.170	0.048	0.225	0.172
$n-6$	2.5	2.6	2.7	2.9	2.7	2.8	3.2	2.2	0.106	0.843	0.525	0.151
$n-3$	0.5	0.5	0.9	1.0	1.3	1.4	1.9	1.5	0.065	0.001	0.681	0.299
$n-6/n-3$	5.6	5.1	2.9	2.8	2.1	2.0	1.9	1.6	0.079	0.001	0.152	0.816
ID14[7]	6.0	2.7	3.3	2.8	2.9	2.9	2.3	2.3	0.189	0.005	0.020	0.011
ID16[7]	10.8	7.4	10.2	7.2	8.8	7.0	7.7	6.8	0.194	0.082	0.001	0.131
ID18[7]	83.3	73.8	81.4	75.3	77.9	72.8	74.2	71.0	0.718	0.019	0.002	0.492
IDCLA[7]	50.8	36.4	51.0	42.5	41.7	36.2	36.9	28.8	1.336	0.005	0.002	0.682

For legend, see Table 3.

not change in adipose tissue and muscle from lambs with linseed supplementation. There was a decrease in the proportions of C18:1*cis*-11 and C18:1*cis*-9 and an increase in almost all the other C18:1 isomers, apart from C18:1*trans*-10 and C18:1*trans*-11, for which the largest variations were observed. The total *trans*-FA tended to increase with linseed supplementation ($P = 0.07$, 0.03, 0.12 in PR, SC and IM, respectively). The proportion of C18:1*trans*-11 represented only about a third of that of C18:1*trans*-10 which was often the major of the *trans*-C18:1 isomers. C18:1*trans*-10 and the sum of the proportions of all *trans*-C18:1 isomers was highest in PR and lowest in IM (C18:1*trans*-10 = 5.0% ± 0.36, min = 1.3, max = 10.1; 3.7 ± 0.28%, min = 0.8, max = 7.6 and 2.2% ± 0.17, min = 0.7, max = 5.2; sum of all *trans*-C18:1 isomers = 8.7% ± 0.54, min = 3.8, max = 19.0; 6.6% ± 0.44, min = 1.9, max = 14.6 and 4.4% ± 0.24, min = 2.0, max = 8.7, in PR, SC and IM, respectively).

With an increase in linseed, no significant variations in the proportions of each even FA were observed in PR, but the sum of the ESFA was significantly lower, mainly in group L9 (Table 3). C16:1*cis*-9, C17:1*cis*-9, C18:1*cis*-11 and to a lesser extent C18:1*cis*-9 were lower in linseed supplemented than in control lambs ($P = 0.08$, 0.08, 0.07, and 0.16, respectively). The other *cis*-C18:1 isomers (C18:1*cis*-12, C18:1*cis*-13, C18:1*cis*-15) and most of the proportions of *trans*-C18:1 isomers (*trans*-6,7,8, *trans*-9, *trans*-10, *trans*-11, *trans*-12, *trans*-13,14, *trans*-15, and *trans*-16) were higher in linseed supplemented than in control lambs.

In SC, most changes in FA proportions in lambs with linseed supplementation appeared to be similar to those observed in PR. The proportion of C18:3$n-3$ was lower in SC than in PR in each group of lambs. However, in SC, with linseed supplementation an increase in the proportions of C20:3$n-3$ was observed (0.008 vs. 0.027%, $P < 0.05$%, for L0 and L9, respectively). The proportions of C18:0 increased with an increasing concentration of linseed in the concentrate. The total proportions of MUFA in SC did not change significantly with linseed supplementation but most *cis*-MUFA decreased (C16:1*cis*-9, $P = 0.17$;

Table 5
Effects of types of concentrate on fatty acid composition of muscle of lambs

