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ARTICLE

Effect of Grape Seed Extract, *Cistus ladanifer* L., and Vegetable Oil Supplementation on Fatty Acid Composition of Abomasal Digesta and Intramuscular Fat of Lambs

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Thirty-six lambs were used in a 6 week experiment to evaluate the effect of vegetable oil blend supplementation (0 vs 60 g/kg of dry matter (DM)) and two dietary condensed tannin sources, grape seed extract (0 vs 25 g/kg of DM) and *Cistus ladanifer* L. (0 vs 250 g/kg of DM), on fatty acid (FA) composition of abomasal digesta and intramuscular polar and neutral lipids. Grape seed extract did not affect the FA profile of abomasal digesta or muscle lipid fractions. *C. ladanifer* had a minor effect in lambs fed diets with no oil but greatly changed the abomasal and muscle FA profiles in oil-supplemented lambs. It decreased 18:0 and increased 18:1 *trans*-11 in abomasal digesta and increased 18:1 *trans*-11 and 18:2 *cis*-9,*trans*-11 ($P = 0.062$) in muscle neutral lipids, resulting in an important enrichment of meat 18:2 *cis*-9,*trans*-11 when compared to other oil-supplemented diets (19.2 vs 41.7 mg/100 g of muscle).

KEYWORDS: Abomasal digesta; biohydrogenation intermediates; condensed tannins; fatty acids; lamb meat; oil supplementation

INTRODUCTION

The supplementation of ruminant diets with lipid sources rich in polyunsaturated fatty acids (PUFA) is an effective approach to improve the nutritional value of meat fat, through decrement of saturated fatty acids (SFA) and enrichment in PUFA, including the health promoters conjugated isomers of linoleic acid (CLA) and *n*-3 PUFA (*1*, *2*). Supplementary C18 PUFA will be extensively metabolized by the rumen ecosystem, producing a complex pattern of isomeric C18 fatty acids (FA), mostly *trans* FA, hereafter named biohydrogenation intermediates (BI). *Trans* FA have been associated with detrimental effects on human health (*3*), although 18:1 *trans*-11, the precursor of 18:2 *cis*-9, *trans*-11 in tissues, might be considered as a neutral or beneficial *trans* FA (*4*).

Several factors modulate rumen biohydrogenation (BH) of PUFA, including the amount and type of lipid supplements (*5*) and basal diet (*6*). More recently, it has been suggested that condensed tannins (CT) might modulate rumen biohydrogenation of PUFA (*7*−*10*). Condensed tannins are plant secondary metabolites with astringency properties. In vitro (*7*, *8*) and in vivo (*9*, *10*) studies showed that some CT sources are effective in the reduction of dietary PUFA ruminal BH, particularly in its last step, resulting in accumulation of 18:1 *trans*-11. Thus, CT supplementation could be a useful strategy to improve the nutritional value of ruminant fat. *Cistus ladanifer* L. was chosen due to its high tannin content and its abundance in marginal fields of Mediterranean countries (*11*). Grape seed extract (GSE) was a commercially available source of purified CT. Interactions between CT and vegetable oil supplementation are fairly unexploited. Therefore, the aim of the present study was to explore the effect of dietary CT sources (GSE and leaves and soft stems of *C. ladanifer* L.), oil supplementation, and their interactions on lamb growth performance, carcass composition, and ruminal biohydrogenation, as evaluated by FA composition of abomasal digesta and intramuscular fat of lambs.

MATERIALS AND METHODS

Animals, Treatments, and Sample Collection. Animal handling followed EU Directive 86/609/EEC concerning animal care. Thirty-six Merino Branco ram lambs were reared on pasture with dams until weaning at approximately 60 days. At weaning day, lambs were transported to the Unidade de Investigação em Produção Animal, Instituto Nacional de Recursos Biológicos (UIPA-INRB, Vale de Santarém, Portugal), where the trial was held. The average initial weight for lambs was 24.8 ± 1.55 kg (mean ± SD). Lambs ($n = 36$) were randomly assigned to 12 pens; 3 lambs per pen and 2 pens per treatment, according to a completely randomized

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experimental design with a 3 × 2 factorial arrangement of treatments. The first factor was CT sources (with three levels): (1) no added CT source, control; (2) 25 g of GSE/kg of dry matter (DM); (3) 250 g of *C. ladanifer* leaves and soft stems/kg of DM. The second factor was oil supplementation (with two levels): 0 and 60 g of oil blend/kg of DM. This 3 × 2 factorial arrangement results in 6 diets: C, basal diet composed of 900 g of dehydrated lucerne/kg of DM and 100 g of wheat bran/kg of DM; CO, basal diet with 60 g of oil blend/kg of DM; GS, basal diet with 25 g of GSE/kg of DM; GSO, basal diet with 25 g of GSE/kg of DM and 60 g of oil blend/kg of DM; CL, basal diet with 250 g of *C. ladanifer*/kg of DM; and CLO, basal diet with 250 g of *C. ladanifer*/kg of DM and 60 g of oil blend/kg of DM. Grape seed (*Vitis vinifera* L.) extract contained 95% proanthocyanidins in DM (AHD International LLC, Atlanta, GA). Leaves and soft stems of *C. ladanifer* shrubs were harvested in Portugal (39° 30′ 36″ N/8° 19′ 00″ W) in March 2008, dried at room temperature, cut in small particles, and milled to a final particle size of 3 mm. The oil blend was composed of a mixture of sunflower and linseed oils in a proportion of 1:2 (v/v). Diets were prepared in an industrial unit, and oil was sprayed over the pellets in a 1000 kg capacity mixer. The chemical composition of the diets and analytical procedures involved are reported in a recently published paper (*12*).

During the trial, lambs were housed and kept on a slatted floor. The trial started after an adaptation period of 7 days to experimental conditions and lasted for 6 weeks. Feed was offered every morning at the rate of 110% of ad libitum intake, a calculation based on daily refusal weighing. Animals were weighed weekly, just before feeding. At the end of the trial, lambs were transported to the experimental abattoir of the UIPA-INRB. After determining live slaughter weight, lambs were stunned and slaughtered by exsanguination. Samples of abomasal digesta were collected immediately post-mortem, freeze-dried, and stored at −80 °C until lipid analysis. After preparation, carcasses were weighed to obtain hot carcass weight, which was used to determine dressing percentage. Carcasses were kept at 10 °C for 24 h and then chilled at 2 °C until the third day after slaughter, at which time carcass traits were evaluated and meat samples collected. The kidney knob channel fat (KKCF) and kidneys were removed. Carcasses were split along the spine and left sides of the carcasses were separated into eight joints (*13*). Chumps and shoulders were dissected into muscle, subcutaneous, and intermuscular fat and bone. Samples of longissimus dorsi muscle were collected at the level of the 13th thoracic vertebra. After removal of the epimysium, muscle samples were minced with a food processor (3 × 5 s), vacuum packed, freeze-dried, and stored at −80 °C until lipid analysis.

Lipid Analysis of Intramuscular Fat and Abomasal Digesta. Intramuscular lipids were extracted using dichloromethane and methanol (2:1 v/v) and separated in neutral (NL) and polar (PL) lipids, by using a solid-phase extraction as previously described (*14*). The NL and PL fractions were transesterified with sodium methoxide in methanol, followed by hydrochoric acid in methanol (1:1 v/v) as described by Raes et al. (*15*). Fatty acid methyl esters (FAME) of abomasal digesta lipids were prepared using one-step extraction transesterification with toluene, according to the procedure reported by Sukhija and Palmquist (*16*). The quantification of muscle and abomasal lipid FAME was performed using nonadecanoic acid (19:0) as internal standard. FAME were analyzed using an HP6890A chromatograph (Hewlett-Packard, Avondale, PA), equipped with a flame ionization detector (GC-FID) and fused silica capillary column (CP-Sil 88; 100 m × 0.25 mm i.d. × 0.20 μm film thickness; Chrompack, Varian Inc., Walnut Creek, CA). Helium was the carrier gas, and the injector split ratio was 1:50. The initial column temperature of 100 °C was held for 15 min, increased to 150 °C at 10 °C/min and held for 5 min, then increased to 158 °C at 1 °C/min and held for 15 min. The temperature was later increased to 175 °C at 1 °C/min and held for 10 min and finally increased to 200 °C at a rate of 1 °C/min and maintained for 40 min. Injector and detector temperatures were 250 and 280 °C, respectively. For the resolution of 18:1 *cis*-9 from both 18:1 *trans*-13 and 18:1 *trans*-14 (that coeluted in our GC-FID conditions), a second temperature program was used. The initial temperature column of 70 °C was held for 4 min, increased to 110 °C at 8 °C/min, and then increased to 170 °C at 5 °C/min, held for 10 min, and finally increased to 220 °C at a rate of 4 °C/min and maintained for 25 min. Thus, the relative amounts of 18:1 *cis*-9 and 18:1 *trans*-13/14 were calculated from the second temperature program and applied to the area of the common peak identified in the initial temperature program. Fatty acids were identified by comparison with commercial FAME standard mixtures (Sigma and Supelco, St. Louis, MO). When no commercial standards were available, elution profiles were compared with published chromatograms obtained with similar analytic conditions (*17*). Moreover, identifications were also confirmed by gas chromatography−mass spectrometry (GC-MS) using a Varian Saturn 2200 system (Varian Inc., Walnut Creek, CA) equipped with a CP-Sil 88 capillary column.

