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## Exploring diversity of oleaginous plants to find potential new sources of oil bodies adapted to climate change

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### ABSTRACT

Global social welfare faces increasing threats from population growth and climate change, particularly impacting food security and economic development, especially for vulnerable groups. Agronomic practices, like crop selection, are essential in addressing these challenges.

Agroforestry, for example, offers a promising solution by both mitigating soil degradation and contributing to sustainable incomes for the local population. Plants adapted to tropical or extreme climatic conditions can make a major contribution to achieving various sustainable development goals. A key factor in their resilience is the presence of oil bodies (OB), lipid storage organelles. Thanks to their unique structure (spherical droplet with a membrane structured with phospholipid monolayer and proteins), composition (triacylglycerols and minor compounds) and physico-chemical properties (pH stability ranges, thermal behavior) can play their lipid storage and protective role in their environment and have attracted considerable research attention. An overview of the OB composition of major crops compared with that of crops grown in non-temperate climates provides a better understanding of the interactions between climate, OB composition, with a particular focus on chia seeds. A wide variety of fatty acid compositions are found in seed or fruit oil from non-temperate climates. Exploring the OB structure that shelters them could explain their adaptation to different climates and the levers that could be used to benefit from them sustainably, considering the exploitation of these lesser-known source plants in virtuous agricultural/agroforestry schemes. Such interest would contribute to the development of larger-scale supply chains to improve the resilience of developing and advanced countries to climate change.

### 1. Introduction

Biodiversity is under threat from both demographic expansion and climate change [1]. The escalating global demographic expansion has heightened the urgency to protect the biodiversity, especially considering the dire threats posed by climate change to vulnerable populations. Amidst these challenges, the importance of fulfilling the United Nations' Sustainable Development Goals (SDG) is increasingly evident (<https://sdgs.un.org/goals>). For example, the SDG 2 "Zero hunger" and SDG 3 "Good health and well-being" have to limit the global deficit of oil and fat consumption, especially in low-income countries [2]. In the face of these issues, developing nations often grapple with the paradox of rising populations and inadequate resources to cope with the disruptive

effects of climate change (European green deal, [https://commission.europa.eu/strategy-and-policy/priorities-2019-2024/european-green-deal\\_fr](https://commission.europa.eu/strategy-and-policy/priorities-2019-2024/european-green-deal_fr)). In particular, agroforestry could offer a promising solution to this paradox.

Indeed, mixing agriculture and forestry could reduce soil degradation and actively contribute to climate change mitigation [3], notably in initiatives like the great green wall, integrating shrubs and trees [4].

Agronomic choice of crops also plays an important role in maintaining biodiversity. For instance, plants adapted to tropical climates or to extreme climatic conditions play a significant role in ensuring local food security. They are an important source of income for farmers and for all the people depending on in the value chain of their exploitation. Furthermore, these climate-smart plants can be pivotal tools in

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mitigating various climatic concerns. For instance, in Africa, the neem tree (*Azadirachta indica*) known for its insecticidal [5] and health effects [6,7] of its extracts demonstrates resistance to arid conditions and flooding, offering solutions against soil erosion and providing shaded areas. *Moringa oleifera* showcases commendable resilience to salinity and heat, finding use in both sustenance and landscaping [8]. *Jatropha curcas*, besides being an additional income source for women, presents an effective erosion deterrent and contributes to local economies through the use of its press cake as fertilizer [9]. Oils and fats from non-temperate oleaginous plants are often the major interest of the exploited species, generally for edible purposes but also for other valorization schemes.

One of the reasons for these characteristics of resistance to external conditions is due to the organelles which house lipids called oleosomes or oil bodies (OB). OB are ubiquitous organelle present mainly in seeds but also in senescing leaves. These lipoprotein assemblies, possess a small diameter (around 0.5–20  $\mu\text{m}$ ), shielded by a monolayer of phospholipids and specific membranous proteins deeply anchored inside the OB [10–13] (Fig. 1). Because the membranous proteins are mainly oleosins (MM ranging between 15 and 20 kDa) which are amphiphilic proteins with very peculiar structural feature including a central hydrophobic hairpin like domain based on a two alpha-helix, OB possess natural emulsifying properties and locate at the water/oil interface. In addition to oleosins, caleosins and steroleosins are others minor interfacial proteins with molecular sizes of 25–35 and above 35 kDa, respectively [14,15]. In terms of functionality, caleosins are able to bind calcium [16] whereas steroleosins in addition to N-terminal lipid anchoring domain have sterol-binding functionality and dehydrogenase domain [17]. OB accumulate during oleaginous seed maturation and are remobilized during seed germination and seedling growth, with triacylglycerol (TAG) being the main nutrients used as metabolic substrates and energy [18].

