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1 Natural diversity in the carotene, tocochromanol and fatty acid composition 2 of crude palm oil

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17 Highlights

- 18 • Considerable intraspecific diversity exists in most crude palm oil compounds
- 19 • The geographical origin of oil palm significantly influences oil composition
- 20 • Palms from Côte d'Ivoire showed the lowest palmitate and highest vitamin E levels
- 21 • High (>500 ppm) carotene contents were found in various origins in West Africa
- 22 • Hybrids of Côte d'Ivoire × Nigeria crosses produce oil of high nutritional value

23

24

25 **Abstract**

26 Crude palm oil (CPO) is extracted from the mesocarp of oil palm (*Elaeis guineensis*) fruits. CPO is
27 widely consumed in many African countries. Due to its high provitamin A carotenoid content, it is
28 also widely used in programmes designed to prevent vitamin A deficiency. *Elaeis guineensis* occurs
29 naturally across a wide geographical range in Africa. We investigated the carotene, tocochromanol
30 (vitamin E) and fatty acid composition of a large set of genotypes representative of this genetic and
31 geographic diversity. We found considerable intraspecific diversity in most lipid traits. Populations
32 from Côte d'Ivoire were distinguished from other origins by their very low palmitate content and high
33 tocochromanol content. Genotypes from Benin, Côte d'Ivoire and Nigeria were characterized by high
34 carotene contents. Finally, hybrids of crosses between genotypes from Côte d'Ivoire and Nigeria
35 produce CPO with exceptionally high provitamin A and vitamin E contents together with low
36 palmitate content.

37

38 **Keywords**

39 Vitamin E; Provitamin A; Palmitic acid; Oil palm, Red palm oil; Geographical origin

40

41 1. Introduction

42 Crude palm oil (CPO), also called red palm oil, is extracted from the mesocarp of *Elaeis guineensis*
43 fruits. CPO has been consumed in Africa for thousands of years (Kay & Kaplan, 2015) and is still
44 widely used in many West African countries (Rafflegeau, Nanda, & Genot, 2018), where it can
45 represent up to 60% of edible oil consumption, as is the case in Cameroon (Rébéna, Rafflegeau,
46 Kanski, Nanda, & Genot, 2019). In countries where CPO is traditionally used for everyday cooking,
47 consumers look for deep colour and high fluidity (Cheyns, Bricas, & Aka, 2004).

48 The two main pigments responsible for the colour of CPO, α - and β -carotenes, are also
49 provitamin A carotenoids. CPO is one of the richest dietary sources of provitamin A and is thus also
50 used in programmes to prevent long-term vitamin A deficiency (Zagré, Delpeuch, Traissac, & Delisle,
51 2003; Burri, 2012; Delisle, 2018). Vitamin A deficiency is a public health concern in numerous
52 developing countries. It can affect up to 80% of the population in sub-Saharan countries and 50% in
53 South East Asia (Murphy, 2007; Hamer & Keusch, 2015). Vitamin A deficiency has a plethora of
54 clinical manifestations (night blindness, growth disturbances, and susceptibility to severe infection)
55 and increases the mortality of young children and mothers (Black et al., 2008). Worldwide, more than
56 half a million children under the age of five die every year due to vitamin A deficiency. The
57 identification of oil palm varieties with a high carotene content could thus not only satisfy consumer
58 demand but also help prevent vitamin A deficiency.

59 A comprehensive literature review revealed that very little is known about intraspecific variability
60 of the carotenoid content of CPO. Most reviews (e.g., Sundram, Sambanthamurthi, & Tan, 2003)
61 provide the same figures for CPO total carotenoid content, i.e. 500-700 ppm, but a closer
62 examination showed that this range of values was based on very few studies. However, a few original
63 studies did show that variations in CPO carotenoid content between oil palm origins can be
64 significantly higher. Among four Nigerian genotypes, carotenoid content was found to vary from 648
65 to 2 226 ppm (Ames, Raymond, & Ward, 1960). Monde et al. (2009) found a higher carotenoid
66 content (1 532 ppm) in a variety originating from Côte d'Ivoire than in a variety belonging to the Deli
67 group (690 ppm). Finally, a range of 450 to 1 250 ppm was reported among 42 progenies collected in
68 Angola (Noh et al., 2002).

69 Because the specific vitamin activity and bioavailability of the different carotenoids varies
70 considerably (Haskell, 2012), carotenoid composition also warrants attention. In the few original
71 studies available, β -carotene and α -carotene were always the two major carotenoids in CPO. β -
72 carotene, which has twice the vitamin A potential of α -carotene, represented 86% of carotenoids in a
73 variety from Côte d'Ivoire (Monde et al., 2009) but 60% and 72% in two Nigerian varieties (Ikemefuna

74 & Adamson, 1984), suggesting the ratio of β -carotene to α -carotene may also vary among oil palm
75 from different origins in Africa.