The methyl esters of CLA isomers were individually analyzed by triple-column silver ion in series (ChromSpher 5 Lipids, 250 mm × 4.6 mm i.d. × 5 μm particle size, Chrompack, Bridgewater, NJ), using an HPLC system (Agilent 1100 Series, Agilent Technologies Inc., Palo Alto, CA) equipped with an autosampler and a diode array detector (DAD) adjusted at 233 nm. The mobile phase was 0.1% acetonitrile in *n*-hexane maintained at a flow rate of 1 mL/min, and injection volumes of 20 μL were used. The identification of the individual CLA isomers was achieved by comparison of their retention times with commercial and prepared standards, as well as with data published in the literature (*18*). In GC analysis the main peak of 18:2 *cis*-9,*trans*-11 coeluted with both 18:2 *trans*-7,*cis*-9 and 18:2 *trans*-8, *cis*-10. As proposed by Kraft et al. (*19*), the HPLC areas of 18:2 *cis*-9,*trans*-11, 18:2 *trans*-7,*cis*-9, and 18:2 *trans*-8,*cis*-10 were added and used to calculate three isomer peaks from GC chromatograms. The amounts of the other CLA isomers were calculated from their HPLC areas relative to the area of the main isomer 18:2 *cis*-9,*trans*-11 identified by GC.

Statistical Analysis. This trial was conducted using a 3 × 2 factorial design, where the 2 factors were CT sources (CT, with 3 levels: control, grape seed extract, and *C. ladanifer*) and vegetable oil blend supplementation (O, with 2 levels: 0 and 60 g/kg of DM). The interaction between CT sources and O was also evaluated (CT × O). The experimental unit used to evaluate dry matter intake (DMI) and FA intake was the pen (3 lambs), whereas individual animals were considered as experimental units for all other variables. The Shapiro−Wilk test was used to evaluate whether data followed a normal distribution. When not normally distributed ($P < 0.05$), data were Box−Cox transformed before further analysis. Data from intake and feed conversion ratio were analyzed using the GLM procedure of SAS (SAS Institute Inc., Cary, NC) with a model that included the main effects and their interaction. Other data were analyzed using the MIXED procedure of SAS, considering oil and CT sources and their interaction as fixed effects and the pen as random effect. The covariance of measurements from lambs within each pen was considered in the model. Lambs were treated as repeated measurements within the pen, and a compound symmetry covariance matrix was assumed. Least-squares means and standard error of means (SEM) are presented in tables. For Box−Cox transformed variables the SEM is presented in tables, although means are back-transformed. Data presented in tables are the least-squares means obtained for each combination of factors levels (diets). Because some variables did not present significant CT × O interactions, the least-squares means for main effects are presented in the text when needed. When only one level of CT source factor differs from the other two and these two are not significantly different, we present only the least-squares mean of the level that was different and the average of least-squares mean for other factor levels.

RESULTS

Feed Intake. Dry matter intake was not affected by treatments, which averaged 1616 g of DM/day (**Table 1**). Dietary oil supplementation resulted in a significant increase of FA intake for lambs receiving the oil-supplemented diets. Diets containing *C. ladanifer* increased ($P = 0.032$) total FA intake when compared to other diets. Despite the great difference in GSE and *C. ladanifer* dietary inclusions (25 vs 250 g/kg of DM), the enrichment of CT into diets was similar. The enrichments in grape seed CT, computed by the difference of CT concentration in grape seed diets and control diets (i.e., GS minus C and GSO minus CO), were 13.9 and 12.6 g/kg of DM for GS and GSO diets, respectively. The enrichments in *C. ladanifer* CT, computed by the difference of CT concentration in *C. ladanifer* diets and control diets (i.e., CL minus C and CLO minus CO), were 12.5 g/kg for both CL and CLO diets.

Growth Performance and Carcass Composition. Treatment did not influence ($P > 0.05$) average daily weight gain (279 g/d),

Table 1. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on Dry Matter and Fatty Acid Intake (Grams per Day) of Lambs

	control		GSE		*C. ladanifer*			P^g		
	0%[a]	6%[b]	0%[c]	6%[d]	0%[e]	6%[f]	SEM	CT	O	CT × O
dry matter intake	1704	1642	1701	1659	1467	1524	89.3	0.143	0.833	0.787
fatty acid intake										
16:0	5.23	9.39	5.28	9.83	6.01	10.1	0.380	0.211	<0.001	0.814
18:0	0.53	3.30	0.61	3.39	0.95	3.62	0.107	0.032	<0.001	0.861
18:1 *cis*-9	5.24	22.9	4.70	22.9	8.11	24.3	0.740	0.033	<0.001	0.424
18:2*n*-6	9.68	37.1	9.91	38.1	16.8	42.9	1.319	0.005	<0.001	0.738
18:3*n*-3	3.61	35.8	4.20	36.4	3.89	38.5	1.114	0.437	<0.001	0.489
total FA	24.5	108.8	24.9	111.1	36.6	120.5	3.64	0.032	<0.001	0.948

[a] Diet C, basal diet composed of 900 g of dehydrated lucerne/kg of DM and 100 g of wheat bran/kg of DM. [b] Diet CO, basal diet with 60 g of oil blend (sunflower and linseed oils, 1:2 v/v)/kg of DM. [c] Diet GS, basal diet with 25 g of GSE/kg of DM. [d] Diet GSO, basal diet with 25 g of GSE/kg of DM and 60 g of oil blend (sunflower and linseed oils, 1:2 v/v)/kg of DM. [e] Diet CL, basal diet with 250 g of *C. ladanifer*/kg of DM. [f] Diet CLO, basal diet with 250 g of *C. ladanifer*/kg of DM and 60 g of oil blend (sunflower and linseed oils, 1:2 v/v)/kg of DM. [g] CT, condensed tannin sources inclusion in diets; O, oil supplementation.

Table 2. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on Growth and Carcass Composition of Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
initial live wt (kg)	24.6	24.9	24.4	24.3	24.3	26.4				
av daily gain (g)	290	308	245	286	257	286	19.7	0.215	0.083	0.835
gain/feed intake ratio	0.17	0.19	0.14	0.17	0.17	0.19	0.012	0.192	0.106	0.785
live slaughter wt (kg)	36.5	37.5	34.4	36.0	34.8	38.1	1.60	0.523	0.145	0.773
hot carcass wt (kg)	15.5	16.6	14.5	15.5	15.6	17.8	0.82	0.127	0.044	0.739
dressing percentage (%)[b]	41.1	43.1	40.2	41.7	42.9	47.0	1.08	0.003	0.009	0.470
muscle (%)[c]	61.6	67.9	59.0	66.7	59.1	53.9	1.39	0.003	0.352	0.050
bone (%)[c]	19.3	17.8	19.7	18.5	19.2	22.4	1.62	0.359	0.890	0.276
muscle/bone ratio[c]	3.25	3.54	3.03	3.35	3.11	2.75	0.219	0.134	0.642	0.227
subcutaneous fat (%)[c]	9.20	8.60	9.28	9.83	10.0	12.5	0.808	0.020	0.235	0.183
intermuscular fat (%)[c]	8.64	10.2	10.2	9.60	10.1	9.73	0.678	0.697	0.732	0.256
KKCF (%)[d]	1.61	2.12	1.63	2.32	2.17	2.99	0.237	0.013	0.002	0.799

[a] See remarks in **Table 1**. [b] Dressing percentage (hot carcass weight × 100/live slaughter weight). [c] Average of chump and shoulder. [d] KKCF, kidney and knob channel fat.

gain/feed intake ratio (0.17), and live slaughter weight (36.2 kg) (**Table 2**). Oil supplementation increased ($P < 0.05$) hot carcass weight (15.2 vs 16.6 kg), dressing percentage (41.4 vs 43.9%), and accumulation of KKCF in carcass (1.80 vs 2.48%). Dressing percentage was higher in lambs fed *C. ladanifer* diets ($P = 0.003$) than in lambs fed the two other diets, which did not differ between each other (44.9 vs 41.5%). When compared to other diets, feeding *C. ladanifer* resulted in a higher ($P = 0.020$) subcutaneous fat percentage (11.3 vs 9.24%) and lower ($P = 0.003$) muscle percentage (56.5 vs 60.9%) in chump and shoulder cuts. KKCF percentage also increased significantly with the inclusion of *C. ladanifer* in the diet ($P = 0.013$) when compared to the other diets (2.58 vs 1.92%).

Abomasal Digesta Fatty Acids. Oil supplementation increased ($P < 0.001$) abomasal FA concentration from 33.4 to 119.2 mg/g of DM (**Table 3**). Lambs fed *C. ladanifer* diets had a higher ($P < 0.001$) abomasal FA concentration than lambs fed control or grape seed diets (89.9 vs 69.5 mg/g of DM).

Individual FA concentration (mg/g of DM) of abomasal digesta was affected by oil supplementation and by the inclusion of CT sources in diets, mainly *C. ladanifer* (**Table 3**). Oil supplementation increased the concentrations of 15:0, 16:0, 17:0, and *iso*-16:0. The 16:0 also increased with *C. ladanifer* diets ($P < 0.001$). The 15:0 was higher ($P < 0.001$) in lambs fed control diets than in lambs fed *C. ladanifer* diets and was intermediate in grape seed diets. There was an interaction between oil and CT sources for *iso*-15:0 ($P = 0.045$), *anteiso*-15:0 ($P = 0.015$), and *iso*-17:0 ($P = 0.036$). Grape seed extract depressed *iso*-15:0, *anteiso*-15:0, and *iso*-17:0, but these responses were neutralized when oil was added. Oil supplementation did not affect the proportion of these FA in lambs fed *C. ladanifer*, and the depressive effect of *C. ladanifer* was present only for *iso*-15:0, which was much lower in lambs fed the CL diet than in lambs fed the C diet. Oil supplementation of control diet decreased the concentration of *iso*-15:0, but did not affect *anteiso*-15:0 and *iso*-17:0.