The adaptation of OB to adverse climatic conditions certainly involved the structure of these organelles, and more particularly their peculiar membranes and its lipid composition. Indeed, these membranes have adjustable composition, notably in terms of chain length and unsaturation of the polar fatty acids (FA), which determine their rheological and resistance properties concerning temperature and humidity. For example, the distribution of OB, lipid composition and FA composition of OB from beach pea nodules, were analysed during different seasons [19,20]. The highest OB, phospholipids and PUFA (polyunsaturated FA) contents were observed in winter, possibly protecting the nodules cell from cold temperature. Moreover, the link between the level of unsaturation and membrane stability has been studied for several decades [21,22]. For instance, studies have demonstrated that

phospholipid unsaturation could improve membrane stability, and that under drought stress for instance, there was an increased formation of unsaturated FA, with omega-3 desaturase playing a significant role in this resistance mechanism [23,24]. Additionally, sterol composition and content, involved cell permeability, also depended on climate and stress factors [25,26] demonstrated that rising temperature increased not only sterol concentrations in olive oil, but also tocopherol (TOH), but decreased the oil content. Similar observations were made regarding TOH content in almonds [27].

Beyond lipid composition, membrane bound proteins also play a crucial role in seed tolerance to adverse effects, e.g. oleosins are pivotal in the freezing, imbibition and dehydration tolerance of the seeds avoiding their fusion and low germination rate [28–30]. OB exhibit high resistance to coalescence in the cell, because they can exert electrostatic repulsions, characteristics that collectively allow the formation of stable emulsions ex-vivo [31].

Despite the putative link between, OB content, characteristics and potential resistance to climatic hazard, most of the studies focusing on OB have about major oilseed and protein crops from temperate region and did not pay attention to minor climate-smart crops nor to OB from major tropical crops except for soya and groundnut [32,33].

The OB from major temperate crops have been studied for food applications, for their natural emulsion droplet structure [12]. As demonstrated in the case of walnut OB, the stability of these extracted organelles is improved when seeds undergo minimally-processing [34]. The use of natural OB structures is an interesting alternative to solvent oil extraction, which involves destructuring these organelles in order to recover the lipids [35]. The preservation of the OB is achievable through the aqueous crushing of the seeds, as highlighted in studies [36–41]. Soya OB is for example widely used in the manufacture of milk, cream and tofu, as well as in gels and for the delivery of bioactive compounds [33,42]. OB are also used in cosmetics or in the pharmaceutical field for its ability to act as carrier for bioactive molecules [43,44].

The OB are also renowned for their ability to improve the oxidative stability of emulsions. In comparison to sodium dodecyl sulphate (SDS) or tween 20 emulsions, the emulsion derived from sunflower for instance exhibited superior oxidative stability [45]. Highly polyunsaturated FA are better protected against oxidation in these OB [46], which typically contain or closely interact with TOH. In particular [47], showed a strong interaction between  $\delta$ TOH and soybean OB in comparison than  $\gamma$ TOH which is the main TOH in seed [48]. investigated the interaction between polyphenol and rice bran OB and it has been shown that the molecules improved both oxidation and emulsification stabilities. The bioaccessibility of TOH and FA from sunflower OB has been assessed *in vivo*, comparing it to Tween 20 or whey protein isolate