76 CPO is also well known for its high vitamin E content (Schroeder, Becker, & Skibsted, 2006; Teh &
77 Lau, 2021). Tocochromanols are a group of four tocopherols and four tocotrienols that collectively
78 constitute vitamin E, an essential micronutrient in the human diet. A specific feature of CPO is its
79 particularly high concentration of tocotrienols, which may account for 80-95% of total
80 tocochromanols (Monde et al., 2009; Irias-Mata et al., 2017). Tocotrienols are the subject of
81 increasing interest because of their health properties (Trela & Szymanska, 2019; Wallert, Börmel, &
82 Lorkowski, 2021). Because tocochromanols and carotenes protect each other from oxidation during
83 storage or cooking (Schroeder, Becker, & Skibsted, 2006), identifying oil palm origins with high
84 tocochromanol content is not only important as a source of vitamin E but also for provitamin A
85 intake. Again, reviews of CPO tocochromanol contents are based on a limited literature and report
86 different ranges: 500-800 ppm (Sundram, Sambanthamurthi, & Tan, 2003) or 600-1 000 ppm (Hoe,
87 Chan, Ramanan, & Ooi, 2020; Goh, Choo, & Ong, 1985). Original studies are rare but provide a
88 different picture of intraspecific variability of CPO vitamin E content. Luo et al. (2020) recently found
89 values ranging between 172 and 1 288 ppm in a set of 161 oil palm individuals collected in different
90 producer countries. Unfortunately, the African origin of the genotypes they studied was not
91 investigated. Low tocochromanol contents (332 to 525 ppm) were found in three varieties grown in
92 Costa Rica (Irias-Mata et al., 2017), but high vitamin E content (1 124 ppm) was found in the
93 genotype of the Deli group studied by Monde et al. (2009).

94 Palm oil is known for its high level of palmitic acid (16:0), meaning it has many advantages for the
95 food industry, including high oxidative stability and a high melting point, making it a good alternative
96 to trans fats (hydrogenated oils). The range of 16:0 content usually reported for palm oil is 39-46%
97 (e.g., Sundram, Sambanthamurthi, & Tan, 2003). However, CPO consumers in Africa want their CPO
98 to be fluid at ambient temperature (Cheyns, Bricas, & Aka, 2004), i.e., a CPO with a low 16:0. Little is
99 known about the intraspecific variability of fatty acid composition in *E. guineensis*. However, a few
100 studies reported that oil palms originating from Côte d'Ivoire may have a 16:0 level lower than 39%
101 (Gascon & Wuidart, 1975; Monde et al., 2009; Montoya et al., 2014).

102 Our knowledge of the variability of CPO carotene, tocochromanol and FA levels linked with the
103 different geographic origins and genetic groups of oil palm thus remains very limited. Oil palm is a
104 native of west and central Africa, from Senegal to Angola along the Atlantic Ocean, and as far as
105 Tanzania in the east. Genetic analyses revealed two major genetic groups within *E. guineensis*: Group
106 I contains collections from Senegal, Guinea, Sierra Leone, and Côte d'Ivoire, while Group II includes
107 all other collections, including those from Benin, Nigeria, Cameroon, Congo, and Angola (Cochard et

108 al., 2009; Bakoumé et al., 2015). A third genetic group, termed Deli, which is of considerable
109 importance for oil palm breeding, contains material introduced from Africa and bred in Indonesia in
110 the middle of the 19th century, but the area of origin of this material in Africa remains unknown
111 (Cochard et al, 2009; Bakoumé et al, 2015). The aim of this study was thus to characterize carotene,
112 tocopherol and FA composition of CPO in a large set of genotypes representing the three genetic
113 groups of oil palm. We analysed 44 genotypes from Angola, Benin, Cameroon, Congo, Côte d'Ivoire,
114 Nigeria, and the group Deli, and assessed diversity within and between origins in each of the three
115 classes of lipid compounds. Twelve inter-group hybrids were further analysed to test whether new
116 genetic combinations could provide CPO with high provitamin A and vitamin E contents and a low
117 16:0 level.