Total C18 FA increased ($P < 0.001$) from 22.8 to 102 mg/g of DM with oil supplementation (**Table 3**). Feeding *C. ladanifer* diets also resulted in a higher content of total C18 FA ($P = 0.002$) when compared to lambs fed control and grape seed diets (72.4 vs 56.4 mg/g of DM). Concentrations of all C18 FA (expressed in mg/g of DM) increased ($P < 0.01$) in abomasal digesta with oil supplementation, with the exception of three CLA isomers (18:2 *trans*-7,*trans*-9, 18:2 *trans*-8,*cis*-10, and 18:2 *trans*-7,*cis*-9), which remained unchanged with oil (data not shown). For selected C18 FA displayed in **Table 3** no significant interactions between oil and CT sources were found ($P > 0.05$). However, *C. ladanifer* diets increased the concentrations of 18:1 *trans*-11, 18:1 *cis*-9, and 18:2*n*-6, whereas grape seed diets had no effect.

The detailed profile of C18 FA (g/100 g of total C18 FA) in abomasal digesta is presented in **Table 4**. Stearic acid (18:0) was the main C18 FA in abomasal digesta for all diets. In lambs fed diets with no oil, 14.4% of total C18 FA were BI, and oil supplementation increased this proportion to 25.5% in lambs fed control and grape seed diets and to 35.9% in lambs fed the *C. ladanifer* diet ($P = 0.031$). For all diets, the major BI was 18:1 *trans*-11, which represented an average of 36.2% total BI.

Table 3. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on Total Fatty Acid Concentration (Milligrams per Gram of Dry Matter) of Abomasal Digesta from Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
total fatty acids	29.8	108.2	26.0	113.8	44.2	135.6	5.31	<0.001	<0.001	0.460
16:0	4.54	8.76	4.41	9.44	6.10	10.8	0.400	<0.001	<0.001	0.611
odd- and branched-chain fatty acids										
15:0 *iso*	0.26 c	0.20 ab	0.20 ab	0.23 bc	0.15 a	0.17 a	0.020	0.008	0.704	0.045
15:0 *anteiso*	0.39 b	0.42 b	0.28 a	0.40 b	0.40 b	0.40 b	0.020	0.009	0.007	0.015
15:0	0.37	0.46	0.29	0.42	0.24	0.33	0.041	0.015	0.005	0.886
16:0 *iso*	0.13	0.14	0.10	0.17	0.09	0.11	0.018	0.078	0.020	0.245
17:0 *iso*[b]	0.10 b	0.09 ab	0.07 a	0.10 b	0.09 ab	0.09 ab	0.041	0.781	0.224	0.036
17:0 *anteiso*	0.07	0.08	0.06	0.07	0.07	0.08	0.012	0.524	0.500	0.999
17:0	0.24	0.31	0.19	0.30	0.21	0.28	0.021	0.260	<0.001	0.501
C18 fatty acids										
18:0	11.4	47.6	8.37	48.2	17.3	41.1	4.080	0.953	<0.001	0.140
18:1 *trans*-11[b]	1.02	6.69	0.91	7.59	1.30	13.5	0.002	0.024	<0.001	0.448
18:1 *cis*-9	1.83	7.02	1.83	7.04	2.57	8.53	0.493	0.049	<0.001	0.683
18:2*n*-6	2.00	6.12	2.26	6.14	3.19	9.51	0.796	0.013	<0.001	0.259
18:2 *cis*-9,*trans*-11	0.03	0.61	0.02	0.46	0.07	0.40	0.060	0.346	<0.001	0.136
18:3*n*-3	0.80	4.57	0.90	4.68	0.90	7.67	0.832	0.121	<0.001	0.138
total	19.4	92.5	16.5	97.2	29.5	115.3	4.48	0.002	<0.001	0.372
others[c]	4.37	6.20	3.96	6.37	7.54	9.50	0.515	<0.001	<0.001	0.835

[a] See remarks in **Table 1**. [b] Variables submitted to Box−Cox transformation; means presented are back-transformed values, although SEM is expressed in transformed scale. [c] The sum of the remaining area (others) includes unidentified peaks.

Independently from the CT inclusion, oil supplementation increased the proportion of most of the C18 FA and decreased only six C18 FA (18:1 *cis*-9, 18:1 *cis*-11, 18:2*n*-6, 18:2 *trans*-8, *trans*-10, 18:2 *trans*-7,*trans*-9, and 18:2 *trans*-8,*cis*-10). Condensed tannin source per se had a minor effect on C18 FA profile, affecting only four FA (18:1 *trans*-6−8, 18:1 *trans*-12, 18:1 *cis*-12, and 18:2 *trans*-11,*trans*-13), although numerous interactions with oil supplementation were observed (12 FA). Adding oil to control and grape seed diets did not affect the proportions of 18:0 and 18:1 *trans*-11. However, when oil was added to the *C. ladanifer* diet, 18:0 decreased 20.4% ($P = 0.016$) and 18:1 *trans*-11 increased 12.5% ($P = 0.018$). In contrast, oil supplementation increased 18:1 *cis*-16, 18:2 *cis*-9,*trans*-11, and 18:3 *cis*-9,*trans*-11, *cis*-15 and the unresolved 18:1*cis*-14 plus 18:1 *trans*-16 in lambs fed control and grape seed diets, but did not affect these FA when added to the *C. ladanifer* diet.

Intramuscular Fatty Acids. In PL, lambs fed *C. ladanifer* diets had a higher ($P = 0.006$) FA concentration (5.27 mg/g of fresh muscle; **Table 5**) than lambs fed control and grape seed diets (4.52 mg/g of fresh muscle). Fatty acid concentration in NL fraction (**Table 7**) was higher ($P = 0.048$) in lambs fed CLO (25.6 mg/g of fresh muscle) than in lambs fed other diets (15.8 mg/g of fresh muscle). The general FA profile (g/100 g of total FA) of PL and NL are presented in **Tables 5** and **7**, respectively, whereas detailed C18 FA profile (mg/g of total FA) of PL and NL are presented in **Tables 6** and **8**, respectively.

Polar Lipids. In lambs fed diets with no oil, the major FA in PL was 18:1 *cis*-9 followed by 18:2*n*-6 and 16:0. However, in lambs fed oil-supplemented diets, the major FA in PL was 18:2*n*-6, followed by 18:1 *cis*-9 and 16:0. Oil supplementation decreased 16:0, 17:0, 14:1 *cis*-9, 16:1 *cis*-9, 17:1 *cis*-9, 20:1 *cis*-11, 20:3*n*-9, 20:3*n*-6, 20:4*n*-6, 22:4*n*-6, branched-chain FA (BCFA), total monounsaturated FA, and total *n*-6 long-chain PUFA (≥C20; LC-PUFA), whereas it increased 18:2*n*-6 and 18:3*n*-3, 20:3*n*-3, total PUFA, and *n*-3 PUFA. Inclusion of *C. ladanifer* in diets increased 20:0, but decreased total SFA from 21.5 to 20.4% total FA. Significant interactions between oil supplementation and inclusion of CT sources in diets were found for minor FA and for *n*-6 PUFA sum ($P = 0.036$). Feeding the CL diet resulted in a higher accumulation of *n*-6 PUFA in PL fraction when compared to C diets. However, lambs fed GS diet had an intermediate value and differed from neither CL- nor C-fed lambs. Oil supplementation increased *n*-6 PUFA in lambs fed control and grape seed diets, but had no effect in lambs fed *C. ladanifer* diet.

The total of C18 FA (**Table 5**) increased with oil supplementation ($P < 0.001$). Grape seed diets resulted in lower total C18 FA than control diets, whereas *C. ladanifer* diets presented an intermediate value ($P = 0.021$). Total BI increased with oil supplementation ($P < 0.001$), ranging from 5.7% total C18 FA in lambs fed diets with no oil to 13.6% in oil-supplemented lambs. Lambs fed *C. ladanifer* diets also showed higher ($P = 0.003$) BI content in PL than lambs fed other diets (11.4 vs 8.76% of total C18). For all diets, 18:2 *cis*-9,*trans*-11 was the predominant CLA isomer, ranging from 86% total CLA in lambs fed diets with no oil to 74% in oil-supplemented lambs.

Oil supplementation increased the proportion of most C18 FA, whereas it decreased only two (18:1 *cis*-9 and 18:1 *cis*-11). Condensed tannin source per se modified only six FA (18:1 *trans*-12, 18:1 *cis*-11, 18:1 *cis*-13, 18:2 *trans*-9,*cis*-12 and 18:2 *cis*-9,*cis*-15 and unresolved 18:2 *cis*-9,*trans*-13 plus 18:2 *trans*-8,*cis*-12). Some interactions between oil supplementation and CT sources were observed for C18 FA. The proportions of 18:0, 18:1 *cis*-15 and unresolved 18:2 *trans*-8,*cis*-13 plus 18:2 *cis*-9,*trans*-12 were not affected when oil was added to *C. ladanifer* diet, although an increase was observed when oil was added to control and grape seed diets. Oil supplementation resulted in a greater increase of 18:2 *trans*-12,*trans*-14 in lambs fed *C. ladanifer* than in lambs fed other diets. 18:2 *cis*-12,*cis*-15 was detected only in lambs fed oil.

