Structured Lipids Improve Fat Absorption in Normal and Malabsorbing Rats

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ABSTRACT The presence of medium-chain fatty acids in dietary fatty acid as well as the triacylglycerol structure may influence the absorption and lymphatic transport of fatty acids. We compared the lymphatic transport and recovery of fatty acids from four intragastrically administered fats based on rapeseed oil and decanoic acid in two rat models of normal absorption and malabsorption, respectively. The fats were: 1) a fat with a regiospecific structure, 2) a similar fat but with a random distribution of fatty acids in the triacylglycerol molecule, 3) a physical mixture of tridecanoic and rapeseed oil and 4) rapeseed oil as control. Lymph samples were collected for 24 h. Significantly higher recoveries were observed of total fatty acids, oleic acid, linoleic acid and linolenic acid from the specific oil in malabsorbing rats and of oleic acid in normal rats fed specific oil compared with those fed rapeseed oil. Furthermore, the recoveries of oleic acid and linolenic acid from the specific oil in normal rats were higher than those from the other oils. In malabsorbing rats, the transport of all fats was ~90% less than that of normal rats. The present study demonstrates improved hydrolysis and absorption of the specific oil compared with the other oils examined both in rats with normal absorption and in rats with malabsorption.

KEY WORDS: • interesterified fats • intestinal absorption • rapeseed oil • decanoic acid • rats

During digestion, triacylglycerols are degraded to sn-2 monoaoylglycerols (sn-2 MAG) and to free fatty acids in the small intestine by pancreatic lipase (Mattson and Beck, 1956, Morley et al. 1973). The sn-2 MAG and long-chain free fatty acids are absorbed by the enterocytes. In the intestinal mucosa cells, the sn-2 MAG are reesterified with fatty acids of exogenous or endogenous origin to form a new population of triacylglycerols (Mattson and Volpenhein, 1964). These are packed into chylomicrons and excreted into the lymph.

The hydrolysis of the triacylglycerol by the pancreatic lipase is affected by chain length and unsaturation of the fatty acids in the sn-1/3 positions (Jandacek et al. 1987, Mattson and Volpenhein, 1964, Morley et al. 1973), with medium-chain triacylglycerols (MCT) being degraded faster than long-chain triacylglycerols (LCT) (Greenberger et al. 1966). After intestinal absorption, medium-chain fatty acids (MCFA) are preferentially transported via the portal vein (Bernard and Carlier, 1991, Kiyasu et al. 1952) to the liver, where they are oxidized.

In the treatment of malabsorption (Hubbard and McKenna, 1987) and postsurgical patients (Kenhoe et al. 1996, Sandström et al. 1995), it is advantageous to have a combination of long-chain fatty acids (LCFA) and MCFA to provide both energy and essential fatty acids (EFA) as in randomized lipids. Randomized lipids thus increased body weight and improved nitrogen balance in thermally injured rats compared with rats fed LCT (Gollaher et al. 1993, Mok et al. 1984, Teo et al. 1989).

Lipids produced via interesterification of vegetable oils with MCFA, with a regiospecific lipase, contain MCFA in the sn-1/3 positions and LCFA in the sn-2 position (specific triacylglycerol). The intake of these fats may result in higher fat acid absorption than randomized fat and thus be useful in the dietary treatment of malabsorption. One reason for the higher absorption is the rapid hydrolysis of the specific lipid, which is comparable to that of MCT (Jandacek et al. 1987). Another reason is that lingual and gastric lipases (Gargouri et al. 1986, Paltauf et al. 1974, Rogalska et al. 1990, Staggers et al. 1981) preferentially hydrolyze fatty acids in the sn-3 position with high activity toward MCFA. Although a number of studies have been published on the absorption of interesterified fatty acids, a direct comparison between rats with normal absorption versus malabsorption using similar fats has not yet been published. In the present study, we examined the lymphatic transport of fatty acids in two different rat models: normal absorption and malabsorption. We compared the lymphatic transport of a specific fat, a randomized fat and a physical mixture, all made from rapeseed oil and decanoic acid (or tridecanoic) and with similar fatty acid profiles, and as the control, rapeseed oil.
MATERIALS AND METHODS