Type of concentrate	L0		L3		L6		L9		SEM	Effect, *P*-value		
Sex	M	F	M	F	M	F	M	F		C[1]	Sex	C × sex
DM, %	25.2	25.6	25.5	26.6	24.8	26.2	24.9	25.8	0.1975	0.514	0.022	0.839
Total FA, %	4.1	4.5	5.4	5.5	4.8	4.5	4.1	4.3	0.293	0.367	0.767	0.684
FA composition, g/100 g of FA												
C14:0	1.9	2.7	2.9	2.9	2.3	2.7	2.2	2.3	0.106	0.119	0.141	0.480
C15:0	0.34	0.41	0.54	0.37	0.37	0.35	0.37	0.33	0.014	0.040	0.168	0.030
C16:0	23.2	24.6	24.3	24.4	24.0	24.4	23.4	24.1	0.212	0.747	0.154	0.751
C17:0	1.4	1.7	1.7	1.4	1.4	1.2	1.4	1.2	0.036	0.013	0.192	0.069
C18:0	13.9	14.8	12.4	13.1	13.8	13.0	13.6	14.7	0.298	0.251	0.436	0.676
C16:1*cis*-9	1.78	1.68	1.98	1.84	1.74	1.85	1.68	1.77	0.046	0.454	0.921	0.675
C17:1*cis*-9	1.19	1.12	1.36	1.04	1.09	0.97	1.05	0.97	0.037	0.214	0.056	0.625
C18:1*cis*-9	41.2	38.7	38.4	40.9	41.2	38.9	37.0	38.3	0.296	0.025	0.671	0.009
C18:1*cis*-11	1.95	1.45	1.61	1.46	1.52	1.57	1.56	1.38	0.041	0.308	0.025	0.159
C18:1*cis*-12	0.16	0.11	0.13	0.11	0.21	0.20	0.24	0.22	0.011	0.004	0.233	0.982
C18:1*cis*-13	0.18	0.09	0.12	0.12	0.15	0.11	0.12	0.12	0.011	0.933	0.160	0.465
C18:1*cis*-15	0.15	0.15	0.25	0.14	0.21	0.19	0.35	0.29	0.016	0.005	0.173	0.638
C18:1*trans*-6,7,8[2]	0.20	0.18	0.32	0.16	0.23	0.17	0.31	0.23	0.017	0.175	0.013	0.523
C18:1*trans*-9	0.26	0.33	0.32	0.24	0.29	0.23	0.37	0.29	0.013	0.280	0.196	0.184
C18:1*trans*-10	1.7	1.8	2.8	2.3	1.7	2.1	3.1	2.0	0.165	0.201	0.391	0.402
C18:1*trans*-11	1.0	0.7	0.7	0.6	0.9	0.7	1.1	1.1	0.106	0.559	0.559	0.974
C18:1*trans*-12	0.17	0.17	0.14	0.14	0.12	0.12	0.21	0.16	0.009	0.075	0.512	0.558
C18:1*trans*-13,14[3]	0.08	0.08	0.12	0.06	0.07	0.08	0.14	0.12	0.007	0.059	0.271	0.436
C18:1*trans*-15	0.28	0.29	0.32	0.28	0.32	0.30	0.46	0.44	0.015	0.003	0.518	0.970
C18:1*trans*-16	0.07	0.09	0.12	0.10	0.18	0.12	0.16	0.18	0.009	0.004	0.552	0.464
C18:2*n* − 6	4.5	3.3	3.8	3.5	3.6	4.7	4.6	3.7	0.151	0.585	0.257	0.054
C18:2*cis*-9,*trans*-11	0.12	0.02	0.05	0.11	0.15	0.09	0.08	0.07	0.016	0.686	0.357	0.419
C18:3*n* − 6	0.05	0.04	0.03	0.03	0.03	0.04	0.02	0.03	0.002	0.018	0.187	0.148
C18:3*n* − 3	0.44	0.51	0.87	0.69	1.01	1.15	1.52	1.15	0.031	0.001	0.163	0.022
C20:2*n* − 6	0.06	0.05	0.07	0.06	0.06	0.65	0.08	0.06	0.002	0.221	0.191	0.239
C20:3*n* − 6	0.14	0.10	0.10	0.09	0.09	0.13	0.10	0.11	0.006	0.486	0.670	0.145
C20:3*n* − 3	0.01	0.02	0.02	0.01	0.02	0.02	0.03	0.02	0.008	0.052	0.591	0.037
C20:4*n* − 6	1.08	0.82	0.64	0.67	0.62	1.00	0.75	0.81	0.005	0.293	0.622	0.214
C20:5*n* − 3	0.16	0.17	0.15	0.15	0.17	0.29	0.21	0.26	0.084	0.072	0.114	0.411
C22:4*n* − 6	0.08	0.06	0.05	0.04	0.04	0.06	0.05	0.05	0.003	0.155	0.919	0.321
C22:5*n* − 3	0.22	0.20	0.20	0.19	0.20	0.30	0.25	0.27	0.092	0.312	0.423	0.495
C22:6*n* − 3	0.06	0.06	0.05	0.06	0.05	0.08	0.06	0.07	0.037	0.837	0.411	0.879
oddFA	3.0	3.3	3.6	2.8	2.9	2.6	2.8	2.6	0.076	0.033	0.074	0.138
ESFA[4]	39.2	42.4	40.0	40.7	40.3	40.3	39.5	41.2	0.307	0.924	0.028	0.030
MUFA[5]	50.9	47.5	49.4	50.1	50.4	48.1	48.3	48.3	0.329	0.490	0.075	0.127
PUFA[6]	7.0	5.4	6.1	5.7	6.1	8.0	7.9	6.7	0.244	0.158	0.498	0.082
n − 6	5.9	4.3	4.7	4.4	4.4	6.0	5.6	4.8	0.205	0.616	0.480	0.069
n − 3	0.89	0.96	1.28	1.90	1.46	1.83	2.07	1.77	0.052	0.001	0.910	0.113
n − 6/*n* − 3	6.8	4.8	3.7	4.0	3.0	3.3	2.8	2.7	0.128	0.001	0.165	0.013
ID14[7]	4.0	3.5	4.3	4.0	4.0	3.9	3.7	3.5	0.121	0.429	0.199	0.959
ID16[7]	7.1	6.4	7.5	7.0	6.7	7.0	6.6	6.8	0.143	0.561	0.544	0.508
ID18[7]	74.8	72.3	75.6	75.7	75.0	74.9	73.2	72.4	0.478	0.150	0.418	0.785
IDCLA[7]	11.1	3.3	6.8	11.9	13.8	10.2	8.2	5.5	1.333	0.500	0.410	0.399