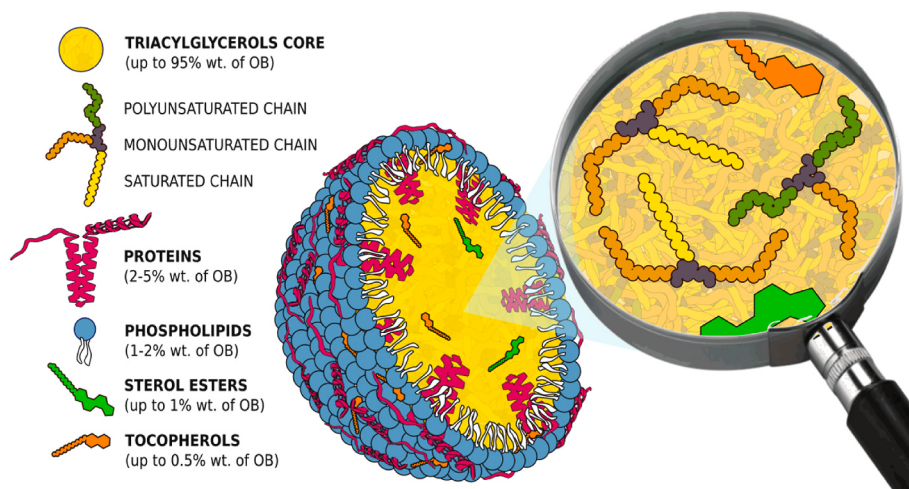


Fig. 1. OB structure.

emulsion [49]. Notably, the hydrolysis process was slower for OB than for the emulsion, suggesting a positive effect on digestion and satiety. These advantages in terms of resistance to digestion and satiety were also reviewed in details [46].

If OB proves advantageous for cosmetic formulations [50], for vectorizing/encapsulating some proteins [51,52] or for increasing the bioavailability of organic liposoluble compounds [53,54], it holds particular promise in facilitating the improved vectorization and stability of essential FA but also valuable minor compounds such as sterols and TOH.

To enhance the opportunities and address societal challenges, other underexploited minor crops as those grown in tropical, semi-arid and arid regions should be identified and developed as potential source of OB of interest for food and non-food applications. In these areas, oilseed and protein crops may encounter significant environmental stresses and it is reasonable to assume that the seeds, along their substantial lipid reserves, have adapted to thrive in such conditions. The diverse properties and applications of OB across various fields, along with their potential role in enhancing plant adaptability to different climates, underscore the importance of investigating OB from seeds originating in tropical or non-temperate regions. These climates present unique challenges and opportunities for agricultural innovation. By focusing on both major crops and minor crops from these regions, we can uncover novel adaptive mechanisms and functionalities of OB that may not be present in temperate-zone plants.

To do so, the main physicochemical parameters and biochemical attributes from OB of crops grown in non-temperate climate will be first presented. Then the putative impact of climate on OB composition in plants grown under different climates and geographical localizations will be discussed. Some oleaginous seeds presenting peculiar biochemical composition and yet not harvested for OB extraction for food or non-food applications will be presented in a third and last part of this review.

### 1.1. Main physicochemical parameters and biochemical attributes of OB from crops in non-temperate climate

We will consider here plants not generally grown in temperate

climate and will concentrate mainly on oleaginous species since they produce seeds having an oil content exceeding 20 % with some exceptions however for some tropical fruit seeds (*Punica granatum*) or amilaceae plant (*Coix lacryma-jobi*) of special interest for OB extraction that will also be presented.

The study of OB from major crops (rapeseed (*Brassica napus*), sunflower (*Helianthus annuus*), soybean (*Glycine max.*), maize (*Zea mays*), sesame (*Sesamum indicum* L.) has been well documented in the last decades (Table 1 and Fig. 2.). Fewer articles concern minor crops, so an overview of some OB from minor species in comparison to well-studied major crops is given.

#### 1.1.1. Yields, conditions of extraction and physicochemical attributes

First, if the OB yields of extraction are considered, it appears that all the studies are still far from achieving industrial requirements (Table 2.). The OB extraction yields being generally omitted or quite low (between 18 and 20 % for *Gevuina avellana* and *Madia sativa*) [62], or medium (42 % and 46.0 % for *Argania spinosa* and *Punica granatum*, respectively [63, 64]). Notably, only *Mauritia flexuosa* L.f. allowed high extraction yields, surpassing 70 % [65].