118

119 **2. Material and methods**

120 *2.1. Plant material and crude oil extraction in Benin*

121 All the genotypes studied were grown at the Agricultural Research Centre for Perennial Plants
122 (*Centre de Recherches Agricoles Plantes Pérennes, CRA-PP/INRAB*) at Pobè, Benin. Passport data
123 (genotype identifier, country and population of origin, genetic group, planting year) of each genotype
124 are given in Supplementary Table 1. The genetic group of each genotype was determined in a
125 previous study (Cochard et al., 2009). We studied 10 genotypes originating from Côte d'Ivoire
126 belonging to two populations (La Mé, seven genotypes, and Yocoboué, three genotypes), five
127 genotypes from Benin (population Pobè), four genotypes from Nigeria (population Aba-Calabar), five
128 genotypes from Congo (population Yangambi), four genotypes from Angola, belonging to two
129 populations (Cuanza and N'Jala, two genotypes each), and 16 genotypes of the group Deli, divided
130 into two sub-groups (Dabou, 13 genotypes) and (Socfin, three genotypes) (Fig. 1). The 12 inter-group
131 hybrids investigated were chosen because at least one of their two parents did not belong to any of
132 the nine populations (including the two Deli sub-groups) in the CRA-PP field genebank (Fig. 1). For
133 each genotype, the objective was to extract and analyse CPO in triplicate from three independent
134 bunches, i.e., collected on three different dates in the period 2017-2019. Each genotype
135 corresponded to single palm tree in the CRA-PP field genebank. In the end, four bunches were
136 harvested and analysed in six genotypes: three bunches in 47 genotypes and only two bunches in
137 three genotypes (Supplementary Table 1). Forty well-developed undamaged fruits were removed
138 from spikelets collected in the centre of each bunch. The fruits were immediately immersed in
139 boiling water for 20 min or until a final temperature of 75-80 °C was reached in the centre of three
140 fruits per bunch measured with a Stuart SCT1 probe thermometer (Cole-Parmer, Stone, UK). After

141 heating, fruits were left to cool to 60 °C (internal mesocarp temperature) and then pressed using a
142 manual 1.2 L screw-press. The extracted crude oil was stirred while still warm and fluid, and 10 mL
143 were sampled and immediately frozen at -20 °C. At this stage of the process, crude oil still contains
144 water and impurities. Unpurified crude oil samples were stored at -20 °C at Pobè for maximum two
145 months.

146

147 *2.2. CPO purification*

148 Unpurified crude oil samples were sent to Montpellier, France, by plane and kept cold during
149 transport using eutectic plates. Prior to lipid extraction, after 15 min in a 40 °C water-bath (Firlabo,
150 Meyzieu, France) to melt all the triacylglycerols, the samples were homogenised. Total lipids were
151 extracted from the samples of crude oil using a modified Folch method as described previously
152 (Laffargue, de Kochko, & Dussert, 2007). Briefly, 3 mL of crude oil was homogenised for 30 s in 20 mL
153 of methylene chloride/methanol (2/1) (analytical grade, Merck, Darmstadt, Germany) using a IKA T25
154 Ultra Turrax homogeniser (Staufen, Germany) prior to filtration (pore size 5) into a glass filter cup.
155 The filtrate was transferred in a 100 mL glass separatory funnel and washed with 5 mL of 0.73% NaCl
156 solution by vigorous hand shaking. After the resulting mixture separated into two phases, the lower
157 phase was recovered and divided into nine aliquots, i.e. three aliquots for each of the three classes of
158 compounds to be analysed (carotenoids, tocochromanols and fatty acids).

159

160 *2.3. Carotenoid analysis*

161 Carotenoid extraction was adapted from the method described previously (Montúfar et al., 2010),
162 which includes a preliminary triacylglycerol (TAG) removal step. Briefly, CPO samples (15 mg) dried
163 under nitrogen ($\geq 99.999\%$, Linde, Lyon, France), using an OASys heating system (Organomation,
164 Berlin, MA, USA) were carefully mixed with 10 mL of acetone (analytical grade, Merck) and left for 60
165 min at -20 °C, leading to TAG crystallisation. After centrifugation (Eppendorf 5810R, Hamburg,
166 Germany) of frozen samples at 900 g and -9 °C for 20 min, TAG were separated by rapid sampling of
167 the upper acetone phase, which contained the carotenoids, and filtered through a 0.2 μm Minisart
168 SRP4 PTFE filter (Sartorius, Göttingen, Germany). The 20- μL carotenoid extract was directly injected
169 into the Agilent Infinity II HPLC system (Santa Clara, CA, USA). The column was a polymeric YMC-30
170 (300 \times 4.6 mm, YMC, Kyoto, Japan). Elution was performed at a flow rate of 1 mL/min as follows: (i)
171 100% A for 1 min, (ii) a linear gradient from 100% A to 10% A and 90% B for 40 min, (iii) a linear
172 gradient to 100% B for 5 min, (iv) a 5-min step with 100% B, and (v) a return to initial conditions for 5
173 min (A = methanol:water [60:40, v/v], B = methanol:methyl tert-butyl ether:water [28.5:67.5:4,

174 v/v/v]). A 15-min rinse step was then carried out using 100% ethyl acetate, followed by re-
175 equilibration with 100% A for 10 min. All solvents were of HPLC grade and were purchased from
176 Merck. The column temperature was maintained at 25 °C. An Agilent G7115A UV-visible photodiode
177 array detector was used to analyse the chromatograms at a detection wavelength of 450 nm.
178 Carotenoids were identified by the combined use of their relative retention times and their
179 wavelength absorption maxima determined using analytical standards (Merck). All analyses were
180 performed in triplicate from three independent carotenoid extractions.

