

Digestibility of Different Plant-derived Oils and their Influence on Fatty Acid Composition in the Liver and Muscle of Juvenile Common Carp (*Cyprinus Carpio*)

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Abstract

We evaluated the digestibility of plant oils and their influence on the growth of and fatty acid composition in common carp. Apparent digestibility coefficients (ADC) of lipids were determined in carp (200.2 ± 40.0 g) fed with cod liver oil (CLO), linseed oil (LO), sunflower oil (SFO), or sesame oil (SO). A 96-day growth trial was then conducted using six isolipidic (from 100 to 101 g/kg diet) diets, namely CLO, LO, SFO, SO, and two blends of plant oils (SLO = SO + LO; SSFO = SO + SFO). Lipid ADC values (0.920-0.972) were similar or slightly lower in the plant oil-based diets than in the CLO-based diet. Growth and feed efficiency (FE) were not influenced by dietary lipids. The fatty acid profile in the liver and muscle reflected those of the dietary lipids. The EPA and DHA proportions were higher in the liver and muscle of the LO and SLO-fed fish than in the other plant oil groups, and lower than in CLO-fed fish ($P < 0.05$). Higher EPA, DHA, and n3/n6 ratio levels in the muscle of fish fed on the linseed oil (LO) diet, as compared to those in fish fed on the other plant oil-based diets, were ideal for human health and suggest that it can be used as a suitable alternative to fish oil.

Keywords

Common carp, vegetable oil, fatty acid profile

Introduction

Globally, the reduction in availability of feed ingredients, especially fish meal and oil, is considered among the main constraints of aquaculture development (Tocher, 2015; Nguyen *et al.*, 2019a, 2019b). Therefore, the strategy of exploring other alternatives such as plant-based products and their valorizations is encouraged. Plant

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ingredients contain some levels of polyunsaturated fatty acids (PUFA) but no long-chain (>18C) polyunsaturated fatty acids (LC-PUFA) (Orsavova *et al.*, 2015; Kutluyer *et al.*, 2017; Castro *et al.*, 2019). Among the LC-PUFAs, some members of the n-3 family, like eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), and of the n-6 family, such as arachidonic acid (ARA), play important roles in fish development and health (Oliva-Teles, 2012; Cornet *et al.*, 2018; Tocher *et al.*, 2019; Nguyen *et al.*, 2021). During the last few decades, many studies have been conducted on the replacement of fish oil with plant oils. In several cases, especially in salmonid species, the reported results were similar, *i.e.* limited or no significant reductions of growth rate or feed utilization when 100% of the fish oil was replaced by plant oil (Peng *et al.*, 2016; Mellery *et al.*, 2017; Nguyen *et al.*, 2019a). On the other hand, for some other fish species, the use of dietary plant oil instead of fish oil has induced a poor growth performance (Geay *et al.*, 2011, 2015; Ren *et al.*, 2012; Ti *et al.*, 2019). Fish LC-PUFA composition is strongly affected by the dietary FA profile (Nayak *et al.*, 2017; Torrecillas *et al.*, 2017; Nguyen *et al.*, 2019a; Ti *et al.*, 2019). Common carp is able to synthesize C20- and C22-PUFAs from C18 PUFA through a series of desaturation and elongation reactions (Oliva-Teles, 2012). Ren *et al.* (2012) and Böhm *et al.* (2014) reported that the FA compositions of different tissues such as muscle, kidney, and liver of common carp fed diets containing high levels of linoleic acid (LA, C18:2n-6) and α -linolenic acid (ALA, C18:3n-3), well known as the precursors of LC-PUFAs, were similar to those of carp fed fish oil. Accordingly, high expression levels of several genes involved in the desaturation and elongation processes were measured in fish fed plant oil diets rich in LA and ALA (corn, sunflower, and linseed oils), such as *fads2* and *elovl5* (Ren *et al.*, 2012; Nguyen *et al.*, 2019b), and *elovl5-a* and *elovl5-b* (Ren *et al.*, 2015). Although studies have focused on how fish oil replaced by plant-derived oils influences the bioconversion capacity of common carp, to our knowledge, the digestibility of such dietary lipid sources in common carp has not yet been assessed.

Linseed, sunflower, and sesame oils may be considered as candidates to replace fish oil based on their high contents in PUFA (Popa *et al.*, 2012; Asghar & Majeed, 2013). Among them, linseed oil has more advantages as it contains a higher level of ALA than the other two oils (Asghar & Majeed, 2013). The combination of different dietary plant oils could provide a better balanced PUFA profile for fish than a pure dietary plant oil (Castro *et al.*, 2016; Kutluyer *et al.*, 2017). However, the reported data are still limited for common carp. Thus, this study was conducted to evaluate the digestibility of different dietary lipid sources in the diet of common carp, and to determine how the PUFA composition of plant oils affects the growth, feed utilization, and tissue FA composition of fish fed these plant-derived oils.

Materials and Methods

Diets

Six iso-nitrogenous (crude protein ranged from 404 to 415 g/kg diet), iso-lipidic (100 to 101 g/kg diet), and iso-energetic (0.018 to 0.019 MJ/kg diet) experimental diets were formulated based on four oil sources: cod liver oil (CLO), linseed oil (LO), sunflower oil (SFO), and sesame oil (SO), and two plant-derived oil blends: SO + LO (SLO, *v:v 1:1*) and SO + SFO (SSFO, *v:v 1:1*). In each diet, the protein source was supplied from casein, gelatin, and wheat gluten. The ingredients were chosen based on the nutritional requirements of common carp (NCR, 2011) and previous studies on the same species (Ren *et al.*, 2012; Nguyen *et al.*, 2019). The formulation, chemical analysis, and the FA profile of the diets are given in **Tables 1 and 2**.