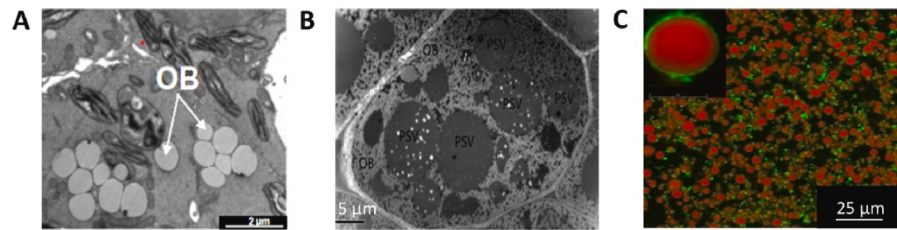
The TAG/protein ratio is an important feature which depends on conditions of extraction. For example, processing *Gevuina avellana* and *Madia sativa* allowed TAG/protein ratio increase from 2.6 to 0.7 to finally reach 29. As with major crops, protein content varies depending on aqueous extraction method. Increasing pH from 6.8 to 11 decreased protein content by 25 % for *Arachis hypogaea* OB (Zaaboul et al., 2018a). Washing *Echium plantagineum* OB with buffer pH 7.5 or with urea (9M) impacted the protein content [72]. The TAG/protein ratios were 38.9, 86.8 and 107.6 for crude OB, water-washed OB and urea washed OB, respectively.

Now diameter, a relative homogeneity in the size of the OB were found for identified species, between 1 and 3 µm for *Coix lacryma-jobi* [69], *Punica granatum* [64] and *Argania spinosa* (Zaaboul et al., 2018b) and between 3 and 10 µm for *Gevuina avellana*, *Madia sativa* [62], *Arachis hypogaea* [66], *Carya illinoensis* [74] and *Pistacia vera* L. [75] (Table 3.). The higher diameters indicated for the OB of other seeds such as *Mauritia flexuosa* L.f. [65], *Persea americana* Mil. [73] and *Cocos*

**Table 1**  
Examples of characteristics of OB from different majors' crops.

seeds	Diameter (µm)	TAG (%)	Proteins (%)	Phospholipids (%)	Free fatty acids (%)	Ref
<b>major crops</b>						
<i>Arachis hypogaea</i> Peanut	2.0	98.2	0.9	0.8	0.1	[55]
<i>Avena sativa</i> Oat	1.1	89.9	0.4	(n.a) <sup>a</sup>	(n.a)	[56]
<i>Brassica napus</i> Rapeseed	0.7	94.2	3.5	2.0	0.4	[55]
<i>Brassica nigra</i> Mustard	0.7	94.6	3.3	1.6	0.2	[55]
<i>Prunus dulcis</i> Almond	2.6	94.4	1.4	1	0.8	[57]
<i>Glycine max.</i> Soybean oil	0.4 <sup>a</sup>	85.9 <sup>b</sup>	8.2 <sup>b</sup>	5.8 <sup>b</sup>	(n.a)	<sup>a</sup> [37] <sup>b</sup> [58]
<i>Gossypium hirsutum</i> L. Cotton seed	1.0	97.0	1.7	1.2	0.1	[55]
<i>Glycine max.</i> Soybean	0.6 <sup>c</sup>	85.9 <sup>d</sup>	5.1 <sup>c</sup>	5.9 <sup>d</sup>	(n.a)	<sup>c</sup> [59] <sup>d</sup> [58]
<i>Helianthus annuus</i> Sunflower	1.0–2.0	96	(–)	2.5	(–)	[60]
<i>Linum usitatissimum</i> Linseed	1.3	97.7	1.3	0.9	0.1	[55]
<i>Oriza sativa</i> L. Rice	1.9–5.8	83.7	11.5	(n.a)	(n.a)	[61]
<i>Sesamum indicum</i> L. Sesame	2.0	97.4	0.6	0.6	0.1	[55]
<i>Zea mays</i> Maize	1.5	97.6	1.4	0.9	0.1	[55]

<sup>a</sup> n.a: non attributed.