181

182 2.3. Tocochromanol analysis

183 Analysis of tocochromanols was adapted from the method described previously (Montúfar et al.,
184 2010). CPO samples (15 mg) dried under nitrogen were carefully dissolved in 500 µL of *n*-hexane and
185 30 µL aliquots of the solution were injected into the Agilent Infinity II HPLC system, which was
186 equipped with an Agilent G7121B fluorescence detector set at an excitation wavelength of 290 nm
187 and an emission wavelength of 330 nm. The HPLC column was a Merck Lichrospher Si-60 (250 × 4.6
188 mm internal diameter, 5 µm particle size). The mobile phase was *n*-hexane/propan-2-ol (99:1, v/v) at
189 a flow rate of 1 mL/min. All the solvents were of HPLC grade and were purchased from Merck.
190 Standard curves were run with commercial standards of α-, β-, γ- and δ-tocopherols (Tocopherol set,
191 Calbiochem, Merck) and α-, β-, γ- and δ-tocotrienols (Cayman Chemical, Ann Harbor, MI, USA). All
192 analyses were performed in triplicate from three independent CPO dissolutions in *n*-hexane.

193

194 2.4. Fatty acid analysis

195 Fatty acid methyl esters (FAME) were prepared according to the ISO-5509 standard from 50 mg CPO
196 samples and analysed using gas chromatography to determine FA composition (Laffargue, de Kochko,
197 & Dussert, 2007). Analyses were performed using an Agilent 7820A Gas Chromatography system with
198 flame ionization detection. A Famewax capillary column (Restek, Lisses, France), (30 m × 0.25 mm ×
199 0.25 m) was used. Analyses were conducted from 185 to 225 °C at 4 °C/min and then kept at 225 °C
200 for 10 min. The carrier gas was helium at 40 cm/s. Both injector and detector were maintained at a
201 temperature of 230 °C. Only peaks identified in the chromatograms with a relative percentage >0.1%
202 were retained. All fatty acid analyses were performed in triplicate from three independent FAME
203 reactions.

204

205 *2.5. Statistical analyses*

206 Genotype means were calculated using two to four biological replicates (two to four bunches
207 collected from the same palm tree on different dates) and three technical replicates per biological
208 replicate. Linear regression and one-way ANOVA were performed using Statistica (Statsoft, Tulsa,
209 USA). Linear regression was used to test the relationships between carotene content, tocochromanol
210 content, the β -carotene to α -carotene ratio, and the percentages of tocotrienols, linoleic acid and α -
211 and β -tocochromanol forms. ANOVA was used to test the effect of the country of origin and the
212 population on all chemical traits measured. When the effect of the country of origin or the
213 population was significant, Duncan's post-hoc multiple comparison test was performed using
214 Statistica. The accuracy of the classifications based on carotene, tocochromanol and fatty acid
215 compositions was also tested using discriminant analysis (DA) and canonical analysis (CA). DA and CA
216 were performed using the following active variables: total carotene content, β -carotene to α -
217 carotene ratio, total tocochromanol content, the percentage of tocotrienols, VTE3 and VTE4
218 activities, and the percentages of 14:0, 16:0, 16:1, 18:0, 18:1 n -7, 18:2, 18:3, 20:0 and 20:1 n -9. The
219 population or the country of origin was the grouping variable. DA and CA were performed using
220 Statistica.

221

222 **3. Results and Discussion**

223 *3.1. Intraspecific variability of carotene, tocochromanol and fatty acid composition of crude palm oil*

224 Total carotene content varied considerably in the 44 genotypes chosen to represent the geographic
225 and genetic diversity of oil palm: from 77 ppm in the genotype Yang5 to 1 275 ppm in the genotype
226 Pobe3 (Fig. 2a; Supplementary Table 2). The CPO carotene content of 16 out of 44 genotypes was
227 above the limit of the range usually reported in the literature (500-700 ppm), thus supporting the
228 possible identification of high provitamin A genotypes, as previously reported by Monde et al. (2009)
229 and Noh et al. (2002). More unexpectedly, we found that more than half the genotypes studied
230 contained less than 500 ppm of carotenes. In five genotypes, CPO carotene content was even less
231 than 200 ppm. We therefore advise caution concerning the origin of the CPO when calculating
232 recommended CPO intakes for use in programmes to prevent vitamin A deficiency (Burri, 2012).