The ingredients were mixed with a blender (B20 mixer; Rudong Hengyu Food Machinery Co., Ltd.; Jiangsu, China) and then subsequently moistened for pelleting (3 or 5 mm pellets). The experimental feed was dried and stored at -20°C until feeding or analysis.

Digestibility trial

The apparent digestibility coefficient (ADC) of the experimental diets (CLO, LO, SFO, and SO) in terms of dry matter (DM) and lipid source

Table 1. Chemical compositions of the experimental diets (g/kg diet as-is)

Ingredients	Experimental diets					
	CLO	LO	SFO	SO	SLO	SSFO
Casein ^a	88.3	88.3	88.3	88.3	88.3	88.3
Wheat Gluten ^b	380.0	380.0	380.0	380.0	380.0	380.0
Gelatin ^c	50.0	50.0	50.0	50.0	50.0	50.0
Modified starch ^d	306.7	306.7	306.7	306.7	306.7	306.7
Cod liver oil ^e	100.0	0.0	0.0	0.0	0.0	0.0
Sunflower oil ^f	0.0	0.0	100.0	0.0	0.0	50.0
Linseed oil ^g	0.0	100.0	0.0	0.0	50.0	0.0
Sesame oil ^h	0.0	0.0	0.0	100.0	50.0	50.0
Premix of vitamins ⁱ	10.0	10.0	10.0	10.0	10.0	10.0
Premix of minerals ^j	65.0	65.0	65.0	65.0	65.0	65.0
Total	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0
Dry matter, DM (g/kg diet)	898	902	901	900	899	902
Crude protein, CP (g/kg diet)	415	404	415	404	404	405
Crude fat, CF (g/kg diet)	100	101	100	100	101	100
Gross Energy, GE (MJ/kg diet)	18.9	17.6	17.6	17.6	17.6	17.6
CP/GE (g/MJ)	21.5	23.0	23.0	23.0	23.0	23.0
CF/GE (g/MJ CE)	5.3	5.7	5.7	5.7	5.7	5.7

Note: CLO: cod liver oil; LO: linseed oil; SFO: sunflower oil; SO: sesame oil; SLO: SO + LO, v/v:1/1; SSFO: SO + SFO, v/v:1/1;

^{a,b,c,f,g,h} Sigma Aldrich, St. Louis, MO, USA

^d Baaboo Food, Ho Chi Minh city, Vietnam

^e Mosselman s.a., Ghlin, Belgium

^f Cai Lan Oils & Fat Industries Co., Ltd

ⁱ The vitamin premix formulation was published in Abboudi *et al.* (2009) (mg/kg of diet) as follows: retinyl acetate, 6.7; ascorbic acid, 1200; cholecalciferol, 1.0; tocopheryl acetate, 342; menadione, 22; thiamin, 56; riboflavin, 120; pyridoxine, 45; calcium-pantothenate, 141; p-aminobenzoic acid, 400; vitamin B12, 0.3; niacin, 300; biotin, 1.0; choline chloride, 3500; folic acid, 15; inositol, 500; canthaxanthin, 50; astaxanthin, 50; butylated hydroxytoluene, 15; butylated hydroxyanisole, 15; α -cellulose, 3250.

^j The mineral premix formulation was published in Abboudi *et al.* (2009) (mg/kg of diet) as follows: $\text{CaHPO}_4 \cdot 2\text{H}_2\text{O}$, 2955; $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$, 2170; NaHCO_3 , 950; $\text{Na}_2\text{SeO}_3 \cdot 5\text{H}_2\text{O}$, 0.11; KCl, 1000; NaCl, 1720; KI, 2; MgCl_2 , 640; MgSO_4 , 340; $\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$, 20; $\text{FeSO}_4 \cdot 4\text{H}_2\text{O}$, 100; $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 4; $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, 100.

were determined indirectly using chromic oxide (Cr_2O_3) as an inert marker in the diets (10g Cr_2O_3 in 1kg diet). The digestibility experiment was carried out in triplicate with portion-size common carp (BW = 200.2 ± 40.0 g) for 14 days. Fish collected from the Research Institute for Aquaculture N°1, Vietnam (RIA1) were acclimatized in the experimental tanks for two weeks. After the acclimatization period, the fish were allocated into the 200L cylindro-conical tanks at a density of 12 fish per tank. During the trial, fish were maintained at temperatures from 26 to 28°C, dissolved oxygen (DO) of 5-6 mg/L, and a natural photoperiod (light:dark, 12:12 h). Fish were fed with the 5 mm pellet size feeds to satiation once daily. Daily feed intake was weighed and recorded.

The faeces were collected for 14 days from the experimental tanks using a continuous automatic device, as published in Choubert *et al.* (1982). For each dietary condition, samples of semi-dry faeces were collected daily and immediately frozen (-20°C). After the 14-day digestibility trial, the faeces were lyophilized by a freeze-drier at -50°C for 48h as described previously (Nowak & Jakubczyk, 2020) and stored at -20°C. The experimental pellets and fish faeces were respectively calculated as follows (NRC, 2011):

$$\text{ADC of DM} = 1 - \frac{\text{Dietary Cr}_2\text{O}_3}{\text{Faecal Cr}_2\text{O}_3}$$

$$\text{ADC of DM} = 1 - \left(\frac{\text{Dietary Cr}_2\text{O}_3}{\text{Faecal Cr}_2\text{O}_3} \times \frac{\text{Faecal lipid concentration}}{\text{Dietary lipid concentration}} \right)$$