For legend, see Table 3.

C17:1*cis*-9, $P = 0.009$; C18:1*cis*-9, $P = 0.063$; C18:1*cis*-11, $P = 0.009$). The decrease in oddFA with linseed supplementation was more pronounced in SC than in PR. L9 oddFA were only about a third of that of L0. In SC, oddFA, were negatively correlated with ESFA ($r = -0.86$, $P < 0.001$, $n = 40$). For changes in the proportions of C18:0, and oddFA in SC the same trend was observed for males and females with linseed supplementation. However, these changes were only significant in males. Opposite to PR and IM, there was a significant decrease in most of the Δ9 desaturase indices in SC (ID14: 4.4 vs. 2.3, $P < 0.01$; ID16: 9.0 vs. 7.2, $P < 0.01$; ID18: 78.6 vs. 72.7, $P < 0.05$; IDCLA: 43.6 vs. 32.8, $P < 0.01$, for L9 and L0, respectively). Within SC, these indices were highly correlated with each other ($P < 0.01$). In PR and IM there were also similarities in their variations. But the correlation coefficient between ID14 and IDCLA was not significant in PR, or for those between ID14 and IDCLA and between ID16 and IDCLA in IM. Between tissues, these coefficients were significant only between PR and IM ($r = 0.397$, $P < 0.01$, $r = 0.399$, $P < 0.01$, and $r = 0.567$, $P < 0.01$, for ID14, ID16, and

ID18, respectively), between SC and PR for IDCLA ($r = 0.464$, $P < 0.01$) and between SC and IM for ID18 ($r = 0.343$, $P < 0.05$).