Neutral Lipids. The major FA in NL were 18:1 *cis*-9, 16:0, and 18:0. Oil supplementation decreased 14:0, 16:0, 17:0, 20:0,

Table 4. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on C18 Fatty Acid Profile (Grams per 100 g of Total C18 Fatty Acids) of Abomasal Digesta from Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
18:0	58.3 b	50.6 b	49.3 b	49.4 b	57.6 b	36.7 a	3.38	0.105	0.002	0.016
18:1 isomers										
*t*6−8	0.64	0.77	0.69	0.81	0.77	1.05	0.063	0.009	0.002	0.329
*t*9[b]	0.47	0.57	0.52	0.60	0.54	0.69	0.692	0.083	0.003	0.763
*t*10[b]	0.93	0.95	1.19	0.87	1.19	0.96	0.181	0.796	0.285	0.632
*t*11	5.43 a	8.06 a	5.96 a	8.44 a	4.88 a	17.4 b	1.866	0.051	<0.001	0.018
*t*12	0.94	1.86	1.08	2.05	1.52	2.16	0.126	0.007	<0.001	0.397
*t*13/14	2.05	4.48	2.44	4.74	2.52	4.23	0.467	0.778	<0.001	0.717
*t*15	0.86 a	2.17 c	0.86 a	2.30 c	1.17 a	1.72 b	0.151	0.671	<0.001	0.014
*c*9	9.56	7.71	11.4	7.31	9.01	7.41	0.671	0.237	<0.001	0.141
*c*11	2.00 c	0.74 a	2.35 d	0.78 a	1.27 b	0.82 a	0.107	<0.001	<0.001	<0.001
*c*12	0.55	1.39	0.65	1.81	0.95	2.44	0.248	0.024	<0.001	0.427
*c*13	0.07	0.13	0.10	0.14	0.09	0.18	0.021	0.289	<0.001	0.496
*c*14 + *t*16	1.05 a	2.03 c	1.09 a	2.02 c	1.32 b	1.42 b	0.076	0.038	<0.001	<0.001
*c*15[b]	0.16	0.60	0.19	0.82	0.16	0.53	0.183	0.139	<0.001	0.777
*c*16	0.18 a	0.34 d	0.22 ab	0.38 d	0.23 bc	0.27 c	0.018	0.041	<0.001	0.002
total	25.0 a	37.9 bc	28.8 abc	33.1 c	25.7 ab	42.5 d	2.123	0.044	<0.001	0.018
18:2 nonconjugated isomers										
*t*11*t*15	0.21	0.58	0.28	0.69	0.08	0.72	0.073	0.402	<0.001	0.151
*c*9*t*13 + *t*8*c*12[c]	0.44	0.35	0.64	0.41	0.69	0.44	0.142	0.472	0.107	0.842
*t*8*c*13 + *c*9*t*12[d]	0.09	0.09	0.13	0.09	0.10	0.07	0.012	0.088	0.072	0.415
*t*9*c*12	0.13 ab	0.18 c	0.16 bc	0.22 d	0.12 a	0.26 e	0.012	0.005	<0.001	0.001
*t*11*c*15	0.34 a	1.56 b	0.36 a	1.93 d	0.29 a	1.73 c	0.042	<0.001	<0.001	0.001
*c*9*c*12	10.6	6.75	14.1	6.43	11.3	8.28	1.281	0.443	<0.001	0.172
*c*9*c*15[b]	0.05	0.20	0.07	0.33	0.06	0.24	0.217	0.116	<0.001	0.806
*c*12*c*15[b]	0.07	0.25	0.08	0.47	0.05	0.32	0.329	0.067	<0.001	0.361
total	11.9	9.98	15.9	10.6	12.7	12.3	1.358	0.245	0.033	0.207
18:2 conjugated isomers										
*t*12*t*14[b]	0.04	0.12	0.04	0.11	0.04	0.16	0.542	0.533	<0.001	0.898
*t*11*t*13[b]	0.03	0.19	0.03	0.17	0.06	0.18	0.171	0.034	<0.001	0.053
*t*10*t*12	0.006	0.12	0.004	0.10	0.02	0.11	0.012	0.518	<0.001	0.648
*t*9*t*11	0.05	0.12	0.05	0.10	0.09	0.12	0.013	0.088	<0.001	0.202
*t*8*t*10	0.04	0.02	0.04	0.02	0.04	0.02	0.004	0.867	<0.001	0.926
*t*7*t*9	0.02	0.004	0.02	0.005	0.02	0.004	0.097	0.862	<0.001	0.642
c/*t*12,14[b,e]	0.02 ab	0.04 b	0.01 a	0.05 b	0.04 b	0.03 b	0.903	0.289	0.005	0.017
c/*t*11,13[f]	0.05	0.33	0.02	0.36	0.02	0.28	0.048	0.666	<0.001	0.717
*t*10*c*12	0.04	0.09	0.04	0.06	0.05	0.09	0.019	0.541	0.018	0.750
*c*9*t*11[b]	0.12 a	0.65 d	0.12 a	0.47 cd	0.22 ab	0.30 bc	0.212	0.787	<0.001	0.034
*t*8*c*10[b]	0.02	0.004	0.02	0.006	0.02	0.004	0.130	0.360	<0.001	0.930
*t*7*c*9	0 a	0.002 b	0 a	0 a	0.005 c	0.002 b	0.0006	<0.001	0.435	0.002
total	0.45	1.71	0.72	1.46	0.68	1.59	0.123	0.275	<0.001	0.359
total 18:2	12.4	11.7	16.3	12.1	13.4	13.9	1.388	0.290	0.217	0.227
18:3 isomers										
*c*9*c*12*c*15	4.20	5.07	5.55	4.91	3.16	6.69	0.854	0.786	0.085	0.066
*c*9*t*11*c*15	0.08 a	0.74 c	0.06 a	0.47 b	0.16 a	0.23a	0.077	0.025	<0.001	0.003
total	4.28	5.81	5.61	5.38	3.31	6.91	0.818	0.841	0.022	0.084
total BI[g]	13.3 a	24.6 b	14.8 a	26.4 b	15.1 a	35.9 c	1.89	0.005	<0.001	0.031

[a] See remarks in **Table 1**. [b] Variables submitted to Box−Cox transformation; means presented are back-transformed values, although SEM is expressed in transformed scale. [c] Peak includes 18:2 *c*9*t*13, 18:2 *t*8*c*12, and 17-cyclo (methyl 11 cyclohexylundecanoate). [d] Peak includes 18:2 *t*8*c*13 and 18:2 *c*9*t*12. [e] Peak includes 18:2 *c*12*t*14 and 18:2 *t*12*c*14. [f] Peak includes 18:2 *c*11*t*13 and 18:2 *t*11*c*13. [g] Total C18 biohydrogenation intermediates, total C18 fatty acids minus 18:0, 18:1 *cis*-9, 18:1 *cis*-11, 18:2*n*-6, and 18:3*n*-3.

iso-15:0, *iso*-16:0, *iso*-17:0, *anteiso*-17:0, 14:1 *cis*-9, 16:1 *cis*-9, 17:1 *cis*-9, 20:4*n*-6, and total SFA, but increased 18:2*n*-6 and 18:3*n*-3, 20:3*n*-9, 20:3*n*-3, 20:5*n*-3, total PUFA, *n*-6 PUFA, and *n*-3 PUFA. Lambs fed *C. ladanifer* diets had the lowest concentrations of *iso*-15:0 and *iso*-16:0, but the highest concentrations of 16:1 *cis*-9 and 20:0. Inclusion of CT sources in diets decreased ($P = 0.002$) the *iso*-17:0 proportion.

Total C18 FA (**Table 7**) increased with oil supplementation in all diets. For diets with no oil, CT source inclusion decreased total C18 FA when compared to control ($P = 0.036$). Total BI increased with oil supplementation ($P < 0.001$), representing 10% of total C18 FA in lambs fed diets with no oil and 21.6% in oil-supplemented lambs.