**Fig. 2.** Microscopic images of OB of rapeseed (A) and soybean (B) by transmission electronic microscopy and of almond (C) by confocal microscopy stained with Nile Red (lipid) and Fast green (protein). The left image includes a zoom (top left corner) on one almond OB showing the protein layer covering the entire surface of the lipid core. Rapeseed OB reproduced with authorization from (Boulard et al., 2015), soybean OB reproduced with authorization from (Han et al., 2013) and almond reproduced with authorization from (Gallier et al., 2012). Abbreviation: OB oil bodies, PSV: protein stocking vesicle. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 2**  
OB yield, lipid content, protein content and ratio lipid/protein.

OB species	OB Yield (%)	Lipid content (% DM <sup>a</sup> )	Protein content (% DM <sup>a</sup> )	Ratio lipid/protein	Ref
<i>Arachis hypogaea</i>	–	–	–	4.91	[66]
Peanut	–	85.5	1.5	–	[67]
<i>Argania spinosa</i>	42	88.1	5.9	–	(Zaaboul et al., 2018b)
Argan	–	–	–	–	[68]
<i>Cannabis sativa</i> L.	–	79.3	1.5	–	[63]
Hemp seeds	–	96.3	2.2	–	[63]
<i>Carya illinoensis</i>	–	95	–	–	[69]
Pecan nut	–	95.9–98.8	1.1–1.3	–	[70]
<i>Coix lacryma-jobi</i>	–	93.4	2.4	–	[71,72]
Job's Tears	–	–	–	–	[71,72]
<i>Curcubita pepo</i>	–	–	–	–	[71,72]
Pumpkin	–	–	–	–	[71,72]
<i>Eschium plantagineum</i>	–	–	–	–	[71,72]
purple viper's-bugloss	–	–	–	–	[71,72]
<i>Gevuina avellana</i>	18.3	–	–	29	[62]
Chilean hazelnut	–	–	–	–	[62]
<i>Madia sativa</i>	20.5	–	–	29	[62]
Coast tarweed	–	–	–	–	[62]
<i>Mauritia flexuosa</i>	73.0	39.8	3.0	–	[65]
L.f.	–	–	–	–	[65]
Buriti	–	–	–	–	[65]
<i>Persea americana</i>	9.8–13.5	–	–	–	[73]
Mil.	–	–	–	–	[73]
Avocado	–	–	–	–	[73]
<i>Punica granatum</i>	46.0	39.5	16.1	–	[64]
Pomegranate	–	–	–	–	[64]

<sup>a</sup> DM: dry matter.

*nocifera* L. [76] can result from both *in-vitro* and *in-vivo* aggregation and subsequent coalescence of smaller OB. A special case is *Simmondsia chinensis* (jojoba), which has not OB but wax bodies, meaning no TAG accumulation but esters of FA and fatty alcohols [77]. The diameter of these wax bodies is around 1.5 μm.

Now considering their colloidal stability, for instance assessing the stability against flocculation of OB after aqueous extraction, it is important to know the isoelectric point (IEP) of their surface protein. This point corresponds to a net null zeta potential, so an absence of electrostatic surface repulsion. The stability of oleosomes against flocculation occurs generally at low pH < IEP-2 or high pH > IEP+2 with zeta potential superior to 30 mV. IEP is not always indicated but in general, the corresponding pH is between 4 and 6 [67]. Therefore, at neutral pH, zeta potentials are generally negative and due to the exposure of negatively charged residues of membranous proteins [80]. For example, the available values gave 4.8, 4–5 and 4–6 for *Arachis hypogaea*, *Eschium plantagineum* and *Argania spinosa*, respectively. However,