In IM with linseed supplementation a significant increase in C20:3$n-3$ ($P = 0.05$) and C20:5$n-3$ ($P = 0.07$) was observed with a concomitant change in the proportions of C18:3$n-3$. With ILW as a covariable, the significance levels for C20:5$n-3$ ($P = 0.015$) and for C22:5$n-3$ ($P = 0.10$) were increased, but C22:6$n-3$ were no longer different. There was a significant decrease in the proportions of C18:3$n-6$ (about 35%, $P = 0.02$). Other long-chain FA of the $n-6$ series (LC$n-6$) did not change significantly with linseed supplementation. C18:3$n-3$ represented almost all of the $n-3$ PUFA in adipose tissue (100% and 97.3% in PR and SC, respectively) and about two-thirds of the total $n-3$ PUFA in muscle (65%), which represents less than a quarter of the total PUFA (24.1, 23.7 and 14.0%, in PR, SC and IM, respectively). Nevertheless, as the proportions of C18:2$n-6$ and total $n-6$ PUFA did not change in adipose tissues and muscle with linseed

Table 6
Pearson correlation coefficients for the fatty acids between main C18:1 isomers and with C18:2$n-6$ and C18:3$n-3$ in perirenal adipose tissue (PR) subcutaneous adipose tissue (SC) and muscle (IM)

PR	*c*9	*c*11	*c*12	*c*13	*c*15	*t*6,7,8	*t*9	*t*10	*t*11	*t*12	*t*13,14	*t*15	*t*16
C18:2$n-6$	−0.23	0.08	−0.09	−0.12	0.14	0.20	0.09	**0.61**	0.08	−0.02	0.01	0.06	−0.09
C18:3$n-3$	**−0.40**	−0.22	**0.58**	**0.34**	**0.82**	**0.64**	**0.51**	**0.49**	0.18	**0.68**	0.30	**0.82**	**0.68**
*c*9		−0.06	−0.20	−0.05	**−0.42**	**−0.56**	**−0.33**	**−0.57**	**−0.39**	**−0.52**	**−0.52**	**−0.47**	**−0.42**
*c*11			0.17	**−0.36**	−0.03	0.11	0.04	0.12	−0.20	−0.03	0.05	−0.05	−0.07
*c*12				**0.54**	**0.81**	**0.42**	**0.44**	−0.05	0.01	**0.61**	0.05	**0.73**	**0.65**
*c*13					**0.35**	0.16	0.15	−0.14	0.19	0.27	0.11	0.41	**0.51**
*c*15						**0.62**	**0.49**	0.30	0.03	**0.81**	0.27	**0.94**	**0.83**
*t*6,7,8							**0.92**	**0.54**	**0.38**	**0.66**	**0.43**	**0.71**	**0.54**
*t*9								**0.32**	**0.42**	**0.50**	0.31	**0.56**	**0.40**
*t*10									0.11	0.29	0.29	**0.31**	0.15
*t*11										0.22	**0.55**	0.15	0.15
*t*12											**0.39**	**0.88**	**0.86**
*t*13,14													**0.41**
*t*15													**0.92**
SC	*c*9	*c*11	*c*12	*c*13	*c*15	*t*6,7,8	*t*9	*t*10	*t*11	*t*12	*t*13,14	*t*15	*t*16
C18:2$n-6$	**−0.41**	0.02	0.25	−0.11	0.26	0.31	0.25	**0.64**	0.09	0.18	0.26	0.13	0.10
C18:3$n-3$	**−0.33**	−0.30	**0.77**	0.06	**0.84**	**0.71**	**0.66**	**0.48**	0.13	**0.79**	**0.54**	**0.80**	**0.71**
*c*9		0.07	−0.19	−0.10	−0.28	**−0.33**	−0.30	**−0.38**	**−0.34**	−0.17	−0.24	−0.22	−0.12
*c*11			0.15	**0.54**	−0.22	−0.09	−0.06	0.01	**−0.40**	−0.30	−0.08	**−0.38**	−0.29
*c*12				0.15	**0.89**	**0.66**	**0.59**	**0.35**	0.08	**0.81**	**0.55**	**0.84**	**0.80**
*c*13					0.04	0.17	0.29	0.10	−0.11	0.02	0.04	−0.03	0.15
*c*15						**0.67**	**0.61**	**0.43**	0.06	**0.85**	**0.52**	**0.89**	**0.79**
*t*6,7,8							**0.94**	**0.73**	**0.33**	**0.78**	**0.59**	**0.72**	**0.67**
*t*9								**0.57**	**0.35**	**0.68**	**0.53**	**0.62**	**0.59**
*t*10									0.24	**0.54**	0.29	**0.46**	0.40
*t*11										0.24	−0.05	0.17	0.20
*t*12											**0.49**	**0.96**	**0.92**
*t*13,14												**0.54**	**0.47**
*t*15													**0.92**
IM	*c*9	*c*11	*c*12	*c*13	*c*15	*t*6,7,8	*t*9	*t*10	*t*11	*t*12	*t*13,14	*t*15	*t*16
C18:2$n-6$	**−0.39**	**0.51**	0.20	0.15	−0.05	0.10	−0.06	0.25	0.11	0.23	0.05	−0.03	−0.25
C18:3$n-3$	**0.47**	−0.21	**0.63**	−0.05	**0.66**	**0.49**	0.25	**0.39**	0.16	0.07	**0.35**	**0.52**	**0.63**
*c*9		0.22	−0.10	**0.33**	**−0.32**	**−0.37**	**−0.35**	−0.28	**−0.39**	**−0.32**	**−0.34**	**−0.43**	−0.13
*c*11			−0.11	0.24	−0.27	−0.05	−0.01	0.11	−0.30	0.20	0.05	**−0.38**	**−0.42**
*c*12				0.06	**0.66**	**0.37**	0.20	0.10	0.04	−0.16	0.31	**0.50**	**0.58**
*c*13					0.07	−0.02	0.04	0.06	**−0.33**	0.01	0.08	−0.08	0.14
*c*15						**0.76**	**0.62**	0.45	0.03	−0.10	**0.68**	**0.66**	**0.76**
*t*6,7,8							**0.66**	**0.53**	0.24	0.02	**0.58**	**0.52**	**0.53**
*t*9								**0.40**	0.08	0.05	**0.68**	**0.47**	**0.40**
*t*10									0.09	0.13	**0.45**	**0.38**	0.26
*t*11										0.22	0.03	**0.40**	0.10
*t*12											0.26	0.21	−0.12
*t*13,14												**0.55**	**0.48**
*t*15													**0.57**