Most C18 FA increased with oil supplementation, whereas only 18:1 *cis*-9 decreased. Condensed tannin source per se had

Table 5. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on Total Fatty Acid Concentration (Milligrams per Gram of Fresh Muscle) and Composition (Grams per 100 g of Total Fatty Acids) of Polar Lipid in Longissimus dorsi Muscle from Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
total fatty acids	4.67	4.02	4.63	4.75	5.46	5.09	0.259	0.006	0.170	0.344
12:0	0.06	0.02	0.07	0.06	0.09	0.10	0.024	0.096	0.506	0.612
14:0	0.50	0.38	0.46	0.38	0.64	0.55	0.128	0.362	0.369	0.985
15:0 *iso*	0.05	0.01	0.03	0.02	0.03	0.02	0.008	0.650	0.004	0.115
15:0 *anteiso*	0.05 b	0.02 a	0.05 b	0.04 ab	0.05 b	0.06 b	0.007	0.117	0.054	0.012
14:1 *cis*-9	0.12	0.11	0.13	0.11	0.13	0.12	0.005	0.343	0.007	0.106
15:0	0.18 b	0.17 a	0.18 b	0.13 a	0.16 b	0.16 b	0.008	0.118	0.006	0.016
16:0 *iso*[b]	0.09	0.07	0.08	0.06	0.07	0.07	0.093	0.121	<0.001	0.381
16:0	12.9	11.0	13.4	10.1	12.8	10.5	0.36	0.809	<0.001	0.170
17:0 *iso*	0.28	0.23	0.28	0.22	0.29	0.22	0.016	0.854	<0.001	0.985
17:0 *anteiso*[b]	0.13	0.08	0.12	0.07	0.12	0.30	0.030	0.380	<0.001	0.625
16:1 *cis*-9	0.69	0.26	0.62	0.28	0.67	0.35	0.042	0.403	<0.001	0.358
17:0	0.73 c	0.57 b	0.74 c	0.43 a	0.66 c	0.44 a	0.027	0.003	<0.001	0.020
17:1 *cis*-9	0.49	0.16	0.45	0.17	0.44	0.18	0.031	0.741	<0.001	0.520
total C18	56.2	60.4	54.7	59.5	55.4	60.1	0.40	0.021	<0.001	0.774
20:0	0.11	0.11	0.13	0.12	0.16	0.13	0.007	<0.001	0.033	0.493
20:1 *cis*-11	0.18	0.12	0.21	0.14	0.19	0.14	0.014	0.155	<0.001	0.869
20:2*n*-6[b]	0.12 a	0.15 bc	0.14 ab	0.14 ab	0.18 c	0.14 ab	0.280	0.079	0.956	0.013
20:3*n*-9	0.84	0.44	0.78	0.60	0.87	0.44	0.088	0.868	<0.001	0.348
22:0	0.03	0.05	0.05	0.05	0.05	0.06	0.008	0.109	0.087	0.204
20:3*n*-6[b]	0.67	0.58	0.74	0.60	0.76	0.56	0.045	0.400	<0.001	0.154
20:3*n*-3[b]	0.05	0.10	0.05	0.10	0.05	0.10	0.347	0.941	<0.001	0.836
20:4*n*-6	5.60	4.59	5.91	5.10	6.19	4.80	0.212	0.108	<0.001	0.391
20:5*n*-3[b]	1.67	2.08	1.79	2.19	1.58	2.10	0.328	0.854	0.055	0.970
22:4*n*-6[b]	0.39 c	0.22 a	0.39 c	0.30 b	0.45 d	0.24 a	0.041	0.045	<0.001	0.006
22:5*n*-3[b]	2.51	2.22	2.47	2.61	2.27	2.18	0.062	0.121	0.486	0.367
22:6*n*-3	0.59	0.54	0.59	0.64	0.54	0.56	0.048	0.379	0.827	0.642
others[c]	15.0	15.4	15.5	16.1	15.2	15.9	0.399	0.338	0.095	0.963
SFA	21.2	22.0	21.0	21.7	20.8	20.1	0.38	0.011	0.365	0.114
MUFA	30.0	20.0	27.7	20.2	26.8	22.9	1.29	0.708	<0.001	0.080
PUFA	30.5	40.9	31.8	41.5	33.6	40.2	1.42	0.679	<0.001	0.372
n-6 PUFA[b]	21.6 a	28.5 d	22.9 ab	27.9 cd	25.1 bc	27.0 cd	0.039	0.446	<0.001	0.036
n-6 LC-PUFA	6.77	5.55	7.18	6.14	7.60	5.74	0.247	0.084	<0.001	0.238
n-3 PUFA	7.03	10.0	7.04	10.8	6.30	10.3	0.537	0.486	<0.001	0.645
n-3 LC-PUFA[b]	4.79	4.89	4.86	5.35	4.38	4.93	0.090	0.539	0.289	0.852

[a] See remarks in **Table 1**. [b] Variables submitted to Box−Cox transformation; means presented are back-transformed values, although SEM is expressed in transformed scale. [c] The sum of the remaining area (others) includes about 11.6% of dimethylacetals and 3.87% unidentified peaks.

minor effects on C18 FA profile in NL fraction, affecting only three FA (18:1 *cis*-9, 18:2 *trans*-11,*trans*-13, and unresolved 18:2 *cis*-9,*trans*-13 plus 18:2 *trans*-8,*cis*-12). However, numerous interactions with oil supplementation were observed (14 FA). Oil supplementation decreased 18:1 *cis*-11 and increased 18:1 *trans*-10, 18:1 *cis*-16, 18:2 *trans*-10, *cis*-12, and unresolved 18:2 *trans*-8, *cis*-13 plus 18:2 *cis*-9,*trans*-12 when added to control and grape seed diets, although it did not affect these FA when added to *C. ladanifer* diets. Oil supplementation increased 18:1 *trans*-11 in all diets, but there was a greater increase in lambs fed *C. ladanifer* diet ($P = 0.003$). Conversely, supplementation of *C. ladanifer* diet with oil resulted in a smaller increase of 18:1 *trans*-12, 18:1 *trans*-15, and 18:1 *cis*-14 plus *trans*-16 than supplementation with oil in other diets. For all diets, 18:2 *cis*-9, *trans*-11 was the predominant CLA isomer, ranging from 81% total CLA in lambs fed oil to 75% in oil-supplemented lambs. Oil supplementation resulted in an important increase ($P < 0.001$) of this CLA isomer in NL for all diets, although there was a tendency (CT × O, $P = 0.062$) for a greater increase in lambs fed CLO diet. The 18:2 *cis*-12, *cis*-15, and 18:3 *cis*-9,*trans*-11,*cis*-15 were detected only in lambs fed oil, although lambs fed GSO showed a higher proportion of 18:2 *cis*-12,*cis*-15 than lambs fed other diets with oil.

DISCUSSION

Growth Performance and Carcass Composition. Lipid supplements are the richest energy-containing feedstuffs, and thus their use in ruminant diets should theoretically increase growth performance. The effects of lipid supplementation on the growth performance of ruminants are inconsistent. Differences have been attributed to negative interactions of lipids with ruminal digestion of structural carbohydrates and to depressions in feed intake (*20*). Previous works reported reductions of feed intake in lambs fed lipid-supplemented diets coupled with no effect (*6*, *21*) or reduction (*22*) on lamb growth. In the present trial, DMI was not affected by oil supplementation, which might explain the tendency of average daily gain to increase ($P = 0.083$) and the significant enhancement in hot carcass weight. Higher fat deposition in carcass has been found in lambs fed diets supplemented with fat (*22*). However, tissue composition of dissected cuts was not affected by oil supplementation, and only the percentage of KKCF in carcass increased.

Condensed tannins might have both adverse and beneficial effects in ruminants, depending on their chemical structure and concentration in diets (*23*). Thus, the reports on the effects of

Table 6. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on C18 Fatty Acid Composition (Milligrams per Gram of Total Fatty Acids) of Polar Lipids in Longissimus dorsi Muscle from Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
18:0[b]	101 a	116 b	98 a	111 b	98 a	97 a	0.02	<0.001	<0.001	0.001
18:1 isomers										
*t*6−8[b]	1.01	1.08	0.96	1.09	1.00	1.19	0.073	0.672	0.059	0.778
*t*9	1.02	1.26	0.87	1.29	1.07	1.56	0.133	0.201	0.002	0.623
*t*10[b]	1.10	1.58	0.86	1.46	1.48	1.71	0.153	0.138	0.021	0.458
*t*11[b]	4.91	10.4	4.92	12.9	5.01	24.9	0.082	0.235	<0.001	0.283
*t*12	2.24	4.54	1.86	4.39	2.64	5.15	0.247	0.015	<0.001	0.871
*t*13/14	2.47	8.36	2.57	8.06	3.20	6.75	0.053	0.689	<0.001	0.081
*c*9	239	116	206	123	221	119	12.2	0.584	<0.001	0.274
*c*11	22.3	19.4	20.2	17.2	18.9	16.0	0.758	<0.001	<0.001	0.998
*c*12	2.53	16.3	1.82	19.1	5.80	18.9	1.471	0.156	<0.001	0.336
*c*13	0.75	0.83	0.62	0.75	0.73	0.75	0.029	0.005	0.003	0.137
*c*14 + *t*16	1.63	2.86	1.56	2.98	1.81	2.85	0.100	0.710	<0.001	0.184
*c*15[b]	0.55 ab	1.20 c	0.46 a	1.53 c	0.66 b	1.46 b	0.083	0.078	<0.001	0.025
*c*16	0.51 ab	0.62 b	0.61 b	0.45 a	0.40 a	0.53 ab	0.059	0.236	0.564	0.037
total	280	187	243	195	264	206	13.9	0.457	<0.001	0.258
18:2 nonconjugated isomers										
*c*9*t*13 + *t*8*c*12[c]	1.86	2.18	1.96	2.71	2.70	3.28	0.179	<0.001	<0.001	0.467
*t*8*c*13 + *c*9*t*12[d]	1.91 a	2.60 b	1.83 a	3.05 b	2.69 b	2.86 b	0.189	0.034	<0.001	0.036
*t*9*c*12	1.09	1.22	1.12	1.15	1.33	1.32	0.078	0.036	0.441	0.658
*t*11*c*15[b]	0.52	1.55	0.58	2.40	0.65	2.65	0.180	0.119	<0.001	0.569
*c*9*c*12[b]	148	230	158	218	174	212	0.051	0.644	<0.001	0.059
*c*9*c*15[b]	0.77	1.03	0.88	1.16	1.01	1.30	0.076	0.010	<0.001	0.914
*c*12*c*15[b]	0	1.65	0	2.77	0	1.89	0.150	0.214	<0.001	0.214
total[b]	154	240	164	231	182	226	0.05	0.470	<0.001	0.058
18:2 conjugated isomers										
*t*12*t*14	0.03 a	0.13 b	0.02 a	0.17 b	0.03 a	0.25 c	0.020	0.015	<0.001	0.024
*t*11*t*13[b]	0.07	0.29	0.05	0.32	0.05	0.23	0.246	0.523	<0.001	0.554
*t*10*t*12	0.01	0.02	0.01	0.02	0.01	0.02	0.003	0.687	0.036	0.951
*t*9*t*11	0.11	0.16	0.10	0.17	0.11	0.21	0.018	0.314	<0.001	0.368
*t*8*t*10	0.03	0.03	0.02	0.02	0.02	0.02	0.004	0.212	0.921	0.632
*t*7*t*9	0.04 b	0.02 a	0.03 ab	0.02 a	0.03 ab	0.03 b	0.004	0.276	0.405	0.049
c/*t*12,14[b,e]	0.03	0.05	0.02	0.08	0.02	0.05	0.464	0.941	<0.001	0.299
c/*t*11,13[f]	0.18	0.76	0.15	1.23	0.16	1.02	0.105	0.142	<0.001	0.075
*t*10*c*12	0.02	0.04	0.01	0.05	0.02	0.08	0.010	0.218	<0.001	0.336
*c*9*t*11	3.86	5.14	3.59	5.87	3.71	7.94	0.799	0.228	<0.001	0.192
*t*8*c*10	0.04	0.06	0.05	0.06	0.05	0.11	0.013	0.058	0.008	0.112
*t*7*c*9	0.12	0.09	0.10	0.12	0.14	0.15	0.021	0.200	0.840	0.642
total	4.55	6.81	4.15	8.14	4.36	10.2	0.948	0.249	<0.001	0.195
total 18:2	159	249	168	240	188	236	8.4	0.529	<0.001	0.061
18:3 isomers										
*c*9*c*12*c*15	22.1	50.7	21.5	53.5	18.7	53.1	2.23	0.761	<0.001	0.434
*c*9*t*11*c*15	0	1.73	0	1.67	0	1.43	0.162	0.612	<0.001	0.612
total[b]	21.8	52.3	21.0	55.7	18.1	54.7	0.09	0.558	<0.001	0.408
total BI[g]	2.97	7.08	2.78	7.76	3.73	9.64	0.462	0.003	<0.001	0.173