233 In all the genotypes studied here, α -carotene and β -carotene were the only two major
234 carotenoids. None of the other minor carotenoids (< 0.5%) reported in the literature (Sundram,
235 Sambanthamurthi, & Tan, 2003) was identified as a major compound in our large sample set,
236 suggesting that the intraspecific diversity in the different types of carotenoids accumulated in the
237 mesocarp of oil palm fruits is very restricted. In contrast, although the majority of genotypes had the

238 β -carotene to α -carotene ratio usually given for CPO, i.e., between 1.5 and 2, the ratio varied
239 considerably among the 44 genotypes studied (Fig. 2b). In the genotype Pobe5, β -carotene content
240 was 7 times higher than that of α -carotene (518 vs 75 ppm, Supplementary Table 2). Such a high ratio
241 was also observed in one of the two origins studied by Monde et al. (2009). Conversely, in the
242 genotype AbaC1, α -carotene represented 60% of the CPO carotenoids. Considering that the vitamin
243 A equivalence of α -carotene is half that of β -carotene (Haskell, 2012), the choice of the source of
244 CPO also appears to be crucial regarding these characteristics. Finally, it is worth noting that the β -
245 carotene to α -carotene ratio was not correlated with the total carotene content of the CPO (Fig. 3).

246 Total tocochromanol content also varied considerably within the panel of genotypes investigated
247 (Fig. 2c; Supplementary Table 3), from 310 to 1 362 ppm, a very similar range to that recently found
248 by Luo et al. (2020) in a very large set of oil palm individuals characterised to identify the molecular
249 determinants of CPO vitamin E content. Taken together, the results of our study and those of Luo et
250 al. (2020) make it possible to propose that the range for the tocochromanol content of CPO is closer
251 to 200-1 400 ppm than to 500-800 ppm (Sundram, Sambanthamurthi, & Tan, 2003) or 600-1 000
252 ppm (Hoe, Chan, Ramanan, & Ooi, 2020; Goh, Choo, & Ong, 1985). We also observed very high
253 variability of the proportion of tocotrienols in the tocochromanols accumulated in the oil palm
254 mesocarp (Fig. 2d). The CPO of four genotypes contained a substantial proportion (35-45%) of
255 tocopherols, presenting a different picture of CPO tocochromanol composition from that previously
256 reported, in which tocotrienols largely prevailed (> 80%; Monde et al., 2009; Peh, Tan, Liao, & Wong,
257 2016; Irias-Mata et al., 2017). Given the pharmacological differences between tocopherols and
258 tocotrienols (Peh, Tan, Liao, & Wong, 2016; Trela & Szymanska, 2019; Wallert, Börmel, & Lorkowski,
259 2021), the present work provides a valuable basis for the identification of genotypes producing
260 tocopherol- or tocotrienol-rich CPO. Moreover, we found no correlation between the tocochromanol
261 content of CPO and the percentage of tocotrienols (Fig. 3), suggesting that these two traits are
262 controlled by distinct genetic determinants.

263 Using the relative percentages of the different tocochromanols, it is possible to estimate the
264 activities of the enzyme VTE3 (2-methyl-6-phytyl-1,4-hydroquinone methyltransferase), which
265 regulates competition between the biosynthetic branch of γ - and α -tocochromanols and that of δ -
266 and β -tocochromanols, and the enzyme VTE4 (tocopherol O-methyltransferase), which converts γ -
267 and δ -tocochromanols into α - and β - tocochromanols, respectively (Hunter & Cahoon, 2007; Munoz
268 & Munné-Bosch, 2019; Supplementary Fig. 1). VTE3 activity was always very high (> 88%) in the panel
269 of genotypes studied here (in other words, α - and γ -tocochromanols were always the major forms of
270 vitamin E; Supplementary Fig. 2). By contrast, VTE4 activity varied considerably among genotypes,
271 ranging from 29% in genotype AbaC4 to 74% in genotype Pobe4 (Supplementary Table 3). As the

272 bioavailability and antioxidant activity of α - and γ -tocochromanols differ significantly (Peh, Tan, Liao,
273 & Wong, 2016), the data presented here may be very important in nutritional considerations of CPO
274 intake. However, a highly significant negative correlation was found between the percentage of
275 tocotrienols and VTE4 activity (Fig. 3), suggesting that in *E. guineensis*, the enzyme VTE4 converts γ -
276 tocopherol into α -tocopherol more efficiently than γ -tocotrienol into α -tocotrienol.

277 Because the tocochromanol and carotene biosynthesis pathways share the same isoprenoid
278 building blocks, they may be in competition (Asensi-Fabado & Munné-Bosch, 2010). No significant
279 correlation was found between total tocochromanol content and total carotene content in our panel
280 of 44 genotypes (Fig. 3), suggesting that there is no competition for geranylgeranyl-PP, the branch-
281 point between the two pathways (Supplementary Fig. 1). This result also suggests that the activation
282 of the upstream pathway, which produces geranylgeranyl-PP in genotypes that accumulate large
283 amounts of either carotenes or tocochromanols, does not necessarily influence the two downstream
284 pathways. However, this analysis also revealed that several genotypes had high concentrations of
285 both carotenes and tocochromanols, suggesting it is possible to select varieties with high provitamin
286 A and vitamin E CPO.