*c*9, *c*11, *c*12, *c*13, *c*15 = C18:1*cis*-9, C18:1*cis*-11, C18:1*cis*-12, C18:1*cis*-13, C18:1*cis*-15. *t*6,7,8, *t*9, *t*10, *t*11, *t*12, *t*13, *t*14, *t*15, *t*16 = C18:1*trans*-6 + C18:1*trans*-7 + C18:1*trans*-8, C18:1*trans*-9, C18:1*trans*-10, C18:1*trans*-11, C18:1*trans*-12, C18:1*trans*-13 + C18:1*trans*-14, C18:1*trans*-15, C18:1*trans*-16.

supplementation, the increase in C18:3$n-3$ led to similar increases in the total proportion of PUFA and to decrease in the $n-6$:$n-3$ ratios, from values above 5.0 in control lambs to values below 2.0 in PR and SC and below 3.0 in IM.

The decrease in the proportions of C18:1*cis*-9 in IM ($P < 0.05$) was greater than in PR and SC, but the decrease in C18:1*cis*-11 was less than in PR and SC. Among other C18:1 isomers, only C18:1*cis*-12, ($P < 0.01$), C18:1*cis*-15, ($P < 0.01$), C18:1*trans*-12, ($P < 0.10$), C18:1*trans*-13,14, ($P < 0.10$), C18:1*trans*-15 ($P < 0.01$), and C18:1*trans*-16, ($P < 0.01$), increased with linseed supplementation. In IM the change in the proportions of C18:1*cis*-9 was not concurrent with changes in the Δ9 index of desaturases. With linseed supplementation the decrease in the total proportion of oddFA ($P < 0.05$) in IM was similar to that in PR.

On the whole, *trans*-octadecenoic isomers, except C18:1*trans*-10 and C18:1*trans*-11, were closely and positively correlated with each other (Table 6). Among *cis*-octadecenoic isomers, C18:1*cis*-15 had the highest positive correlation coefficients with *trans*-octadecenoic isomers, except C18:1*trans*-10 and C18:1*trans*-11. Conversely, C18:*cis*-9 was negatively correlated with most *trans*-octadecenoic isomers in these tissues. Yet, these coefficients were significant with all *trans*-octadecenoic isomers in PR, but only with C18:1*trans*-6-7-8, C18:1*trans*-10 and C18:1*trans*-11 in SC and were not significant with C18:1*trans*-10 and C18:1*trans*-16 in IM. C18:2$n-6$ was positively correlated with C18:1*trans*-10 ($r = 0.61$, $P < 0.01$, $r = 0.64$, $P < 0.01$, and $r = 0.25$; $P = 0.13$, in PR, SC and IM, respectively). C18:3$n-3$ was negatively correlated with C18:1*cis*-9 in PR, SC and IM and positively correlated with C18:1*cis*-12 and most of the *trans*-octadecenoic isomers.