[a] See remarks in **Table 1**. [b] Variables submitted to Box−Cox transformation; means presented are back-transformed values, although SEM is expressed in transformed scale. [c] Peak includes 18:2 *c*9*t*13, 18:2 *t*8*c*12, and 17-cyclo (methyl 11 cyclohexylundecanoate). [d] Peak includes 18:2 *t*8*c*13 and 18:2 *c*9*t*12. [e] Peak includes 18:2 *c*12*t*14 and 18:2 *t*12*c*14. [f] Peak includes 18:2 *c*11*t*13 and 18:2 *t*11*c*13. [g] Total C18 biohydrogenation intermediates, total C18 fatty acids minus 18:0, 18:1 *cis*-9, 18:1 *cis*-11, 18:2*n*-6, and 18:3*n*-3.

dietary CT on growth performance of lambs are inconsistent (*10*, *24*, *25*). Our results show that the inclusion of 25 g/kg of DM of grape seed extract or 250 g/kg of DM of *C. ladanifer* in diets did not affect growth performance. This is the first report on the effects of dietary inclusion of *C. ladanifer* on lamb growth performance. As far as we know, the effect of GSE on lamb growth seems to be restricted to one trial (*26*). These authors found that 33 g/day of GSE, supplied as liquid supplement, reduced weight gain but not carcass gain when the basal diet was white clover and had no effect when the basal diet was perennial ryegrass. As the average daily intake of grape seed CT in our trial was approximately 24 g, no depression of growth performance was expected.

C. ladanifer is a very abundant shrub in marginal fields of Mediterranean countries, but practically it is not used in direct grazing. This fact is probably due to its high content in anti-nutritional compounds, arising from the secondary metabolism of plants, such as CT and essential oils, which are very abundant

Table 7. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on Total Fatty Acid Concentration (Milligrams per Gram of Fresh Muscle) and Composition (Grams per 100 g of Total Fatty Acids) of Neutral Lipid in Longissimus dorsi Muscle from Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
total fatty acids	15.8 a	16.2 a	15.5 a	17.0 a	14.9 a	25.6 b	1.80	0.048	0.009	0.016
12:0[b]	0.33	0.39	0.48	0.31	0.34	0.30	0.098	0.398	0.235	0.085
14:0	3.91	3.69	4.29	3.54	4.63	3.47	0.198	0.456	<0.001	0.078
15:0 *iso*	0.12	0.10	0.11	0.10	0.09	0.08	0.005	<0.001	<0.001	0.724
15:0 *anteiso*	0.17	0.19	0.19	0.16	0.16	0.14	0.018	0.292	0.527	0.359
14:1 *cis*-9	0.10	0.09	0.11	0.08	0.13	0.09	0.007	0.319	<0.001	0.254
15:0	0.43	0.48	0.47	0.41	0.44	0.38	0.038	0.586	0.424	0.245
16:0 *iso*	0.16	0.16	0.17	0.14	0.14	0.11	0.008	<0.001	0.002	0.146
16:0[b]	21.2	20.6	25.9	20.5	27.0	22.0	0.029	0.059	<0.001	0.843
17:0 *iso*[b]	0.34	0.30	0.31	0.28	0.31	0.25	0.001	0.002	<0.001	0.680
17:0 *anteiso*	0.54	0.42	0.52	0.37	0.50	0.38	0.030	0.383	<0.001	0.838
16:1 *cis*-9	1.15	0.86	1.21	0.85	1.39	0.93	0.040	0.001	<0.001	0.109
17:0	1.07	0.90	1.05	0.86	1.00	0.83	0.049	0.328	<0.001	0.967
17:1 *cis*-9	0.43	0.32	0.43	0.29	0.45	0.29	0.017	0.527	<0.001	0.472
total C18	63.7 b	68.8 c	61.3 a	68.7 c	60.4 a	68.0 c	0.50	0.002	<0.001	0.036
20:0	0.14	0.12	0.17	0.14	0.28	0.18	0.023	<0.001	0.012	0.159
20:1 *cis*-11	0.12 bc	0.09 a	0.12 bc	0.11 ab	0.12 bc	0.13 c	0.006	0.018	0.275	0.016
20:2*n*-6[b]	0.05	0.05	0.05	0.04	0.05	0.05	0.204	0.321	0.078	0.246
20:3*n*-9[b]	0.05 a	0.21 c	0.05 a	0.23 c	0.05 a	0.10 b	0.084	<0.001	<0.001	<0.001
22:0	0.01	0.01	0.03	0.03	0.02	0.02	0.010	0.239	0.888	0.930
20:3*n*-6	0.05	0.03	0.06	0.04	0.04	0.05	0.011	0.644	0.425	0.520
20:3*n*-3	0.05	0.06	0.04	0.06	0.05	0.06	0.005	0.445	0.001	0.691
20:4*n*-6	0.18	0.16	0.19	0.16	0.17	0.15	0.014	0.405	0.039	0.812
20:5*n*-3	0.06	0.10	0.07	0.08	0.05	0.09	0.014	0.732	0.023	0.650
22:4*n*-6	0.03	0.07	0.01	0.01	0.02	0.01	0.031	0.349	0.663	0.649
22:5*n*-3	0.19	0.19	0.22	0.20	0.15	0.20	0.026	0.477	0.678	0.464
22:6*n*-3	0.06	0.07	0.06	0.07	0.05	0.06	0.015	0.728	0.416	0.969
others[c]	1.49	2.06	2.54	2.54	2.08	2.16	0.330	0.088	0.436	0.655
SFA	48.8	43.0	49.0	43.3	49.8	42.5	1.08	0.961	<0.001	0.674
MUFA	42.7	42.4	41.3	41.7	41.0	43.6	0.66	0.295	0.096	0.257
PUFA	6.35	12.5	6.69	12.4	6.65	11.5	0.450	0.589	<0.001	0.414
n-6 PUFA	2.75	4.52	2.93	4.11	3.13	3.78	0.236	0.743	<0.001	0.071
n-6 LC-PUFA[b]	0.30	0.28	0.29	0.24	0.26	0.24	0.338	0.281	0.137	0.338
n-3 PUFA	1.47	3.40	1.51	3.11	1.28	2.94	0.242	0.406	<0.001	0.773
n-3 LC-PUFA[b]	0.36	0.42	0.18	0.40	0.39	0.36	0.077	0.524	0.138	0.682

[a] See remarks in **Table 1**. [b] Variables submitted to Box−Cox transformation; means presented are back-transformed values, although SEM is expressed in transformed scale. [c] The sum of the remaining area (others) includes unidentified peaks.

in a characteristic gum resin exuded by the plant, also known as labdanum (*11*, *27*). Thus, we expected that the high incorporation of *C. ladanifer* in diets (250 g/kg of DM) would result in greater depression in lamb growth performance. However, our results show that *C. ladanifer* may be successfully incorporated in lambs' diets without compromising animal performance, reinforcing the interest of its use in small ruminant nutrition. *C. ladanifer* affected the composition of the weight gain, increasing fat deposition probably due to the highest fat content in these diets.