287 Palmitic (16:0) and oleic (18:1 n-9) acids were the major FA in all genotypes (Fig. 2f and 2g;
288 Supplementary Table 4), followed by stearic (18:0) and linoleic (18:2) acids (Fig. 2h and 2i). Other
289 minor FA (<1%), including vaccenic (18:1 n-7), linolenic (18:3) and arachidic (20:0) acids, were also
290 detected (Supplementary Table 4). Considerable intraspecific variation was found in the levels of
291 16:0 and 18:1 (Fig. 2f and 2g), higher than that reported previously (Gascon & Wuidart, 1975;
292 Montoya et al., 2014). Indeed, although a few studies previously pointed to a low 16:0 level in some
293 oil palm varieties, e.g. 31% in Monde et al. (2009), we did not expect to identify genotypes with 25-
294 26% of 16:0. Percentages of 16:0 and 18:1 were highly ($R=0.92$) negatively correlated
295 (Supplementary Fig. 3), as previously reported (Montoya et al., 2015). Moreover, the percentage of
296 18:0 was also negatively correlated with that of 16:0 (Supplementary Fig. 3). This finding may have
297 consequences for the melting temperature of low 16:0 CPO, since 18:0 also increases the melting
298 point of triacylglycerols. In palm oil, 18:0 is mostly incorporated in PSO triacylglycerols (P=16:0,
299 S=18:0, O=18:1; Chen et al., 2007) and PSO has a melting point as high as that of PPO (Berry, 2009).
300 The 18:2 level was not correlated with that of any of the other FA, in agreement with the distinct
301 pathways involved in the biosynthesis of 16:0, 18:0 and 18:1 in the plastid on one hand, and of 18:2
302 in the endoplasmic reticulum on the other (Dussert et al., 2013).

303 Because tocochromanols and carotenoids are strong lipid antioxidants, they are believed to be
304 accumulated by plants in seeds and fruits to protect polyunsaturated FA against peroxidation. For
305 instance, a significant relationship was found between the α -tocopherol content and the percentage

306 of 18:2 in 14 oil crops (Kamal-Eldin & Andersson, 1997). Within our representative sample of oil palm
307 diversity, neither total carotene content nor tocochromanol content was significantly correlated with
308 the percentage of 18:2 (Fig. 3).

309

310 *3.2. Differences in crude palm oil composition among oil palm origins*

311 Significant effects of the country of origin ($P=0.0067$) and of the population of origin ($P=0.0092$) on
312 the total carotene content of CPO were observed (Fig. 4), although within-country and within-
313 population variability was high in some origins: e.g., 245-992 ppm in Aba-Calabar (Nigeria). Two
314 populations contained only genotypes with high (>500 ppm) carotene content, Yocoboué in Côte
315 d'Ivoire and Pobè in Benin (Fig. 4). However, the populations La Mé (Côte d'Ivoire), Aba-Calabar
316 (Nigeria) and Deli Dabou also contained genotypes that produced a CPO rich in carotenes and were
317 thus categorised at an intermediate level according to the Duncan test. Our results are consistent
318 with those of the few previous studies which compared a limited number of origins. CPO from some
319 Nigerian genotypes had high carotene contents (Ames, Raymond, & Ward, 1960) and the variety
320 from Côte d'Ivoire analysed by Monde et al. (2009) had a higher carotene content than the variety in
321 the Deli group. No significant differences between the different groups were observed in the β -
322 carotene to α -carotene ratio (Supplementary Fig. 4).

323 Although significant ($P=0.04$), the effects of the country and of the population of origin on the
324 CPO tocochromanol content were lower than those found for carotene content (Fig. 4). However, the
325 two populations from Côte d'Ivoire, La Mé and Yocoboué, were again distinguishable because they
326 contained genotypes with very high tocochromanol contents (ca. 1 000 ppm). The Deli Dabou group
327 was classified in an intermediate position, with several genotypes with high tocochromanol contents
328 (> 800 ppm), in agreement with the high level found in the Deli genotype investigated by Monde et
329 al. (2009). The dispersion of the percentage of tocotrienols was high in some populations, including
330 in La Mé (Côte d'Ivoire) and Yangambi (Congo) (Fig. 5). However, the effect of the country of origin
331 was highly significant ($P=0.0062$) and the chance of identifying varieties with a substantial percentage
332 of tocopherols appears to be greater in Côte d'Ivoire and Benin, while the Deli group showed
333 homogeneously high CPO tocotrienol levels.

334 The most spectacular difference between the origins studied was in 16:0 and 18:1 contents
335 ($P=0.0000$ for both country and population effects; Fig. 5 and Supplementary Fig. 5). The population
336 La Mé from Côte d'Ivoire was clearly separated from all the others with a 16:0 content $< 35\%$ in all
337 genotypes (Fig. 5). This finding is in agreement with previous observations by Monde et al. (2009)
338 and Gascon and Wuidart (1975). However, it is worth noting that only one genotype from Yocoboué,

339 the other population from Côte d'Ivoire, had a low palmitate content, highlighting the specificity of
340 the CPO FA composition in the La Mé population.