4. Discussion

4.1. Growth performance and carcass composition

The results show a lack of effect of linseed supplementation on growth rate during the short fattening period, and are in agreement with studies on ovines and bovines (Demirel et al., 2004).

4.2. Lipid composition of adipose tissues and muscles

The total FA content of muscle found was in the range of most reported values in lamb (Lough et al., 1992; Ponnampalam et al., 2002; Solomon, Lynch, Paroczay, & Norton, 1991) although they are higher than in others (Aurousseau, Bauchart, Calichon, Micol, & Priolo, 2004; Demirel et al., 2004; Nuernberg et al., 2005). Some of the discrepancies could be due to effects of ME intake, losses in energy with experimental conditions and age at weaning and slaughter. Under similar environmental conditions and at the same age, increases in lipid content of the diet did not affect muscle lipid content (Bolte, Hess, Means, Moss, & Rule, 2002; Lough et al., 1992; Solomon et al., 1991). The fat and saturated FA supplied by 100 g of lamb muscle would provide about 5 g of total fat and less than 2 g of total saturated FA, less than 6% and 10%, respectively, of the recommended amounts (AFSAA, 2001; German & Dillard, 2004).

Proportions of C18:3$n-3$ and $n-3$ PUFA in adipose tissues and muscles of lambs supplemented with linseed were consistent with other results (Cooper et al., 2004; Demirel et al., 2004; Wachira et al., 2002). The higher linolenic acid content in PR than in SC was consistent with the preferential growth rate of tissues from FA synthesis pathways, with take up of blood FA with lipoprotein lipase rather than growth by endogenous synthesis (Ingle, Bauman, & Garrigus, 1972; Vézinhet, Nougues, & Teyssier, 1983). Lambs fed concentrate supplemented with 9% linseed led to less linolenic acid in adipose tissue and muscle than in lambs raised on pasture or with very high roughage diets (Bas & Morand-Fehr, 2000; Aurousseau et al., 2004; Daniel et al., 2004; Nuernberg et al., 2005). This is probably because linolenic acid was supplied over a shorter period than for grazing lambs and only in the latter period of growth compared to grazing lambs which had more linolenic acid at their disposal during the pre-weaning and growing periods. The increase in LC$n-3$ was lower than generally reported when feeding diets rich in linolenic acid. Nevertheless, this increase in LC$n-3$ in IM showed that elongation and desaturation could occur with linseed fed to a low extent, that was sufficient to improve the production of the active metabolites EPA (eicosapentaenoic acid, C20:5$n-3$) and DPA (docosapentaenoic acid, C22:5$n-3$), but not for DHA production (docosahexaenoic acid, C22:6$n-3$). These results agree with those reported earlier where linolenic acid was supplied in the late finishing period of lambs (Aurousseau et al., 2004; Demirel et al., 2004; Wachira et al., 2002). Feeding linseed had no effect on linoleic acid proportions in adipose tissue and muscle, probably because the supply of linoleic acid in the four groups of lambs was similar. Likewise, proportions of LC$n-6$ in muscles were little affected by feeding linseed, apart from less C18:3$n-6$, the first product of the $n-6$ PUFA series obtained by the action of Δ6 desaturase on linoleic acid. The lack of a marked effect of high linolenic acid availability on linoleic acid and LC$n-6$ in tissues in this study contrasted with previous results obtained with similar linoleic acid contents in the diet (Demirel et al., 2004; Wachira et al., 2002). Competition for common metabolic enzymes, desaturase and elongase, caused an imbalance between these two PUFA series. This had consequences on the balance between production of pro-thrombotic and pro-inflammatory metabolites on the one hand, and on production of anti-thrombotic and anti-inflammatory metabolites on the other hand (Simopoulos, 2004). The $n-6$:$n-3$ ratios below 4.0, in adipose tissues and muscle of lambs fed linseed supplemented diets was within the recommendations for the balance between the PUFA series. Yet, with respect to the recommended intake of $n-3$ PUFA, the supply of $n-3$