Ruminal Biohydrogenation. We did not obtain quantitative information on rumen outflow of C18 FA; thus, definite conclusions on rumen biohydrogenation balance are not possible. Nevertheless, as lambs had similar feed intake and lipid supplements generally do not affect rumen fluid and particle passage ratio (*28*), large differences in digesta flow to abomasum are not expected. However, some caution is still needed because there is no information on the effects of GSE and *C. ladanifer* on rumen outflow. The profile of C18 FA in abomasal digesta provides an insight on ruminal biohydrogenation pattern (i.e., relative distribution of substrates and products), allowing an evaluation of the effects of oil supplementation and CT on modulation BH process. Modification of the BH pattern would reflect the metabolic pathways in use and microbial equilibriums in the rumen.

Dietary supplementation with oil rich in PUFA, by increasing the substrate availability for BH, is the most effective approach to increase BI outflow of rumen (*20*) and their transfer to milk and deposition in tissues. As expected, oil supplementation increased the concentration (mg/g of DM) of substrates (18:3*n*-3, 18:2*n*-6, and 18:1 *cis*-9), most BI, and the main end product (18:0). Dramatic changes in BH pattern due to oil supplementation, with strong accumulation of 18:1 *trans*-11 and low concentrations of 18:0, have been reported in vitro (*29*). However, these changes are usually much less expressive in vivo, except when fish oil is used (*30*). The changes in BH pattern, with increasing dietary PUFA concentration, have been explained by a putative toxic effect of PUFA on rumen bacteria, particularly on those catalyzing the last reductive step (*5*). However, the present data of BH pattern show that, although oil supplementation increased most BI, no effects of oil supplementation were observed for 18:0 and 18:1 *trans*-11, except in lambs fed CLO diet. This is due to a large variability of those FA proportions within each diet. Nevertheless, despite the type (rich in 18:3*n*-3) and amount (60 g/kg of DM) of oil used, no dramatic changes in 18:0 were observed,

Table 8. Effect of Dietary Condensed Tannin Sources (Control, Grape Seed Extract (GSE), and *C. ladanifer*) and Oil Supplementation (0 and 6% of Added Oil in DM) on C18 Fatty Acid Composition (Milligrams per Gram of Total Fatty Acids) of Neutral Lipids in Longissimus dorsi Muscle from Lambs

	control		GSE		*C. ladanifer*			P^a		
	0%[a]	6%[a]	0%[a]	6%[a]	0%[a]	6%[a]	SEM	CT	O	CT × O
18:0	176	166	164	172	159	152	6.48	0.063	0.549	0.352
18:1 isomers										
*t*6−8[b]	2.09	3.79	2.06	3.85	2.16	3.97	0.057	0.999	<0.001	0.715
*t*9	2.71	4.19	2.63	4.32	2.70	4.07	0.087	0.566	<0.001	0.177
*t*10[b]	3.18 a	6.96 c	3.07 a	5.27 bc	4.32 b	5.01 bc	0.045	0.308	<0.001	0.042
*t*11	18.0 a	39.7 b	20.1 a	43.5 b	18.6 a	69.8 c	4.30	0.004	<0.001	0.003
*t*12	3.31 a	8.62 c	2.96 a	8.70 c	3.76 a	6.61 b	0.434	0.192	<0.001	0.006
*t*13/14	5.63 b	16.7 d	4.82 a	17.9 e	5.59 b	12.2 c	0.265	<0.001	<0.001	<0.001
*t*15[b]	2.32 a	6.36 c	2.47 a	7.02 c	2.39 a	3.95 b	0.028	0.002	<0.001	0.004
*c*9	346	228	332	272	326	284	5.8	0.032	<0.001	0.264
*c*11	9.60 c	6.54 a	8.86 c	6.84 ab	7.67 b	7.24 ab	0.366	0.251	<0.001	0.005
*c*12	3.13 ab	9.72 c	2.35 a	13.2 c	3.96 b	10.2 c	0.406	0.011	<0.001	<0.001
*c*13	1.14	1.17	1.00	1.42	1.01	0.99	0.101	0.122	0.095	0.079
*c*14 + *t*16[b]	4.17 a	7.78 c	3.96 a	7.80 c	3.92 a	5.69 b	0.045	<0.001	<0.001	0.005
*c*15	1.78 a	3.50 c	1.70 a	4.44 d	1.52 a	2.95 b	0.165	<0.001	<0.001	0.001
*c*16	0.67 a	1.18 c	0.60 a	1.24 c	0.69 ab	0.87 b	0.064	0.054	<0.001	0.005
total	404 bc	404 bc	388 ab	398 ab	384 a	418 c	6.5	0.249	0.012	0.048
18:2 nonconjugated isomers										
*t*11*t*15	0.58	1.48	0.73	2.10	0.66	1.98	0.185	0.125	<0.001	0.393
*c*9*t*13 + *t*8*c*12[b,c]	4.36	7.10	4.37	7.96	4.10	6.35	0.326	0.027	<0.001	0.139
*t*8,*c*13 + *c*9*t*12[b,d]	2.34 a	4.20 c	2.39 a	4.38 c	2.99 ab	3.28 bc	0.045	0.939	<0.001	0.017
*t*9*c*12	0.61	1.10	0.61	1.31	0.64	1.15	0.065	0.252	<0.001	0.204
*t*11*c*15	2.74	8.72	2.67	10.7	2.78	8.78	0.624	0.259	<0.001	0.204
*c*9*c*12	24.4	42.0	26.4	38.6	28.7	35.3	2.12	0.843	<0.001	0.053
*c*9*c*15[b]	0.79	1.44	0.59	1.82	0.58	1.23	0.147	0.239	<0.001	0.215
*c*12*c*15[b]	0 a	1.90 b	0 a	3.09 c	0 a	1.66 b	0.126	0.049	<0.001	0.049
total	36.0 a	68.2 c	37.8 a	70.3 c	41.4 a	60.1 b	2.35	0.378	<0.001	0.010
18:2 conjugated isomers										
*t*12*t*14	0.17	0.48	0.16	0.52	0.15	0.50	0.015	0.497	<0.001	0.166
*t*11*t*13[b]	0.28	0.68	0.23	0.68	0.21	0.42	0.130	0.040	<0.001	0.355
*t*10*t*12[b]	0.03	0.08	0.03	0.07	0.04	0.06	0.094	0.645	<0.001	0.144
*t*9*t*11[b]	0.21	0.40	0.23	0.37	0.21	0.50	0.081	0.185	<0.001	0.065
*t*8*t*10	0.03	0.04	0.03	0.04	0.03	0.03	0.005	0.327	0.062	0.596
*t*7*t*9	0.05	0.05	0.05	0.04	0.05	0.06	0.005	0.450	0.375	0.136
c/*t*12,14[b,e]	0.09 a	0.34 c	0.07 a	0.42 c	0.07 a	0.19 b	0.186	0.012	<0.001	0.023
c/*t*11,13[f]	0.38	1.70	0.34	2.07	0.30	1.63	0.177	0.395	<0.001	0.435
*t*10*c*12[b]	0.02 a	0.10 c	0.02 a	0.06 bc	0.03 b	0.05b	0.857	0.397	<0.001	0.018
*c*9*t*11	7.49	13.5	8.78	13.7	7.47	18.5	1.319	0.178	<0.001	0.062
*t*8*c*10	0.23	0.28	0.20	0.32	0.16	0.33	0.044	0.958	0.004	0.378
*t*7*c*9[b]	0.36	0.70	0.43	0.76	0.44	0.84	0.057	0.149	<0.001	0.793
total[b]	9.27	18.1	10.4	18.9	8.59	22.3	0.125	0.775	<0.001	0.310
total 18:2	45.3	86.6	48.4	89.3	50.6	83.3	2.51	0.504	<0.001	0.174
18:3 isomers										
*c*9*c*12*c*15	11.1	29.8	11.3	27.1	9.82	25.4	2.051	0.392	<0.001	0.697
*c*9*t*11*c*15	0.94	2.62	1.10	1.77	0.86	1.99	0.267	0.327	<0.001	0.182
total	12.2	33.2	12.7	29.7	11.0	28.2	1.804	0.247	<0.001	0.481
total BI[g]	6.07	13.8	6.05	15.3	6.46	15.7	0.523	0.188	<0.001	0.371

[a] See remarks in **Table 1**. [b] Variables submitted to Box−Cox transformation; means presented are back-transformed values, although SEM is expressed in transformed scale. [c] Peak includes 18:2 *c*9*t*13, 18:2 *t*8*c*12, and 17-cyclo (methyl 11 cyclohexylundecanoate). [d] Peak includes 18:2 *t*8*c*13 and 18:2 *c*9*t*12. [e] Peak includes 18:2 *c*12*t*14 and 18:2 *t*12*c*14. [f] Peak includes 18:2 *c*11*t*13 and 18:2 *t*11*c*13. [g] Total C18 biohydrogenation intermediates, total C18 fatty acids minus 18:0, 18:1 *cis*-9, 18:1 *cis*-11, 18:2*n*-6, and 18:3*n*-3.

which is not consistent with a toxic effect of PUFA on BH bacteria. The BCFA have been proposed as markers for the rumen microbial ecosystem (*31*). Only slight effects of oil supplementation were detected on BCFA concentration in abomasal digesta, which is consistent with no general toxicity to rumen bacteria. Moreover, when rumen FA concentration is high, rumen bacteria tend to incorporate exogenous FA, decreasing the de novo FA synthesis (*31*). Therefore, the lack of depression on BCFA concentration in the abomasal digesta might be indicative of higher microbial matter yield.