Test fat. Rapeseed oil (Aarhus Oliefabrik A/S, Aarhus, Denmark) and decanoic acid (Sigma Chemical, St. Louis, MO) were used as substrates for lipase catalyzed interesterification (Lipozyme IM; Novo Nordisk A/S, Bagsvaerd, Denmark), whereas rapeseed oil and tridecanoin (Grünaü GmbH, Illertissen, Germany) was used for chemical interesterification with sodium methoxide as catalyst. The interesterifications were performed as batch processes by S. Balchen at the Department of Biotechnology, The Technical University of Denmark. The lipase-catalyzed interesterification resulted in regiospecific triacylglycerols with 10:0 mainly located in the sn-1/3 positions, whereas the chemical interesterification resulted in a random location of fatty acids in the triacylglycerol molecules. A physical mixture was made from rapeseed oil and tridecanoin by simple mixing, and rapeseed oil was used as the LCT control (Chri et al. 1998). The diet contained ~4% fat. The rats were randomly divided into eight groups.

Tubing. A clear vinyl tubing (I.D. 0.5 mm, O.D. 0.8 mm) was used for cannulation of the main mesenteric lymph duct (Dural Plastics and Engineering, Cricley Electrical Products Pty., New South Wales, Australia). Silicone tubing (I.D. 1.0 mm, O.D. 3.0 mm) was used as a feeding tube, and polyethylene tubing (I.D. 0.28 mm, O.D. 0.6 mm) was used for cannulation of the common bile and pancreatic ducts (both from Polystan, Værløse, Denmark).

Surgery, administration of fat and collection of lymph. The Danish National Committee for Animal Experiments approved the experiments. Rats weighing 245–300 g were anesthetized with pentobarbital (100 mg/L) injected intraperitoneally (~0.1 mL/100 g body wt) and subjected to cannulation of the main mesenteric lymph duct with clear vinyl tubing (Bollmann et al. 1948). A gastrotomy tube was inserted 2 cm into the fundus region of the stomach and fixed with a purse-string suture. Rats used in the malabsorption examination were further subjected to cannulation of the common bile duct. After surgery, the rats were placed in individual restraining cages (Bollmann 1948) and kept hydrated via infusion of 3 mL of saline/h (normal rats 0.15 mol/L NaCl, malabsorbing rats 0.15 mol/L NaCl, 0.004 mol/L KCl, 0.28 mol/L glucose) administered through the gastrotomy tube and had free access to drinking water.

The rats recovered from surgery overnight. On the next day, 270 mg of oil was administered as a bolus through the gastroscopy feeding tube followed by 0.5 mL of saline. The fats to the malabsorbing rats were emulsified with a solution of taurocholate, whereas the normal rats (with only lymph cannulation) received pure oil. Fat emulsions were prepared by sonicating 270 mg of oil with 0.3 mL of a 20 mmol/L EDTA-H2O solution; E. Merck, Darmstadt, Germany) that had been kept hydrated via infusion of 3 mL of saline (normal rats 0.15 mol/L NaCl, malabsorbing rats 0.15 mol/L NaCl, 0.004 mol/L KCl, 0.28 mol/L glucose) administered through the gastrotomy tube and had free access to drinking water.

One-hour lymph samples were collected from −1 h (i.e., 1 h before fat administration) through 8 h and one sample from 8 to 24 h for the normal rats. For the malabsorbing rats, a sample from 8 to 23 h and a 23- to 24-h sample were collected. The lymph was collected in a 23°C room temperature in tubes (containing 100 μL of a 100 g NaCl EDTA-H2O per L solution; E. Merck, Darmstadt, Germany) that protected it from direct light. The samples were stored at −20°C until further processing.

| TABLE 1 |
| The fatty acid compositions in triacylglycerols and sn-2 monoacylglycerols of test oils |