PUFA was low, less than 80 mg for 100 g of muscle and between 150 and 250 mg with the added intake of linolenic acid, which is less than 10% of $n-3$ PUFA recommendations (2–3 g per day, of which 2/3 to 3/4 might come from linolenic acid; AFSAA, 2001; Wijendran & Hayes, 2004). Moreover, there was a specific requirement for LC$n-3$, which were more potent than linolenic acid for protective action against cardiovascular risks, carcinogenesis, retinal, immune and neurological functions (Sinclair, Attar-Bashi, & Li, 2002; Calder, 2003; Mozaffarian et al., 2005). Yet, the intake of linolenic acid and LC$n-3$ PUFA must be limited, at least in men, due to adverse reports on the risk of prostate cancer (Brouwer, Katan, & Zock, 2004).

Although the level of oleic acid intake increased with linseed diet content, its proportion was lowest in adipose tissue and muscle of lambs fed the highest linseed diet. This could be due to a lower uptake from blood and/or lower synthesis from stearic acid by the action of Δ9 desaturase, as suggested by the lower desaturase indices (ID18). This inhibition of steoryl-CoA desaturase in adipose tissue and muscle by feeding linseed is consistent with findings on rodents of greater inhibition of steoryl-CoA desaturase with linolenic than with linoleic acid (Sessler, Kaur, Palta, & Ntambi, 1996). The lower proportion of oleic acid in muscle could also result from competitive exclusion (Wachira et al., 2002). This decrease in oleic acid content could be unfavourable for the HDL:LDL cholesterol ratio (Lagrost et al., 1999; Sacks & Katan, 2002). The lower proportion of C18:1*cis*-11 in adipose tissues with linseed supplementation was similar to results found in bulls fed linseed (Raes et al., 2004) and in lambs fed high-oleate or high-linoleate safflower seeds (Bolte et al., 2002). These results seem to disagree with those of Aharoni, Orlov, and Brosh (2004), who fed cattle crushed raw flax. But under their analytical conditions C18:1*cis*-11 was unresolved from C18:1*cis*-12, which could lead to misinterpretation because of opposite changes in these two FA. The decrease in the proportions of C18:1*cis*-11 could result from lower production in the rumen by isomerization and hydrogenation of unsaturated FA, but also from lower availability of palmitoleic acid which is a primary product of C18:1*cis*-11 synthesis by elongation.