only *Mauritia flexuosa* L.f. IEP was found at lower values, between pH 2 and 3 [65]. This result could come from a more pronounced exhibition of membranous phospholipids whose pKa are low with high differences between zeta potential at pH 2 and pH 9 (6.3 mV vs. –48.8 mV, respectively). Even if the IEP was not measured, OB of *Coix lacryma-jobi* aggregate when pH decreased from 7.5 to 6.5 indicating low potential zeta at this 6.5 [69]. For *Anacardium occidentale* OB, a basic pH of 8.6 allow a zeta potential superior to - 40 mV [72,81] studied *Eschium plantagineum* OB and showed that zeta potential decreased from 30 at pH 4 to –45 mV at pH 7 and IEP was between pH 4 and 5 depending on OB preparation. The flocculation of *Arachis hypogaea* OB with pH changes was observed through an increase of particle diameters from a pH increase from 3 (~6 μm) to 5 (~15 μm), with a decrease of particle diameters from pH 5 to 7 (~4 μm) indicating the presence of larger particles (aggregates) at pH close to the IP (4.8) [66]. *Argania spinosa* OB had also a small diameter (1.9 μm) at native pH (7.0), but the diameter increased to 25 μm at the isoelectric point of pH = 5.1 (Zaaboul et al., 2018b). *Sesamum indicum* L. OB remain as discrete particles at pH 7.5 but aggregate at pH 6.5 [82]. Regarding *Cocos nocifera* L., the volume-average size of OB was above 20 μm at IEP but remained superior to 10 μm from pH 3 to 7 with zeta potential between –20 mV and +20 mV [76]. Another study confirmed a low and negative zeta potential observed at native pH (6.1), which could also explain a high volume-average particle size  $D[4,3] = 18.9$  [78]. However, the presence of a significant second population between 1 and 10 μm shall indicate that a majority of OB were between 1 and 10 μm in this case. High diameters are also measured for *Persea americana* Mil. but seems not homogenous [73]. A bimodal distribution was also observed for *Mauritia flexuosa* L.f., but it could result to cell debris or aggregation of OB [65].

pH is not the only factor acting on oil-droplets surface charges and consecutive electrostatic repulsion forces. Presence of ions in the vicinity of OB can also annihilate or increase their surface potential, having then also an influence on zeta potential. Ionic strength can then have an important effect on OB stability. For instance, it was observed for *Arachis hypogaea* that zeta potential decreased with increasing NaCl concentration and that stability was reached below 10 mM [66]. However, ionic strengths from 0 mM to 150 mM of NaCl did not impact the stability of *Madia sativa* and *Gevuina avellana* [62].

When high particle sizes did not only result from flocculation but also from a significant coalescence, as observed for *Carya illinoensis*, *Argania spinosa* and *Cocos nocifera* L. OB for example, this propension to coalescence close to their IEP point indicates a poor steric repulsion and/or mechanic resistance, which are generally offered by the synergetic action of phospholipids and membranous proteins [83]. However, surrounding proteins can also play a role in OB stability. Washing OB with water at different pH, saline solutions or chaotropic agents influences the interactions with proteins present in their direct environment. The removal of these proteins could decrease depletion forces but may have a beneficial or deleterious effect on zeta potential, impacting OB resistance to aggregation. For instance, washing and purification of OB

**Table 3**

Diameters ( $\mu\text{m}$ ) and  $\zeta$ -potential (mV) at different pH on the medium and iso-electric point (IEP) from OB species.