<table>
<thead>
<tr>
<th>Test oils</th>
<th>Triacylglycerols</th>
<th>2-Monoacylglycerols</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Specific oil²</td>
<td>Randomized oil³</td>
</tr>
<tr>
<td>Fatty acid</td>
<td>mol/100 mol</td>
<td></td>
</tr>
<tr>
<td>10:0</td>
<td>40.5</td>
<td>40.9</td>
</tr>
<tr>
<td>16:0</td>
<td>2.5</td>
<td>2.9</td>
</tr>
<tr>
<td>18:1(n-7)</td>
<td>1.1</td>
<td>1.1</td>
</tr>
<tr>
<td>18:1(n-9)</td>
<td>34.0</td>
<td>33.1</td>
</tr>
<tr>
<td>18:2(n-6)</td>
<td>1.7</td>
<td>1.9</td>
</tr>
<tr>
<td>18:3(n-3)</td>
<td>14.1</td>
<td>12.7</td>
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<tr>
<td>20:0</td>
<td>4.5</td>
<td>5.8</td>
</tr>
<tr>
<td>20:1</td>
<td>0.5</td>
<td>0.3</td>
</tr>
<tr>
<td>22:0</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td>22:1</td>
<td>0.2</td>
<td>0.2</td>
</tr>
</tbody>
</table>

1 Data represent the means of two determinations.
2 Specific oil: 10:0 located in sn-1/3 positions and long-chain fatty acids in sn-2 position.
3 Randomized oil: like the specific oil but with a random distribution of fatty acids in the triacylglycerol molecule.
4 Physical mixture: mix of tridecanoin and rapeseed oil.
5 ND, not detected.
RESULTS

Absorption profiles. The lymphatic transport of fatty acids during 24 h of four different oils was examined in the mesenteric lymph.

The absorption of the fatty acids decanoic acid [10:0], oleic acid [18:1(n-9)] and linoleic acid [18:2(n-6)] was faster in normal rats than in malabsorbing rats (Figs. 1, 2). The initial baseline level of 18:2(n-6) was higher than those of 10:0 and 18:1(n-9) due to the endogenous contribution of 18:2(n-6). Normal rats absorbed 10:0 rapidly, with maximum transport 2 h after administration of the specific oil, randomized oil and physical mixture. After maximum transport, which occurred earlier than the maxima for 18:1(n-9) and 18:2(n-6), the level of 10:0 in the lymph decreased slowly and returned to baseline within 24 h. Maximum absorption of 18:1(n-9) and 18:2(n-6) occurred after 3 h for the specific oil and the physical mixture and after 5–6 h for rapeseed oil and randomized oil in normal rats. In Figure 1, the AUC from 0 to 8 did not differ between the randomized oil and the physical mixture, but the appearance of the curves differed due to the steep increase and decrease for the physical mixture, whereas the randomized oil curve was flatter. This may explain the similar accumulated transport and recoveries over 24 h.

The malabsorbing rats had slower absorption of 10:0 than the normal rats. Maximum transport was reached between 5 and 7 h but returned to baseline within 24 h. Maximum absorptions of 18:1(n-9) and 18:2(n-6) were probably between 8 and 23 h. The exact time of maximum absorption could not be identified because we collected one sample from 8 to 23 h. Furthermore, it was not possible to determine whether maximum absorption of the different oils occurred at the same time. The lymphatic transport profiles of total fatty acids 10:0, 18:1(n-9) and 18:2(n-6) were significantly lower in malabsorbing rats than in normal rats both during the first 8 h (AUC P < 0.003, Figs. 1, 2) and for accumulated transport after 24 h (P < 0.006, Table 2). The transport profile of total fatty acids was similar to that of 18:1(n-9) (data not shown).

Normal rats

Accumulated lymphatic transport. The accumulated lymphatic transport (in mg) of total fatty acids after 24 h did not differ among the four groups (Table 2).

Recoveries of fatty acids. The recoveries of fatty acids calculated from the amount of each fatty acid administered and the amount of fatty acids transported in the mesenteric lymph express the lymphatic transport for the four oils in another way (Table 3). The recoveries of 18:1(n-9) and linolenic acid [18:3(n-3)] in rats fed the specific oil were higher than those of the rats fed the randomized oil, physical mixture or rapeseed oil (P < 0.05). The recovery of 18:2(n-6) was different in rats fed specific oil and rapeseed oil, with the
highest recovery in the former ($P < 0.05$, Table 4). No significant differences were observed between the physical mixture group and the randomized oil group (Fig.1, Tables 2 and 4).

The three oils containing 10:0 (specific, randomized and physical mixture) had similar recoveries of 10:0 in the mesenteric lymph after 24 h.