With linseed supplementation the accumulation of total C18:1 isomers was 1.5 times (in SC) to twofold higher (in PR) in adipose tissue than in muscle. These results agree with most previous results reported on beef and lamb (Raes et al., 2004; Wachira et al., 2002). In this experiment, the C18:1*trans*-10:C18:1*trans*-11 ratio, much higher than 1.0, could result mainly from the high concentrate level in the diet and fat supplementation. A marked increase in the C18:1*trans*-10 proportion in fat tissues with fat supplementation was only observed with a low forage: concentrate ratio and more with fat rich in linoleic acid compared with oleic or linolenic acids (Bessa, Portugal, Mendes, & Santos-Silva, 2005; Hristov, Kennington, McGuire, & Hunt, 2005; Palmquist, St-Pierre, & McClure, 2004). When the same type of concentrate was offered with meadow hay without restriction, hay intake was less than 20% DM (Normand, Bas, Berthelot, & Sauvant, 2005). In this experiment straw was the only forage offered to lambs and it might even be assumed that the straw intake was less than 10% DM. Moreover, as there was no large variations in the linoleic acid contents of the four diets it could be that in this experiment, the concentrate based-diet is mainly responsible for a greater production of C18:1*trans*-10 than C18:1*trans*-11. C18:1*cis*-15 and all *trans*-C18:1 isomers, except C18:1*trans*-10 and C18:1*trans*-11, were positively associated with the proportions of linolenic acid in tissues and thus with the linolenic acid content in the diet but not with oleic or linoleic acids. C18:1 isomers, with the double bond nearest to the methyl part of the acids, are produced during isomerization and biohydrogenation of linolenic acid, (Body, 1976). Similarly, C18:1*cis*-15, C18:1*trans*-13,14, C18:1*trans*-15 and C18:1*trans*-16 were enhanced in bulls fed a 9.4% linseed concentrate compared to a concentrate richer in $n-6$ fatty acids containing 2.5% palm fat (Raes et al., 2004). Lambs fed linseed supplemented concentrate seemed to yield meat with adverse effects on health because of higher *trans*-FA contents. *Trans*-FA have unfavourable effects on HDL cholesterol, blood coagulating factor, atherogenicity and coronary heart disease than ESFA and particularly stearic acid (Odegaard & Pereira, 2006; Sacks & Katan, 2002; Stender & Dyerberg, 2004; Willett, 2006). The supply of *trans*-FA per 100 g of muscle is moderate considering maximum intake recommendations for total *trans*-FA. But, assuming lamb meat has an extra 10% of fat deposit; it could supply a larger amount of these recommendations (AFSAA, 2005; Mozaffarian, Katan, Ascherio, Stampfer, & Willett, 2006). *trans*-FA had adverse effects on PUFA and particularly on $n-3$ PUFA for cardiovascular disease (Dyerberg, Christensen, Eskesen, Astrup, & Stender, 2006; Innis, 2006). With a same level of *trans*-FA intake, *trans*-FA from ruminant products were supposed to have less unfavourable effects than *trans*-FA from industrial products, but this difference appeared to be of low amplitude (Mensink, 2005; Jakobsen et al., 2006). As physiological effects of *trans*-FA differed from that of *cis*-FA there was no warrant to consider associating *trans*-FA with SFA rather than with *cis*-FA for meat health evaluation.

The proportions of C18:2*cis*-9,*trans*-11, were in the lower range of values reported in other studies. The lack of change in the proportions of this CLA with linseed supplementation was in agreement with results with soybean oil supplemented diets (Beaulieu, Drackley, & Merchen, 2002). In contrast, up to a twofold increase of this CLA was reported as a result of dietary unsaturated fat supplementation in other studies (Aharoni et al., 2004; Bolte et al., 2002; Wachira et al., 2002). An increase in the proportion of this CLA with unsaturated fat supplementation was only observed in pasture feeding, or at least with significant dietary forage in the diets, but not in feedlot fed animals with *ad libitum* access to concentrate-based cereal diets (Bessa et al., 2005; Bolte et al., 2002; Raes et al., 2004; Scollan et al., 2006). The lack of enhancement of this

CLA, as a proportion of total FA, probably resulted from ruminal output of this linoleic isomer and its substrate C18:1*trans*-11 being too low. As C18:2*cis*-9,*trans*-11 has numerous health benefits, such as reducing the risk of cancer, atherosclerosis, diabetes, obesity and inflammation (Ochoa et al., 2004; Wahle, Heys, & Rotondo, 2004), C18:1*trans*-11, the main precursor of this CLA could be considered as a beneficial *trans*-FA. The inability to measure the very small amount of C18:2*trans*-10, *cis*-12 in adipose tissue and muscle with GLC/FID alone, was in agreement with studies on feedlot fed lambs (Palmquist et al., 2004). Beaulieu et al. (2002) found a moderate increase in the proportions of C18:2*trans*-10, *cis*-12 in adipose tissue and muscles of beef fed diets supplemented with 5% soybean oil, but the values reported appear very low, particularly in muscles.

5. Conclusion

In this study, linseed supplementation increased linearly the proportions of linolenic acid in adipose tissue and muscle, but had a very limited effect on LC$n-3$. Consequently, supplying linseed to lambs resulted in an increase in the PUFA content of adipose tissue and muscle, and a $n-6$:$n-3$ PUFA ratio, below 4, which is desirable for human nutrition. In contrast, effects of linseed supplementation on lambs reared on an unlimited-feed concentrate diet was to increase the proportions of most *trans*-octadecenoic isomers which is questionable for consumer health. Further work is needed to clarify the beneficial potential of linseed supplementation on the quality of meat from lambs reared under intensive conditions.

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