Table 2. Fatty acid profile (g/kg diet as-is) of the experimental diets

	Diet					
	CLO	LO	SFO	SO	SLO	SSFO
C14:0	3.0	0.2	0.2	0.1	0.1	0.1
C16:0	11.7	8.2	6.5	12.1	9.7	8.9
C18:0	2.1	3.5	2.8	5.8	4.3	3.7
C18:1n-9	15.3	19.5	20.5	40.0	28.5	26.9
C18:1n-7	4.2	0.9	0.7	1.2	1.0	0.9
C18:2n-6	12.4	21.0	29.8	46.2	33.5	49.4
C20:0	0.1	0.2	0.2	0.7	0.4	0.3
C18:3n-6	0.1	0.0	0.0	0.0	0.0	0.1
C20:1n-9	9.6	0.0	0.2	0.3	0.1	0.3
C18:3n-3	1.0	43.1	0.3	0.9	19.1	1.0
C18:4n-3	1.3	0.0	0.1	0.1	0.0	0.1
C20:2n-6	0.3	0.0	0.0	0.0	0.0	0.0
C22:0	0.1	0.2	0.6	0.2	0.2	0.5
C20:3n-6	0.1	0.0	0.0	0.0	0.0	0.0
C22:1n-9	4.4	0.0	0.0	0.0	0.0	0.0
C20:3n-3	0.6	0.0	0.0	0.0	0.0	0.0
C20:4n-6	0.3	0.0	0.0	0.0	0.0	0.0
C20:4n-3	0.5	0.0	0.0	0.0	0.0	0.0
C20:5n-3	5.8	0.0	0.0	0.0	0.0	0.0
C24:0	0.2	0.2	0.2	0.1	0.2	0.1
C24:1-9	0.5	0.0	0.0	0.0	0.0	0.0
C22:4n-6	0.0	0.0	0.0	0.0	0.0	0.0
C22:5n-6	0.2	0.0	0.0	0.0	0.0	0.0
C22:5n-3	0.8	0.0	0.0	0.0	0.0	0.0
C22:6n-3	8.4	0.0	0.0	0.0	0.0	0.0
<i>Total</i>	91.4	97.6	62.8	108.5	97.7	92.8
Σ SFA	17.8	12.9	11.1	19.3	15.2	13.8
Σ MUFA	41.7	20.6	21.5	42.0	29.8	28.3
Σ PUFA	32.0	64.1	30.3	47.2	52.8	50.6
Σ C18 n-6 PUFA	12.6	21.0	29.8	46.2	33.6	49.5
Σ C18 n-3 PUFA	2.2	43.1	0.4	1.0	19.2	1.0
Σ LC-PUFA	21.5	0.0	0.0	0.0	0.0	0.0
Σ n-6 LC-PUFA	0.8	0.0	0.0	0.0	0.0	0.0
Σ n-3 LC-PUFA	16.3	0.0	0.0	0.0	0.0	0.0
LA/ALA	13.1	0.5	92.6	49.3	1.8	49.5
Σ n-3PUFA	18.5	43.1	0.4	1.0	19.2	1.0
Σ n-6 PUFA	13.4	21.0	29.8	46.2	33.6	49.5
n-3/n-6	1.4	2.1	0.0	0.0	0.6	0.0

Abbreviations: See Table 1 for nomenclature of the experimental diets. SFA: saturated fatty acid; MUFA: mono-unsaturated fatty acid; PUFA: poly-unsaturated fatty acid; LC-PUFA: long chain poly-unsaturated fatty acid.

Feeding trial

Facilities and fish

Common carp juveniles were collected from the RIA1 and acclimated in an indoor tank for one week. During the acclimatization period, fish were fed commercial feed (Cargill, 7434, 35% crude protein). After the acclimation period, 370 fish (initial body weight, IBW = 28.6 ± 1.3 g) were randomly allocated into 18 glass tanks of 120 L with the same biomass of 0.58kg per tank (corresponding to 20 or 21 fish per tank) at the onset of the feeding experiment. Fish were fed to satiation twice a day (08:00 and 14:00) with the experimental feeds CLO, LO, SFO, SO, SLO, or SSFO (in triplicate) for 96 days. Daily feed intake was recorded. During the experimental period, the rearing conditions such as temperature (26-28°C), DO (5-6 mg/L), and natural photoperiod (light:dark 12:12h) were maintained stable. The tanks were siphoned daily to exclude the fish faeces, and the water in each tank was renewed daily (about 30% of the total volume).

Sample collection

After the 96-day feeding trial, fish were fasted 24 h before sampling. The total number of fish and the fish body weights were recorded to calculate the survival rate and other husbandry parameters. Three fish per tank were anaesthetized with clove oil (50 mg/L; Sigma-Aldrich, USA) and dissected for the liver and dorsal muscle sampling for fatty acid composition analyses. The tissues were directly frozen in liquid nitrogen and stocked in a deep freezer (-80°C).

Total lipid extraction and FA measurement

The experimental feed was homogenized and the lipids were extracted with chloroform/methanol (2:1, v:v) according to the methods published by Folch *et al.* (1957), and modified by Christie (1982). The lipids of fish muscle and liver were extracted by chloroform/methanol/water (2/2/1.8, v/v/v) using the methods described by Bligh & Dyer (1959). Tridecanoic acid (Sigma-Aldrich, USA) was utilized as an internal standard to quantify the FA content. The extracted lipids were converted into FA methyl esters through methylation, separated

by gas chromatography, and measured according to Mellery *et al.* (2017). The GC trace (Thermo Scientific, Milan, Italy) was prepared with a capillary column of 100m x 0.25mm, and 0.2µm film thickness (RT 2560, Restek, Bellefonte, PA, USA). The hydrogen gas vector was inserted at 200 kPa. The flame ionization detector (FID, Thermo Scientific) was maintained at 255°C. The temperature program was applied as described by Mellery *et al.* (2017). The peak area of each fatty acid identified based on its retention time in the capillary column was analyzed by comparing the retention times and those of the methyl ester standards. Data were analyzed using ChromQuest software 3.0 (Thermo Finnigan, Milan, Italy). The results were expressed in mg/g DM.