Malabsorbing rats

Accumulated lymphatic transport. Differences between the specific oil and rapeseed oil groups in accumulated lymphatic transport were observed only for total fatty acids and 18:1(n-9) ($P < 0.05$, Table 3).

Recoveries of fatty acids. Higher recoveries of all of the examined fatty acids as well as total fatty acids were found in rats fed the specific oil compared with those fed the rapeseed oil ($P < 0.05$, Table 5).

DISCUSSION

In thermally injured rats, compared with LCT, MCT and a physical mixture of LCT and MCT (Mok et al. 1984, Selleck et al. 1994), randomized lipids containing MCFA and LCFA improved nitrogen balance, increased the gain in body weight and normalized serum albumin (DeMichele et al. 1988 and 1989, Teo et al. 1989). LCFA did not influence the effects of randomized oils on nitrogen balance regardless of whether the LCFA were from vegetable oils (DeMichele et al. 1988 and 1989, Mok et al. 1984) or fish oil (Selleck et al. 1994, Teo et al. 1989).

Interesterification using an sn-1/3 specific lipase produces fat with regiospecific locations of fatty acids within the triacylglycerol molecules. Interesterification of LCT with MCFA results in a specifically structured lipid with LCFA in the sn-2 position and MCFA located mainly in the sn-1/3 positions. This kind of specifically structured triacylglycerol was hydrolyzed as rapidly as MCT in vitro, and the absorption into an isolated, irrigated loop of the small intestine was 2.5 times higher than that of an LCT analogue (Jandacek et al. 1987).

In malabsorbing rats, the lymphatic transport of 18:2(n-6) from a specific oil was higher during an 8-h experiment than the transport of 18:2(n-6) from a randomized oil, a physical mixture or the native soybean oil (Christensen et al. 1995).

This study demonstrated a faster uptake and transport of the specific fat than of the randomized fat. On the other hand, in normal rats, Jensen et al. (1994) observed that the level of 18:2(n-6) in the sn-2 position of the lymph lipids after a bolus of randomized oil was two thirds of the level found after a bolus of specific lipid, even though only one third of the 18:2(n-6)

### TABLE 2

<table>
<thead>
<tr>
<th>Fatty acid</th>
<th>Total fatty acids</th>
<th>10:0</th>
<th>18:1(n-9)</th>
<th>18:2(n-6)</th>
<th>18:3(n-3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Administered oil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Specific oil</td>
<td>327.3 ± 16.3</td>
<td>21.8 ± 1.7</td>
<td>90.8 ± 7.6</td>
<td>77.7 ± 4.8</td>
<td>12.7 ± 0.5</td>
</tr>
<tr>
<td>Randomized oil</td>
<td>259.6 ± 30.8</td>
<td>20.6 ± 3.0</td>
<td>65.6 ± 7.8</td>
<td>60.3 ± 6.7</td>
<td>11.6 ± 1.3</td>
</tr>
<tr>
<td>Physical mixture</td>
<td>242.5 ± 23.7</td>
<td>18.0 ± 1.5</td>
<td>63.8 ± 6.8</td>
<td>58.6 ± 6.1</td>
<td>11.2 ± 1.2</td>
</tr>
<tr>
<td>Rapeseed oil</td>
<td>271.5 ± 28.5</td>
<td>—</td>
<td>83.5 ± 12.4</td>
<td>66.0 ± 8.9</td>
<td>14.6 ± 2.5</td>
</tr>
</tbody>
</table>

1 The values represent the means ± SEM, $n = 6$ or 7.
was in the sn-2 position of the randomized oil and all of the 18:2(n-6) of the specific oil was in the sn-2 position. They suggested that better hydrolysis of the randomized oil could account for this observation. Tso et al. (1995) observed a reduced uptake of sn-2 linoleate from a specific oil (8:0/18:2/ 8:0) compared with the randomized analogue in normal rats. This was not the result of limited hydrolysis but rather reflected the inability of the small intestine to resynthesize triacylglycerol after absorption of sn-2-MAG and free fatty acids because of a low supply of LCFA for triacylglycerol resynthesis.

The conflicting results for specific fat compared with randomized fat may result from differences in the oils and the experimental conditions. Here, we extend the examinations of lymphatic transport of four test oils to include both rats with normal absorption and malabsorbing rats.