Our major objective was to test the ability of CT sources to differentially modulate the BH pattern in control and oil-supplemented lambs. Grape seed CT extract (25 g/kg of DM) had no effect on BH pattern, except for slight changes in minor nonconjugated

18:2 and conjugated 18:3. As far as we know, this is the first report on the effects of grape seed CT extract on ruminal BH. At the present stage, it is not clear whether a higher dose of grape seed CT could modify the BH pattern. Vasta et al. (*9*, *10*) obtained significant responses for BH pattern with much higher doses of quebracho CT (ranging from 40 to 65 g/kg of DM of CT supplied by ca. 100 g/kg of DM quebracho powder). Even if no antinutritive effects of CT would manifest in such high doses, the dilution of nutrient content of diet and consequent low growth performance would be a major restriction for its practical application. In fact, the use of these high doses of quebracho in lamb diets resulted in decreased growth performance (*10*, *24*).

C. ladanifer had no major effects on BH pattern in lambs fed no oil, but greatly changed the BH pattern in oil supplementation lambs, with a depression of 18:0 and accumulation of 18:1 *trans*-11, without changing the 18:2 *cis*-9,*trans*-11. This indicates an inhibition of the last reductive step of BH and is thus consistent with previous reports that used other CT sources (*7*−*10*). Diets with *C. ladanifer* had higher C18 FA content, leading to a higher C18 FA intake and concentration in abomasal digesta. However, this fact should not explain the BH pattern modifications observed because, as discussed above, the increase of FA intake did not induce major changes in BH pattern.

The supply of CT through *C. ladanifer* diets was similar to that of grape seed diets. However, CT are heterogeneous compounds with quite variable structure and size, which is reflected by their reactivity and impact on digestion (*23*), as well as on microbial ecosystem. It has been reported that the effect of tannins on microorganisms is species and tannin type dependent (*32*, *33*). Therefore, differential responses between GSE and *C. ladanifer* on BH may be due to a different CT composition. Moreover, other secondary compounds in leaves and soft stems of *C. ladanifer* may be responsible for changes in the BI pattern. The *C. ladanifer* is an aromatic shrub that secretes abundant amounts of gum resin containing several flavonoids other than proanthocyanidins and terpenoids (*27*, *34*). Some of those compounds might be responsible for rumen BH effects, and further studies using *C. ladanifer* extracts must be conducted to clarify.

The BCFA concentration in abomasal digesta did not differ between lambs fed CL and CLO diets, suggesting that no general depression in bacterial biomass flow had occurred. Accumulation of *trans* octadecenoates in the rumen could be an adaptative response of rumen ecosystem to environmental stress stimuli, as suggested by Bessa et al. (*35*), probably without involving major microbial community changes. Nevertheless, the mechanism responsible for oil × *C. ladanifer* interaction is not clear, and further studies are needed.

Intramuscular Lipid Fractions. The total intramuscular FA content is determined mostly by the amount of FA in the NL fraction, whereas the level of FA in the PL fraction is considered to be fairly constant or slightly increased with degree of muscle fatness (*36*). In general, lipid supplementation in lamb diets had no effect or slightly increased intramuscular FA (*6*, *21*, *22*, *37*−*39*). In the present trial, oil supplementation did not change the intramuscular FA content, except in lambs fed *C. ladanifer*. Although CLO lambs had a higher FA intake than others, this does not seem to explain the 60% increase in intramuscular NL. Once again, the reason is unclear as to what may be the explanation for the higher muscle lipogenic activity in CLO lambs. Nevertheless, the higher FA intramuscular deposition in these lambs could be related to changes in rumen BH pattern (less 18:0 and more 18:1 *trans*-11). In fact, exogenous 18:0 inhibits the acetate incorporation into FA ovine adipose tissue in vitro as reported long ago by Vernon (*40*). Therefore, a reduction in 18:0 availability, as suggested by our data, might stimulate de novo FA synthesis. It was recently reported that the supplementation of diets with 18:1 *trans*-11 reduced the relative abundance of hepatic FA synthesis enzymes in obese rats (*41*). However, as far as we know, there are no studies regarding the effect of increased 18:1 *trans*-11 availability on muscular lipogenic regulation in ruminants. Vasta et al. (*24*) reported increased expression levels of Δ^9-desaturase protein in muscle of lambs fed fresh vetch supplemented with quebracho. Moreover, this dietary treatment also reduced 18:0 and increased 18:1 *trans*-11 levels in intramuscular fat.

As expected (*1*), the FA pattern of NL fraction was characterized by a high proportion of SFA and MUFA, whereas the PL fraction showed a high proportion of PUFA. The 18:2*n*-6, 18:3*n*-3, and LC-PUFA were preferentially deposited in the PL fraction, but the 18:3*n*-3 was distributed more equally between NL and PL fractions, as previously reported (*42*). In contrast, 18:0, 18:1 *cis*-9, and most *trans* C18 FA, including CLA isomers, were preferentially incorporated in NL. The PL are membrane components, so its FA composition is under regulatory control to maintain proper membrane fluidity and function. Therefore, FA composition in PL is less influenced by dietary factors than NL (*1*). However, diet manipulation changed similarly the FA composition of both lipid fractions, reflecting the BH pattern observed in abomasal digesta, although modulated by endogenous syntheses.

As suggested by FA concentration in abomasal digesta, oil supplementation increased 18:1 *trans*-11, 18:2 *cis*-9,*trans*-11, and most of the other BI in both PL and NL. The accumulation of CLA in intramuscular fat, as a response to the supplementation of diets with oil rich in 18:2*n*-6 and 18:3*n*-3, has previously been reported (*6*, *22*, *37*, *38*). However, oil supplementation of *C. ladanifer* diet resulted in a higher accumulation of 18:1 *trans*-11 in NL fraction than in lambs fed other diets. The 18:2 *cis*-9,*trans*-11 also tended ($P = 0.062$) to be highest in lambs fed CLO diet, mainly due to the increase of 18:1 *trans*-11 availability for endogenous desaturation, because its concentration in abomasal digesta was not superior to other oil-supplemented diets. This is fully consistent with the fact that 18:2 *cis*-9,*trans*-11 in tissues results mostly from the conversion of 18:1 *trans*-11 by endogenous Δ^9-desaturase (*1*). The preferential deposition of 18:1 *trans*-11 and 18:2 *cis*-9,*trans*-11 into NL has been previously reported (*36*). Lambs fed CLO diet had more NL in the muscle and higher concentration of 18:1 *trans*-11 and 18:2 *cis*-9,*trans*-11 in NL, resulting in a relevant enrichment of these FA in muscle compared to other oil-supplemented diets (189.5 vs 70.6 and 41.7 vs 19.2 mg/100 g of muscle for 18:1 *trans*-11 and 18:2 *cis*-9,*trans*-11, respectively). About 19% of dietary 18:1 *trans*-11 may be converted into 18:2 *cis*-9,*trans*-11 by Δ^9-desaturase in humans (*43*). Therefore, when considering the 18:1 *trans*-11 content of CLO lamb meat, the potential 18:2 *cis*-9,*trans*-11 supply would increase by 36 mg/100 g of muscle, summing a total of 77.8 mg/100 g of muscle.

The dietary inclusion of lipid sources rich in 18:2*n*-6 and 18:3*n*-3 increased *n*-6 and *n*-3 PUFA content in PL and reduced saturated FA in NL. However, PUFA increase in muscle PL was caused exclusively by increased 18:2*n*-6 and 18:3*n*-3 deposition, because *n*-3 LC-PUFA were unchanged and the *n*-6 LC-PUFA decreased. This can be explained either by an inhibitory effect of *n*-6 PUFA and *n*-3 PUFA on Δ^6- and Δ^5-desaturase expression (*44*) or by competition between 18:2*n*-6 and 18:3*n*-3 for desaturation and elongation enzymes due to the preference of those enzymes for 18:3*n*-3 (*45*). Recently, it also was reported that supplementation of diet with linseed oil decreases the Δ^6-desaturase protein level in cattle muscle (*46*). These, or other, mechanisms regulating the incorporation of these highly unsaturated FA in membranes are probably linked to the homeostasis of membrane fluidity,

but may constitute a limitation to dietary strategies designed for LC-PUFA enrichment of ruminant meat.

The increase of CLA content in lamb meat in response to supplementation of diets rich in forage with vegetable oils has been extensively shown (*6*, *22*, *38*, *39*). However, in the present study we found that inclusion of *C. ladanifer* in oil-supplemented diets, but not of grape seed tannins, resulted in higher health-benefiting FA content in lamb meat than with only oil supplementation. *C. ladanifer* did not compromise animal performance, which reinforces the interest of its use in association with vegetable oils in nutritional strategies to improve the nutritional value of lamb meat.

ABBREVIATIONS USED

BCFA, branched-chain fatty acids; BI, biohydrogenation intermediates; BH, biohydrogenation; CLA, conjugated isomers of linoleic acid; CT, condensed tannins; DM, dry matter; DMI, dry matter intake; FA, fatty acids; FAME, fatty acid methyl esters; KKCF, kidney and knob channel fat; LC-PUFA; long-chain polyunsaturated fatty acids; NL, neutral lipids; PL, polar lipids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids.

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