Calculations of the studied parameters

The studied variables, namely specific growth rate (SGR, %/day), biomass gain (WG, %), feed efficiency (FE), survival rate (SR, %), feed intake (g DM/100g of fish), lipid intake (g DM/100 g of fish), protein intake (g DM/100g of fish), digestible lipid intake (g DM/100g of fish), FA intake (mg DM/ 100g of fish), and digestible FA intake (mg DM/fish), were calculated, respectively, as follows:

Biomass gain =

$$100 \times \frac{(\text{Final biomass} - \text{initial biomass})}{\text{Initial biomass}} ;$$

$$\text{SGR} = 100 \times \frac{\text{Ln}(\text{FBW}) - \text{Ln}(\text{IBW})}{T} ;$$

$$\text{FE} = \frac{\text{Final biomass} - \text{initial biomass}}{\text{Consumable feed quantity}} ;$$

$$\text{Feed intake} = \frac{\text{Consumable feed quantity}}{100 \text{ g of fish}} ;$$

$$\text{SR} = 100 \times \frac{\text{Final number of fish}}{\text{Initial number of fish}} ;$$

$$\text{Lipid intake} = \frac{\% \text{ of lipid in diet}}{\text{Feed intake}} ;$$

$$\text{Protein intake} = \frac{\% \text{ of protein in diet}}{\text{Feed intake}} ; \text{ and}$$

$$\text{Digestible lipid intake} = \text{lipid intake} \times \text{ADC} ;$$

$$\text{Fatty acid intake} =$$

$$\text{FA content in diet} \times \text{lipid intake} ;$$

$$\text{Digestible FA intake}$$

$$= \text{ADC} \times \frac{\text{FA content in diet}}{\text{Lipid intake}}$$

where, IBW and FBW are the initial body weight and final body weight (g/fish), respectively, and T is the duration of the feeding trial (number of days). The fish biomasses were expressed in g fish/tank, and consumable feed quantity in g feed/tank.

Chemical analyses

Dry matter (DM), crude protein, crude lipid, and gross energy (GE) contents of the experimental diets in the digestibility trial as well as in the nutritional trial were determined following conventional analytical procedures (AOAC 954.01, 920.39, AOAC, 1995): DM was measured by drying at a temperature of 105°C for 24 h, ash content by incineration at a temperature of 550°C for 12h, and crude protein content (N x 6.25) by the Kjeldhal method procedures. The GE of the diets was measured with an adiabatic calorimeter (e2K, USA). The quantification of the chromium III (trivalent) concentration involved digestion of organic matter, solubilization of chromium, and determination of chromium concentration by photometry (Czarnocki *et al.*, 1961). Total lipids of the carp muscle content (g/100 g tissue) were extracted and quantified using the Soxhlet method (AOAC 920.39, AOAC 1995; directive 98/64/CE, European Commission, 1998) with diethyl ether as the extraction solvent.

Data presentations and statistical analysis

The data were presented as means \pm SD and pooled standard error of the mean (SEM). Mean values were firstly checked for homogeneity by the univariate test. The homogeneous data were then analyzed using one-way ANOVA, followed by an LSD post-hoc test in which the number of tanks for each diet was used as a statistical unit ($n = 3$). The differences between experimental conditions were significant when the P value was <0.05 . Data were processed using STATISTICA 5.0 software.

Results

Digestibility and digestible fatty acid intake

Results of the 14-day digestibility trial are shown in **Table 3**. No differences were found for

the ADC of DM. The ADC values of dietary lipids were high for all treatments (ranging from 0.920 to 0.972). The lipid ADC of the SFO and CLO groups were similar. In contrast, the ADC values of the LO and SO groups were slightly, but significantly ($P < 0.05$), lower than those of the CLO and SFO diets.

The digestible intakes of oleic acid, LA, ALA, ARA, EPA, and DHA were calculated thanks to the total feed intake, the dietary lipid content, and the lipid ADC (**Table 3**). Significant differences among the diets were observed for the C18 PUFA ($P < 0.05$). Digestible intakes of ARA, EPA, and DHA were restricted to the CLO-fed fish, thereby precluding any comparison. The OA digestible intake for the CLO-fed fish was similar to LO-fed fish but lower than those fed on the SO, SLO, and SSFO diets ($P < 0.05$). The LA digestible intake for the CLO-fed group was also lower ($P < 0.01$) than in the other plant oil-based diets. Moreover, the LA digestible intake for the SSFO-fed fish was higher ($P < 0.05$) than for those fed on the SLO diet. Concerning ALA, both the intake and its digestible fraction for LO-fed fish were several times higher ($P < 0.001$) than those for the CLO, SFO, SO, and SSFO-fed groups, and two times higher ($P < 0.05$) than the SLO group.

Fish growth performance

During the growth trial, differences ($P < 0.05$) in the value of FBW among the experimental groups were observed whereas other husbandry parameters such as biomass gain (ranging from 58 to 89%), SGR (from 0.5 to 0.7%/day), and FE (from 0.30 to 0.38) were similar for all treatments. The average survival rate ranged from 90 to 100%, however, no significant differences were detected among treatments (**Table 4**).