In normal rats, the maximum absorptions of 18:1(n-9) and 18:2(n-6) were obtained after 3 h for the specific oil and physical mixture and after 5–6 h for rapeseed and randomized oils. This difference in the time of maximum transport may result from both differences in rates of hydrolysis and absorption and malabsorbing rats. The improved recoveries of 18:1(n-9), 18:2(n-6) and 18:3(n-3) in normal rats of the specific oil group may reflect a better hydrolysis of the specific oil due to the location of 10:0 in the sn-1/3 positions (Jandacek et al. 1987). However, the endogenous contribution of fatty acids also influenced the lymphatic transport, especially of 18:2(n-6) (Mansbach and Dowell 1992, Savary and Constantin 1967), which is evident from the recovery of total fatty acids (121%) and 18:2(n-6) (175%) from the specific oil. Low recoveries of the exogenous 18:3(n-3), were observed, but the recovery was high from the specific oil, which indicates a better hydrolysis and absorption of the specific oil over 24 h than of the other oils tested. Experiments conducted in our laboratory (Maj-Britt Fruekilde, unpublished data) showed a contribution of endogenous fatty acids from the bile to the lymph, which in addition to the exogenous fatty acids from the dietary oil may account for the 121% recovery of total fatty acids from the specific oil. However, the endogenous fatty acids from the bile and the exogenous fatty acids account for only ~129% (Maj-Britt Fruekilde, personal communication) of the 175% 18:2(n-6) recovered from the specific oil. Endogenous fatty acids from other sources (e.g., adipose tissue) thus may contribute to the lymphatic transport of fatty acids. The differences in lymphatic transport of fatty acids after the intake of the various oils may therefore result from both differences in rates of absorption and different mobilizations of endogenous fatty acids (Porsgaard et al. 2000).

The three manufactured oils had similar contents of 10:0, lower than that for the specific oil. This indicates that the triacylglycerol structure of the oil and the presence of 10:0, and not the level of the individual fatty acid in the oil, were the major determinants of the amount of fatty acids absorbed and transported.

### TABLE 3

<table>
<thead>
<tr>
<th>Administered oil</th>
<th>Fatty acid</th>
<th>10:0</th>
<th>18:1(n-9)</th>
<th>18:2(n-6)</th>
<th>18:3(n-3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Specific oil</td>
<td></td>
<td>39.1</td>
<td>4.6</td>
<td>7.6</td>
<td>11.6</td>
</tr>
<tr>
<td>Randomized oil</td>
<td></td>
<td>28.3</td>
<td>2.8</td>
<td>4.9</td>
<td>8.4</td>
</tr>
<tr>
<td>Physical mixture</td>
<td></td>
<td>31.8</td>
<td>3.3</td>
<td>5.4</td>
<td>9.4</td>
</tr>
<tr>
<td>Rapeseed oil</td>
<td></td>
<td>25.2</td>
<td>4.5</td>
<td>8.3</td>
<td>1.2</td>
</tr>
</tbody>
</table>

1 The values represent the means ± SEM, n = 4–6. Values in a column without common superscript letters are different, P < 0.05.

### TABLE 4

<table>
<thead>
<tr>
<th>Administered oil</th>
<th>Fatty acid</th>
<th>10:0</th>
<th>18:1(n-9)</th>
<th>18:2(n-6)</th>
<th>18:3(n-3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Specific oil</td>
<td></td>
<td>121.2</td>
<td>27.3</td>
<td>84.7</td>
<td>175.3</td>
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<tr>
<td>Randomized oil</td>
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<td>96.1</td>
<td>25.1</td>
<td>62.1</td>
<td>150.1</td>
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<tr>
<td>Physical mixture</td>
<td></td>
<td>89.8</td>
<td>27.3</td>
<td>55.4</td>
<td>134.2</td>
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<tr>
<td>Rapeseed oil</td>
<td></td>
<td>100.6</td>
<td>27.3</td>
<td>55.7</td>
<td>116.6</td>
</tr>
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</table>