341 Discriminant analysis and canonical analysis were also used to assess the accuracy of classification
342 based on carotene, tocopherol and fatty acid composition. Highly significant classifications were
343 obtained when either the population or the country of origin was used as the grouping variable, as
344 estimated by P values (<0.0000) associated with Wilks' lambda coefficients (0.00037 and 0.00250,
345 respectively). Percentages of correct classifications were very satisfactory with both grouping
346 variables (Supplementary Fig. 6). Among the 44 palm genotypes analysed, only two were
347 misclassified in both analyses. The CF1-CF2 score plots obtained by canonical analysis of CPO
348 composition clearly separated countries or populations from one another (Supplementary Fig. 6).

349 On the basis of the carotene, tocopherol and FA composition of CPO, the material from Côte
350 d'Ivoire was distinguished from the other oil palm origins among the germplasm we studied. Using
351 microsatellite genetic markers, Cochard et al. (2009) first showed that populations from Côte d'Ivoire
352 form a distinct genetic group. Their genetic divergence likely results from a major arid phase in the
353 Dahomey gap to the west of Benin between 20000 and 14000 BP. Our data suggest that this genetic
354 separation of West African populations also led to changes in the composition of the oil stored in the
355 fruits of *E. guineensis*. For this reason, it would be interesting to explore the CPO composition of
356 other group I origins, such as populations from Senegal or Guinea. Based on our recent study of fruit
357 lipid composition in 144 palm species, we hypothesise that these changes reflect genetic drift rather
358 than adaptation (Guerin et al., 2020). However, one cannot exclude a role for carotenoids as pigments
359 to attract dispersers, assuming that the fauna differed on the two sides of the Dahomey gap. Genetic
360 studies also provide evidence that the Deli group (group III) derived from group II, which
361 encompasses Benin, Nigeria, Congo and Angola (Cochard et al., 2009; Bakoumé et al., 2015). The
362 composition of CPO fits this hypothesis, since no major chemical differences were identified that
363 distinguished the Deli genotypes from those from these four countries.

364

365 *3.3. Identifying genotypes that satisfy CPO consumers and may help in programmes to fight vitamin* 366 *deficiency*

367 Cheyns, Bricas, and Aka (2004) reported that CPO consumers in Côte d'Ivoire prefer fruits harvested
368 in native palm groves that produce fluid and deep coloured CPO to fruits produced by modern
369 varieties. This traditional usage was confirmed by our data, which showed that genotypes from Côte
370 d'Ivoire had low 16:0 and high carotene contents (Fig. 4 and 5). This prompted us to investigate
371 whether some origins combine high levels of provitamin A and vitamin E and a low level of 16:0. We

372 sorted the 44 genotypes according to decreasing carotene contents and retained those with a 16:0
373 content of less than 35% (Table 1). As expected, eight of the nine genotypes that satisfied the 16:0
374 threshold used were from Côte d'Ivoire. Among these eight genotypes, two genotypes from La Mé
375 and one from Yocoboué had both carotene and tocopherol contents higher than 500 ppm.
376 Therefore, oil palm populations from Côte d'Ivoire represent a valuable reservoir to identify varieties
377 that satisfy both traditional CPO demand for cooking (Cheyns, Bricas, & Aka, 2004; Rafflegeau,
378 Nanda, & Genot, 2018; Rébéna, Rafflegeau, Kanski, Nanda, & Genot, 2019) and the requirements of
379 action programmes against vitamin A deficiency (Zagré, Delpeuch, Traissac, & Delisle, 2003; Burri,
380 2012), combined with increasing vitamin E intake. For instance, the genotype Lamex1 showed ca. 700
381 ppm carotenes, 1 200 ppm tocopherols and a total saturated FA percentage lower than 40%.

382 However, none of genotypes from populations of restricted origin combined the extreme values
383 found in each of the three classes of molecules: > 1 000 ppm for both carotenes and tocopherols
384 and < 35% for 16:0. Consequently, we further investigated 12 hybrids maintained in the CRA-PP field
385 genebank at Pobè, Benin (Supplementary Tables 2-4). The hybrids were chosen because one of their
386 two parents originated from populations that were not represented in the genebank (Fig. 1): Ekona,
387 Mayang and Widikum in Cameroon, Eala and Sibiti in Congo, and a population from Nigeria, whose
388 exact location remains uncertain (and is therefore simply called 'Nigeria'). Two of the 12 hybrids had
389 particularly high carotene contents together with a low level of palmitate (Table 1). They both
390 originated from a cross between individuals from the populations La Mé and Nigeria. Moreover, the
391 hybrid LamexNige1 had the highest carotene content (1 564 ppm) among the 56 genotypes
392 evaluated, exceptionally high vitamin E content (1 330 ppm) and low total saturated FA (38.4%),
393 since it combined low 16:0 (32.3%) and low 18:0 (6.1%) levels. Crosses between La Mé and Nigeria
394 origins thus offer the opportunity to both meet CPO consumer requirements and have very high
395 vitamin contents.