Fatty acid composition

The n-3 PUFA precursor ALA was abundant in the LO and SLO-based diets but almost absent in the other diets, whereas the n-6 PUFA precursor LA content was comparable in the LO, SFO, and SLO diets, higher in the SO and SSFO diets, and the lowest in the CLO diet. The LA/ALA ratio was high in the SFO (92.5), SO

Table 4. Growth, feed utilization, and survival rates of fish eating different dietary lipid sources for 96 days

Parameters	Diet						SEM	P-value
	CLO	LO	SFO	SO	SLO	SSFO		
IBW (g/fish)	29.1 ± 0.4	29.1 ± 0.3	28.8 ± 2.3	27.8 ± 1.1	27.9 ± 2.1	28.9 ± 0.4	0.31	0.765
FBW (g/fish)	47.8 ^{ab} ± 2.7	49.4 ^{ac} ± 4.7	54.6 ^c ± 3.0	45.0 ^a ± 1.1	50.8 ^{bc} ± 2.3	50.8 ^{bc} ± 3.4	1.00	0.039
Biomass gain (%)	58.9 ± 15.0	63.6 ± 14.1	89.4 ± 21.9	60.3 ± 12.1	73.6 ± 19.5	72.4 ± 16.6	4.04	0.275
SGR (%/day)	0.5 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.5 ± 0.0	0.6 ± 0.1	0.6 ± 0.1	0.02	0.255
FE	0.3 ± 0.0	0.4 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.1	0.01	0.176
SR (%)	90.1 ± 8.6	92.5 ± 6.6	97.2 ± 4.8	95.7 ± 4.0	98.4 ± 2.7	100 ± 0.0	1.33	0.399

Note: See Tables 1 and 2 for the diet nomenclature. IBW: initial body weight; FBW: final body weight; SGR: specific growth rate; FE: feed efficiency, SR: survival rate. Data were transformed in Arcsine (\sqrt{X}) for SR and in Log for FBW before statistical analysis. Data are represented as mean ± SD and SEM, $SEM = (SD/n)/\sqrt{n}$. Data within the same row with common superscript letters display non-significant differences ($P > 0.05$).

(49.3), and SSFO (49.5) diets, and low in the CLO (13.6), LO (0.5), and SLO (1.8) diets (Table 2).

Liver fatty acid profiles were determined after the feeding trial (Table 5). Accordingly, no differences in the total fatty acid, SFA, and MUFA levels were recorded. In contrast, differences were found in the C18 PUFA content ($P < 0.05$). The C18 PUFA level in the LO-fed fish was higher ($P < 0.05$) than in the CLO, SFO, SO, and SSFO ones. Particularly, the n-3 C18 PUFA level in the LO-fed fish was higher ($P < 0.05$) than what was observed in the other groups. Regarding the LC-PUFA level, the lowest value was recorded in the SO group, whereas the CLO-fed fish reached the highest content. A similar result was displayed for the n-3 LC-PUFA content. On the other hand, the CLO-fed fish displayed the lowest value of n-6 LC-PUFA content, whereas the highest contents were recorded in the SFO, SO, and SSFO groups. Consequently, the total liver n-3 PUFA content and the n-3/n-6 ratio were highest ($P < 0.05$) in fish fed on the LO diet and the lowest for the SFO, SO, and SSFO conditions.

Fish fed on the dietary LO and SLO exhibited the highest amounts of liver ALA content ($P < 0.05$). In the same trend, the contents of EPA and DHA in the liver of fish fed the LO and SLO diets were also more abundant ($P < 0.05$) than in the other plant oil-fed groups but lower than those recorded in the CLO group ($P < 0.05$). Despite the deficiency of the LO diet in

DHA and EPA, the livers of fish fed on the LO diet contained a relatively high n-3 LC PUFA level (4.7 mg/g for DHA and 2.0 mg/g for EPA). Significant differences were also recorded regarding the liver ARA content, with higher levels found in fish fed dietary SFO, SO, SLO, and SSFO than in the CLO and LO-fed fish ($P < 0.05$) (Table 5).

The lipid content in the carp muscle was high (about 15g/100g of fresh matter) without any differences among the experimental conditions ($P > 0.05$). Regarding the FA composition of the dorsal muscle (Table 6), no differences were observed in the SFA proportion. About the MUFA group, the most abundant FA in the muscles of the SO, SLO, and SSFO-fed fish belonged to oleic acid. The LA level was highest in the SFO group (27.1g/100g FA) while the lowest value was observed in the CLO group (10.0g/100g FA) ($P < 0.05$). The highest ALA content was found in the muscle of LO-fed fish, followed by SLO group, and the lowest values were recorded in the other experimental groups ($P < 0.05$). Similar to the liver fatty acid composition, even if EPA and DHA were absent in all the plant-derived oil diets, the contents of EPA and DHA in the muscle of carp fed on the LO diet were higher than in the other plant oil-fed groups, even though these proportions were reduced as compared to the CLO-fed fish. The highest n-3/n-6 ratio was observed in fish fed on the LO diet (1.5), followed by the CLO diet (1.0), the SLO diet (0.4), and the SO and SSFO diets (0.1) ($P < 0.05$).