1 The values represent the means ± SEM, n = 6 or 7. Values in a column without common superscript letters are different, P < 0.05.
but the specific oil had only 19.6 mol/100 mol 10:0 in the sn-2 position, whereas the randomized oil and the physical mixture had 45.3 and 46.6 mol/100 mol, respectively. If dietary 10:0 from the sn-1/3 positions was absorbed directly to the portal vein (Bernard and Carlier 1991, Kiyasu et al. 1952), we would expect the specific oil to result in less 10:0 appearing in the lymph compared with the randomized oil and physical mixture (Ikeda et al. 1991). Actually we observed similar amounts of 10:0 in the mesenteric lymph from the three oils, which may reflect better hydrolysis and higher absorption of the specific oil, as well as acyl migration in the triacylglycerol molecules during hydrolysis.

In the malabsorbing rats, there was no endogenous fatty acid contribution from the bile due to the surgical technique (Mansbach and Dowell 1992). A higher lymphatic transport of 18:2(n-6) in the rats fed the specific oil compared with the other groups was observed, suggesting a better hydrolysis of the specific oil or greater mobilization of endogenous fatty acids.

Christensen et al. (1995) observed a significantly improved lymphatic transport of 18:2(n-6) in malabsorbing rats fed a specific oil compared with a randomized oil, a mix of soybean oil and MCT (all with similar overall fatty acid profiles) and a soybean oil. We observed only significant differences between the specific oil and the rapeseed oil groups in lymphatic transport. The differences between our results and those of Christensen et al. (1995) may arise from the following factors: 1) their specific oil had no detectable MCFA in the sn-2 position, 2) most of the MCFA in their oils were 8:0 with a higher chyloportal partition than 10:0 (Christensen et al. 1995), 3) they used rats anesthetized during the experiment, 4) that had a thoracic lymph duct cannulation and 5) the duration of the experiment was only 8 h. We used 1) a specific oil with 19.6 mol/100 mol MCT in the sn-2 position, 2) with 10:0 as MCFA, 3) unanesthetized rats 4) with a main mesenteric lymph duct cannulation, and 5) the structured fats were manufactured from rapeseed oil and therefore had only 21.9 mol/100 mol 18:2(n-6), which increased the relative importance of endogenous fatty acids during the 24 h of the experiment.

Our specific oil was a pilot scale batch product that was less specific than the laboratory scale products used by Jensen et al. (1997 and 1998). The higher level of LCFA in the randomized oil (sn-1/3 positions) in our specific oil compared with the randomized oil and the specific oil in normal rats. However, differences in contents of 18:2(n-6) and 18:1(n-9) may also have influenced absorption and lymphatic transport. Linoleic acid is a major endogenous fatty acids in the baseline lymph (Porsgaard et al. 1999). Oils with either 18:2(n-6) or 18:1(n-9) as major LCFA may differently mobilize endogenous fatty acids transported by the lymph.

Recovery of fatty acids after 24 h in malabsorbing rats fed 270 mg of various oils

<table>
<thead>
<tr>
<th>Fatty acid</th>
<th>Administered oil</th>
<th>Total fatty acids</th>
<th>10:0</th>
<th>18:1(n-9)</th>
<th>18:2(n-6)</th>
<th>18:3(n-3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Specific oil</td>
<td>14.5 ± 1.3</td>
<td>5.7 ± 1.0</td>
<td>7.1 ± 1.0</td>
<td>26.1 ± 2.5</td>
<td>12.7 ± 2.1</td>
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<tr>
<td>Randomized oil</td>
<td>10.4 ± 1.2</td>
<td>3.4 ± 0.5</td>
<td>4.6 ± 0.7ab</td>
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<tr>
<td>Physical mixture</td>
<td>11.8 ± 1.9</td>
<td>5.0 ± 1.0</td>
<td>4.7 ± 0.9ab</td>
<td>20.5 ± 5.1ab</td>
<td>7.5 ± 1.9ab</td>
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<tr>
<td>Rapeseed oil</td>
<td>9.3 ± 0.6a</td>
<td>—</td>
<td>3.0 ± 0.2a</td>
<td>14.0 ± 1.3a</td>
<td>4.8 ± 0.5a</td>
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</tr>
</tbody>
</table>

1 Values represent the means ± SEM, n = 4–6. Values in a column without common superscript letters are different, P < 0.05.

LITERATURE CITED