OB species	Diameter ( $\mu\text{m}$ ) (pH)	$\zeta$ -potential (mV) (pH)	IEP	Ref
<i>Arachis hypogaea</i> Peanut	pH = 3.0: 6 pH = 4.0: 14 pH = 5.0: 15 pH = 7.0: 4	pH = 3.0: $\zeta$ -potential $\approx +36$ mV pH = 4.0: $\zeta$ -potential $\approx -25$ mV pH = 5.0: $\zeta$ -potential $\approx -5$ mV pH = 7.0: $\zeta$ -potential $\approx -25$ mV	4.8	[66]
<i>Argania spinosa</i> Argan	pH = 2.0: 2.61 pH = 5.5: 23.4 pH = 7.0: 1.91	pH = 2.0: $\zeta$ -potential = +17.7 mV pH = 8.0: $\zeta$ -potential = -32.25 mV	5.1	(Zaaboul et al., 2018b)
<i>Cannabis sativa</i> L. Hemp seeds	3.2	pH = 4.0: $\zeta$ -potential = +20 mV pH = 7.0: $\zeta$ -potential = -32.8 mV pH = 10.0: $\zeta$ -potential = -68.7 mV	4-45	[68]
<i>Carya illinoensis</i> Pecan nut	2-5	pH = 9.0: $\zeta$ -potential = -19.83 mV	-	[63]
<i>Cocos nucifera</i> L. Coconuts	Polydispersed 1-20	pH = 6.1: $\zeta$ -potential = -13 mV	4	[78]
<i>Coix lacryma-jobi</i> Job's Tears	0.5-2	-	-	[69]
<i>Curcubita pepo</i> Pumpkin	pH = 3.0: 1.2 pH = 7.4: 0.4 pH = 9.0: 0.9	pH = 3.0: $\zeta$ -potential = +30 mV pH = 7.4: $\zeta$ -potential = +40 mV pH = 9.0: $\zeta$ -potential = 0 mV	3-3.5	[79]
<i>Eschium plantaginum</i> Purple viper's- bugloss	1-3	pH = 4.0: $\zeta$ -potential $\approx +30$ mV pH = 7.0: $\zeta$ -potential $\approx -45$ mV	4.5-5	[71,72]
<i>Gevuina avellana</i> Chilean hazelnut	5-10	-	-	[62]
<i>Madia sativa</i> Coast tarweed	5-10	-	-	[62]
<i>Mauritia flexuosa</i> L.f. Buriti	Bimodal distribution 0.7-20/20-178	pH = 2.0: $\zeta$ -potential = +6.3 mV pH = 9.0: $\zeta$ -potential = -48.8 mV	2-3	[65]
<i>Persea americana</i> Mil. Avocado	Bimodal 11-12	pH = 3.0: $\zeta$ -potential = +12 mV pH = 6.1: $\zeta$ -potential = -13 mV	3.5-4	[73]
<i>Pistacia vera</i> L. Pistachios	3.6	-	-	[75]
<i>Punica granatum</i> Pomegranate	0.2-3.1	-	-	[64]
<i>Simmondsia chinensis</i> Jojoba	1.5	-	-	[77]

increased the zeta potential for *Cocos nucifera* L., indicating stability [78]. For *Eschium plantaginum*, it was observed that removal of extraneous proteins at neutral pH had no effect on the surface charges but could increase stability against flocculation at low pH (5.5-7) [72]. For *Sesamum indicum* L., purified OB aggregated at pH 6.5 but without coalescence indicating a good steric hindrance of surface oleosins [82]. However, the impact of washing, removal of extraneous proteins, on stability is nuanced, as observed in several studies. Removal of these proteins can at the same time increase electrostatic repulsion and decrease steric force, being then beneficial against flocculation but deleterious for coalescence as it was observed for maize germ and flaxseed OB [41,84]. Their presence can modify the IEP, as observed for *Eschium plantaginum* (from pH 5 to pH 4.5) but does not change in this case the tendency to aggregate or to coalesce [72].

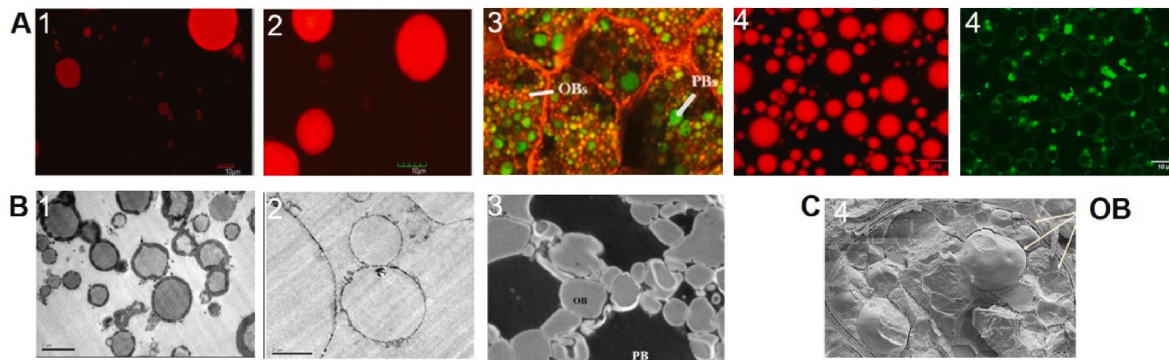
Finally, even if the OB from non-temperate crops have a similar size range to temperate crops OB (Fig. 3.), their response to pH and salinity changes and their resistance to coalescence offer a large palette of behaviors, inducing obvious changes in the extent of their potential industrial applications, especially for vectorizing or diffusing their valuable lipids.