Discussion

Digestibility of the different liquid sources

A high concentration of C16:0 and C18:0 in animal lipids has a negative effect on the DM and lipid digestibility of fish (Menoyo *et al.*, 2003). Among the experimental diets, the SFO diet contained a low level of both C16:0 and C18:0 compared to the other tested diets, which may explain its higher ADC values than the LO diet. In contrast, the SO diet, abundant in both these SFA, displayed the lowest lipid ADC value. The digestible ALA intakes of the LO and SLO diets were higher than in the other diets, whereas the digestible LA intakes were higher in the SFO, SO, SLO, and SSFO diets than the others. The contents of these PUFAs in the all plant oil-based diets were higher than in the CLO diet. The differences in lipid digestibility as shown in the current study should be considered during the establishment of feed formulation in carp. In the case of using a fat source with a low lipid digestibility, it is suggested to use a higher dietary fat level than the theoretical lipid requirement in common carp. This supplementation may not only compensate for the low lipid digestibility but also potentially increase the FA content in fish tissues. In contrast, the dietary lipid amount may be reduced with a high lipid ADC value.

Growth performance

In this study, no significant reductions for FBW of carp fed plant-derived oil diets as compared to CLO-fed fish were observed (**Table 4**). Moreover, fish fed on the SFO diet displayed the highest value of FBW, even higher than the CLO group. This observation demonstrates the possibility of dietary plant-derived oils instead of fish oil in carp diets. In the current study, the protein and carbohydrate ingredients were similar; therefore, the fish body weight may be affected by only the lipid source. Moreover, the differences in FBW among the dietary treatments displayed similar trends to those of the lipid source digestibility (**Table 3**). Indeed, the SO diet had the lowest lipid digestibility and supported the lowest FBW while the SFO diet had the highest lipid digestibility and supported the best fish growth. Usually, the digestibility of

fish oil is higher than that of plant-derived oils (Francis *et al.*, 2007) but according to our results, similar ADC values were recorded between the SFO and CLO diets, indicating that common carp is able to digest and absorb plant-derived oils as well as fish oil. In our study, the CLO-based diet did not support the highest growth rate in common carp, suggesting that the FA profile is not a strict limiting factor for optimal growth in this species. The same observation has been reported in previous studies for the same species (Ren *et al.*, 2012; Yildirim *et al.*, 2013; Nguyen *et al.*, 2019b, 2019a), as well as for other species such as halibut (*Hippoglossus hippoglossus*) (Haugen *et al.*, 2006), Arctic charr (*Salvelinus alpinus*) (Tocher *et al.*, 2006), African catfish (*Clarias gariepinus*) (Sourabié *et al.*, 2018), rainbow trout (*Oncorhynchus mykiss*) (Thanuthong *et al.*, 2011), and marble goby (*Oxyeleotris marmorata*) (Ti *et al.*, 2019). In the present study, the relatively high growth performance of SFO-fed fish may be linked to the highest contents of ARA in the liver and muscle, and this was caused by a higher digestibility of LA in the SFO diet than in the other diets. Ma *et al.* (2018) also demonstrated that ARA supplementation could affect fish growth *via* an increase in the availability of circulating proteins and glucose in yellow catfish (*Pelteobagrus fulvidraco*).

Fatty acid profile of carp tissues

Fish oil-based diets are rich in LC-PUFA, especially in EPA and DHA, while plant oil-based diets usually do not contain these FA (Oliva-Teles, 2012). However, most plant-derived oils are rich in C18 PUFA (Torstensen *et al.*, 2005). Among them, a few (e.g. linseed oil or camelina oil) contain a high level of ALA, the precursor of EPA and DHA (Oliva-Teles, 2012). In the current study, the FA profile of fish liver was significantly affected by the FA composition in the diets. Interestingly enough, the richness of ALA in the dietary LO and SLO induced a high level of EPA and DHA in fish liver compared to other plant oil-fed fish. On the other hand, the ARA amount in the fish livers increased as the LA amount in the diet increased. The ARA contents in the SFO, SO, SLO, and SSFO-fed

Table 5. Content of the FA groups (mg/g) in the livers of fish eating different dietary fat sources for 96 days