396

397 **4. Conclusions**

398 Given the major economic importance of oil palm, information on the natural diversity and
399 nutritional potential reported in this study should encourage the oil palm community to continue
400 efforts to characterise CPO composition in the other major oil palm gene banks around the world,
401 including that maintained in Malaysia (Bakoumé et al., 2015). To date, breeding efforts in oil palm
402 have been almost entirely focused on yield and disease resistance (Murphy, 2007). Although
403 successful in terms of these traits, they may have led to a loss in oil fluidity and in concentrations of
404 provitamin A carotenoids in modern varieties. Our investigations showed that crosses between

405 selected origins can combine several key nutritional properties of CPO, not only with respect to
406 vitamins, but also its saturated FA level, whose role in health is frequently questioned and could
407 improve consumer acceptance in Western countries (Murphy, 2007). It is also worth noting that the
408 selection of oil palm varieties combining low palmitate and high provitamin A and vitamin E contents
409 would facilitate both the production of red palm olein and the extraction of CPO phytonutrients
410 (Hoe, Chan, Ramanan, & Ooi, 2020).

411

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418

419 **Author contributions**

420 **Stéphane Dussert**: Conceptualization, Funding acquisition, Methodology, Supervision, Writing -
421 Original Draft. **Fabienne Morcillo**: Conceptualization, Funding acquisition, Methodology, Supervision,
422 Writing - Review & Editing. **Virginie Vaissayre**: Methodology, Investigation. **Julien Serret**:
423 Investigation. **Sylvie Avallone**: Methodology, Investigation. **Hubert Domonhédó**: Resources. **Florence**
424 **Jacob**: Conceptualization.

425

426 **Declaration of interest**

427 All authors declare no conflicts of interest exist.

428

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536

537 **Figure captions**

538 **Figure 1.** Origin of the oil palm genotypes studied here. The natural range of *E. guineensis*
539 corresponds to the area hatched in blue. The populations collected and the number of genotypes per
540 population studied are given in the green boxes. The size of the two subgroups of the Deli group,
541 whose exact African origin is unknown, is given in the grey box. Hybrids between populations of
542 different countries are indicated in the blue boxes.

543 **Figure 2.** Distribution of CPO (a) carotene content, (b) β -carotene to α -carotene ratio, (c)
544 tocopherol content, (d) tocotrienol percentage (e) VTE4 activity, and (f) 16:0, (g) 18:1, (h) 18:0
545 and (i) 18:2 levels in the 44 genotypes chosen to represent the geographic and genetic diversity of oil
546 palm.

547 **Figure 3.** Relationships between the different components of the carotene, tocopherol and fatty
548 acid composition of CPO in the 44 genotypes representative of the geographic and genetic diversity
549 of oil palm.

550 **Figure 4.** Effects of the country and the population of origin on CPO carotene and tocopherol
551 contents. Countries or populations followed by the same letter do not differ significantly according to
552 Duncan's post hoc test.

553 **Figure 5.** Effects of the country and the population of origin on CPO tocotrienol and 16:0
554 percentages. Groups, countries, or populations followed by the same letter do not differ significantly
555 according to Duncan's post hoc test.

556

Table 1. CPO composition of the 12 genotypes with a palmitate level below 35%. α -C and β -C: α -carotene and β -carotene. Tocols: tocochromanols. PRO: population of restricted origin.

Type	Genotype	Carotenes (ppm)	β -C to α -C ratio	Tocols (ppm)	Tocotrienols (%)	VTE4 activity (%)	16:0 (%)	18:0 (%)	18:1 (%)	18:2 (%)
Hybrid	LameXNige1	1564	1.5	1330	70.2	58.5	32.3	6.1	49.0	10.7
Hybrid	LameXNige2	1172	1.7	756	66.4	55.9	33.5	6.5	48.4	9.6
PRO	Lame1	698	1.2	1214	64.6	58.2	32.1	7.5	45.6	12.6
PRO	Lame7	601	2.1	495	69.5	55.6	28.8	10.4	51.9	7.1
PRO	Lame4	590	1.0	881	57.9	66.5	30.5	8.4	45.7	13.8
PRO	Yoco3	515	1.2	985	68.6	57.0	30.2	10.2	49.1	8.8
PRO	Lame2	493	1.3	956	69.3	55.2	26.6	7.6	53.5	10.6
PRO	Lame5	439	5.5	310	83.9	34.5	28.1	9.6	44.8	16.0
PRO	Lame3	338	2.9	526	81.7	45.2	25.7	10.9	52.3	9.4
PRO	Lame6	243	1.4	498	71.7	53.6	33.0	10.3	47.8	7.3
Hybrid	LameXSibi1	207	0.5	486	79.3	49.0	32.2	7.4	47.4	11.3
PRO	Cuan1	199	1.9	678	75.1	52.4	34.8	4.2	48.6	10.3