	Experimental diets						SEM	P-value
	CLO	LO	SFO	SO	SLO	SSFO		
Total	360.4 ± 29.7	326.3 ± 47.6	263.3 ± 50.8	292.5 ± 40.3	337.5 ± 57.1	332.2 ± 43.4	18.30	0.330
SFA	94.5 ± 7.9	66.5 ± 10.6	66.1 ± 14.5	70.9 ± 10.5	77.6 ± 14.1	80.1 ± 11.7	4.71	0.207
MUFA	219.9 ± 21.9	183.5 ± 35.8	141.8 ± 28.3	177.5 ± 29.6	199.7 ± 40.4	198.2 ± 29.8	12.63	0.234
PUFA	32.5 ^a ± 3.7	65.3 ^c ± 5.9	45.6 ^{ab} ± 9.1	34.4 ^a ± 2.6	51.7 ^{bc} ± 14.2	44.3 ^{ab} ± 6.2	2.77	0.003
C18 n-6 PUFA	17.5 ± 3.1	27.0 ± 3.1	35.1 ± 8.9	25.7 ± 2.6	32.4 ± 10.0	34.9 ± 5.0	2.23	0.090
C18 n-3 PUFA	1.6 ^a ± 0.6	27.7 ^c ± 3.2	0.5 ^a ± 0.2	1.3 ^a ± 0.3	10.3 ^b ± 4.3	1.3 ^a ± 0.3	0.60	<0.001
LC-PUFA	13.4 ^d ± 2.7	10.6 ^c ± 0.9	10.0 ^{bc} ± 1.4	7.4 ^a ± 0.3	9.0 ^{ac} ± 0.8	8.1 ^{ab} ± 0.6	0.45	<0.001
n-6 LC-PUFA	2.7 ^a ± 0.3	3.8 ^{ab} ± 0.5	8.9 ^e ± 1.5	6.1 ^{cd} ± 0.3	4.9 ^{bc} ± 0.6	6.9 ^d ± 0.5	0.25	<0.001
n-3 LC-PUFA	10.7 ^d ± 2.5	6.7 ^c ± 0.4	1.07 ^a ± 0.2	1.3 ^a ± 0.1	4.1 ^b ± 0.3	1.3 ± 0.2 ^a	0.25	<0.001
n-3 PUFA	12.3 ^b ± 3.1	34.5 ± 3.2 ^c	1.6 ^a ± 0.2	2.6 ^a ± 0.4	14.4 ^b ± 4.4	2.5 ^a ± 0.3	0.78	<0.001
n- 6 PUFA	20.2 ^a ± 3.4	30.8 ^{ab} ± 3.4	44.0 ^b ± 10.4	31.8 ^{ab} ± 2.8	37.3 ^b ± 10.3	41.7 ^b ± 5.4	2.42	0.026
n-3/n-6	0.6 ^c ± 0.1	1.1 ^d ± 0.1	0.0 ^a ± 0.0	0.1 ^a ± 0.0	0.4 ^b ± 0.0	0.1 ^a ± 0.0	0.01	<0.001
OA (C18:n-9)	152.3 ± 17.3	150.9 ± 27.2	120.0 ± 23.5	148.4 ± 23.4	169.1 ± 33.0	167.2 ± 25.6	10.20	0.371
LA (C18:2n-6)	17.2 ± 3.1	26.4 ± 3.0	33.2 ± 8.5	24.4 ± 2.5	31.4 ± 9.8	32.9 ± 4.8	2.15	0.123
ALA (C18:3n-3)	1.1 ^a ± 0.4	26.7 ^c ± 3.2	0.5 ^a ± 0.2	0.6 ^a ± 0.1	9.7 ^b ± 4.1	0.6 ^a ± 0.2	0.55	<0.001
ARA (C20:4n-6)	0.9 ^a ± 0.1	1.0 ^a ± 0.1	4.4 ^d ± 0.7	3.8 ^c ± 0.2	2.3 ^b ± 0.2	5.5 ^e ± 0.2	0.10	<0.001
EPA (C20:5n-3)	2.7 ^c ± 0.8	2.0 ^b ± 0.3	0.2 ^a ± 0.1	0.3 ^a ± 0.1	0.7 ^a ± 0.2	0.3 ^a ± 0.1	0.10	<0.001
DHA (C22:6n-3)	8.0 ^d ± 1.7	4.7 ^c ± 0.4	0.9 ^a ± 0.1	1.0 ^a ± 0.1	3.4 ^b ± 0.3	1.0 ^a ± 0.2	0.19	<0.001

Note: See Tables 1, 2, and 3 for the diet nomenclature and abbreviations. Data are represented as mean ± SD and SEM, SEM = (SD/n)/√n. Data within the same row with common superscript letters display non-significant differences (P > 0.05).

Genetic diversity of *Chanos chanos* (Forsskål, 1775) from natural populations in Vietnam

Table 6. Contents of lipid (g/100g fresh muscle) and fatty acid groups (g/100g fatty acids) in the dorsal muscle of fish fed different oil sources for 96 days

	Diet						SEM	P-value
	CLO	LO	SFO	SO	SLO	SSFO		
<i>Lipid content</i>	15.1 ± 3.8	13.6 ± 2.3	14.1 ± 5.3	17.2 ± 1.3	13.3 ± 2.0	16.3 ± 2.2	1.12	0.929
<i>FA content</i>								
SFA	25.6 ± 0.7	19.4 ± 0.6	21.5 ± 0.3	20.8 ± 1.0	25.2 ± 3.4	21.9 ± 0.5	0.44	0.079
MUFA	48.6 ^b ± 1.0	36.4 ^a ± 0.5	42.6 ^b ± 1.0	46.9 ^b ± 4.0	48.1 ^b ± 1.7	44.0 ^b ± 1.7	0.68	0.009
PUFA	11.8 ^a ± 0.4	37.1 ^c ± 1.5	29.1 ^b ± 1.4	21.3 ^a ± 1.1	26.8 ^b ± 0.7	26.9 ^{bc} ± 0.2	0.36	<0.001
C18 n-6 PUFA	10.3 ^a ± 0.3	15.2 ^b ± 0.2	28.6 ^e ± 1.4	21.6 ^c ± 1.2	19.7 ^c ± 0.3	26.0 ^d ± 0.2	0.24	<0.001
C18 n-3 PUFA	1.7 ^a ± 0.1	21.9 ^c ± 1.3	0.7 ^a ± 0.1	1.0 ^a ± 0.1	6.6 ^b ± 0.7	1.0 ^a ± 0.2	0.16	<0.001
LC-PUFA	12.2 ^b ± 0.8	6.7 ^a ± 0.9	5.9 ^a ± 0.5	4.7 ^a ± 0.2	5.2 ^a ± 0.2	6.0 ^a ± 1.0	0.25	<0.001
n-6 LC-PUFA	1.9 ^a ± 0.2	1.6 ^a ± 0.3	5.5 ^b ± 0.4	4.2 ^b ± 0.4	2.3 ^a ± 0.1 ^a	5.4 ^b ± 1.0	0.16	<0.001
n-3 LC-PUFA	10.9 ± 0.7 ^d	5.5 ^c ± 0.7	0.9 ^a ± 0.1	1.2 ^a ± 0.1	3.2 ^b ± 0.2	1.1 ^a ± 0.1	0.13	<0.001
n-3/n-6	1.0 ^c ± 0.0	1.6 ^d ± 0.1	0.1 ^a ± 0.0	0.1 ^a ± 0.0	0.4 ^b ± 0.0	0.1 ^a ± 0.0	0.01	<0.001
OA (C18:n-9)	30.5 ^{ab} ± 0.7	30.2 ^a ± 0.5	35.6 ^{bc} ± 1.0	39.2 ^c ± 3.3	40.3 ^c ± 1.6	36.3 ^c ± 1.6	0.59	0.005
LA (C18:2n-6)	10.0 ^a ± 0.3	14.8 ^b ± 0.2	27.1 ^e ± 1.3	19.3 ^c ± 1.0	19.5 ^c ± 0.8	24.7 ^d ± 0.2	0.25	<0.001
ALA (C18:3n-3)	1.1 ^a ± 0.1	21.0 ^c ± 1.4	0.5 ^a ± 0.1	0.9 ^a ± 0.1	6.1 ^b ± 0.5	0.9 ^a ± 0.2	0.16	<0.001
ARA (C20:4n-6)	0.9 ^a ± 0.1	0.7 ^a ± 0.2	2.5 ^b ± 0.2	1.9 ^b ± 0.1	1.0 ^a ± 0.1	2.6 ^b ± 0.5	0.08	<0.001
EPA (C20:5n-3)	2.5 ^d ± 0.2	1.1 ^c ± 0.1	0.2 ^a ± 0.0	0.2 ^a ± 0.0	0.5 ^b ± 0.0	0.2 ^a ± 0.0	0.02	<0.001
DHA (C22:6n-3)	6.6 ^c ± 0.5	2.4 ^b ± 0.5	0.4 ^a ± 0.2	0.6 ^a ± 0.1	1.7 ^b ± 0.1	0.6 ^a ± 0.1	0.10	<0.001

Note: See Tables 1 and 2 for the abbreviations

fish were even higher than the CLO-fed ones suggesting a good ability of common carp to biosynthesize LC-PUFA from PUFA precursors including ARA from LA and EPA, and DHA from ALA. Similar observations have been previously reported in the same species (Zupan *et al.*, 2016; Nguyen *et al.*, 2019b). In the immune system, ARA is a precursor to producing several important pro-inflammatory mediators such as prostaglandin and leukotriene (Nguyen *et al.*, 2021) suggesting that modification in the immunomodulation of fish fed these lipid sources was caused by differences in accumulated ARA levels in fish tissues.

The FA composition found in carp muscle indicates that the accumulation of LC-PUFA biosynthesized from the LA and ALA precursors was efficient, considering the relatively high level of EPA and DHA in the LO and SLO-fed fish muscles. These EPA and DHA amounts were higher than in data previously reported in the same species (Stancheva & Merdzhanova, 2011; Zupan *et al.*, 2016) suggesting that these lipid sources led to a fish flesh source enriched in important LC-PUFAs for human health. Furthermore, the contents of EPA and DHA in the LO and SLO fish were similar to those in the muscle of wild rainbow trout from Dospat Dam Lake (Bulgaria) (Stancheva & Merdzhanova, 2011), which is known as a fish naturally rich in n-3 LC-PUFA. The lowest values of the EPA and DHA contents were in the muscle and liver of fish fed on the SFO diet, which contained the highest LA/ALA ratio. Paulino *et al.* (2018) also reported that the EPA and DHA amounts in tambaqui decreased as the dietary LA/ALA ratio increased. Besides, the muscles of fish fed the plant oil-based diets were abundant in oleic acid. This MUFA has been known to prevent cardiovascular diseases (Peterson *et al.*, 1994; Sales-Campos *et al.*, 2013) indicating the nutritional value of flesh carp fed these plant oils. In the current research, the highest n-3/n-6 ratios were found in the muscles of the LO and CLO-fed fish (1.6 and 1.0, respectively). Interestingly enough, these n-3/n-6 ratios were higher than those previously reported in the same species (Stancheva & Merdzhanova, 2011; Hong *et al.*, 2014). These results are of particular importance

as far as human nutrition is concerned. The n-3/n-6 ratio in the human diet is related to controlling markers of metabolic problems, including inflammation, insulin sensitivity, and adiposity (Burghardt *et al.*, 2010). According to different authors (Gómez Candela *et al.*, 2011; Bhardwaj *et al.*, 2016), humans have been evolutionarily adapted to a diet with an n-3/n-6 ratio close to 1. This trend was observed in the muscle of CLO-fed fish as well as the LO-fed group. This observation supports the suitability of linseed oil as a terrestrial vegetable fat instead of fish oil in carp feeding, not only in terms of culture performance but also from a human nutrition perspective.

Conclusions

The total substitution of fish oil by terrestrial vegetable oils did not affect the growth rate in common carp, but it did impact the lipid digestibility and tissue fatty acid profiles. The digestible α -linolenic acid intake was higher with the linseed oil-containing diets while of the intake of digestible linoleic acid was higher with the sunflower and sesame oil ones. These differences seemed associated with the differential long-chain polyunsaturated fatty acid endogenous bioconversion capacity of polyunsaturated fatty acids such as the higher digestible α -linolenic acid intake induced higher eicosapentaenoic acid and docosahexaenoic acid contents in carp tissues, while higher digestible linoleic acid intake induced only higher arachidonic acid content. The DHA and EPA content values, and the n3/n6 ratio in carp muscle were adequate for human nutrition in the LO diet suggesting the use of this fat source as an alternative to fish oil in the common carp diet.

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