### 1.1.2. Biochemical features

TAG composition analysis reveal distinct FA profiles among these OB (Table 4.). Lauric acid is prominent in *Cocos nucifera* L. (around 50 %), while palmitic acid (PA) is high in *Hippophae rhamnoides* L. pulp (35-40 %), *Persea americana* Mil. (up to 39 %) and *Mauritia flexuosa* L.f. (up to 70 %). Rich sources of alpha linolenic acid (ALA) include *Hippophae rhamnoides* L. (up to 37 %) and *Eschium plantaginum* (28 %). *Punica granatum* stand out for its high content of punicic acid (PuA) (79-84 %), oleic acid (OA) is abundant in *Gevuina avellana* (up to 39 %), *Arachis hypogaea* (up to 58 %), *Coix lacryma-jobi*, (38-51 %). Notably, *Ricinus communis* is a unique case exhibiting a high content in ricinoleic acid (RiA) (up to 74 %).

While the structure of OB contributes to protecting valuable TAG against oxidation [63], a high content in TOH could also be an interesting point. Some seed oils have TOH content exceeding 1000 ppm, such as *Sesamum indicum* L. (up to 5292 ppm), *Punica granatum* (1350-5250 ppm), *Hippophae rhamnoides* (2736-4303 ppm) and *Mauritia flexuosa* L.f. (1041 ppm) (Table 5.). In contrast, other seeds have mild content as *Madia sativa* (760-856 ppm), still above values generally found in "traditional" edible oils (60-420 for palm, 180-240 for rapeseed, 320-590 for sunflower, 180-250 for corn oil) [105]. *Gevuina avellana* is the sole specie with a high amount of gamma tocotrienol ( $\gamma\text{T3}$ ) form (>90 %), known for its antioxidant effects with potential pharmaceutical applications for cancer and neurodegeneration [106, 107]. The  $\gamma\text{TOH}$  isomer is preponderant in various seeds while the alpha form prevails in others (*Madia sativa* (up to 96 %), or *Arachis hypogaea* (77 %)). For *Arachis hypogaea*, a change in TOH isomer was observed with pH of the medium, with a majority of alpha form at pH 6.8-8 while a higher pH increased Gamma form (Zaaboul et al., 2018a). Both alpha and gamma isomers could demonstrate antioxidant activities even at low concentrations (100 ppm) in oil in water emulsion [108], but it is still difficult to differentiate their respective efficiency in the protection of an OB, even if their persistence in OB has already been demonstrated [38,109].

As vector of active components, OB are also naturally rich in other valuable compounds as phytosterols, these compounds being generally liposoluble. They are particularly known for their cholesterol-lowering properties [110] and they can also demonstrate anti-cancer properties [104]. They are particularly in high amount in *Sesamum indicum* L. (7000 ppm), *Pistacia vera* L. (5000 ppm) and *Hippophae rhamnoides* (>6000 ppm) but are also concentrated in *Madia sativa* (3000 ppm), *Punica granatum* (4000), *Argania spinosa*, (around 1500 ppm), *Carya illinoensis* (2000 ppm), *Ricinus communis* (2300 ppm), *Anacardium occidentale* (1990 ppm), and *Eschium plantaginum* (2000 ppm) while the content is inferior for *Coix lacryma-jobi* (around 500 ppm).



**Fig. 3.** Microphotographs of confocal (A), TEM (B) and Cryo scanning electron microscopy (SEM) (C) from OB of *Madia sativa* (1), *Gevuina avellana* (2) reproduced with authorization from Ref. [62], (3) peanut reproduced with authorization from (Zaaboul et al., 2018), (4) coconut reproduced with authorization from Ref. [78]. For the microphotographs of confocal OB are stained red by Nile red and protein are stained by fast green FCF. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 4**  
Fatty acid composition, TOH and sterol content of OB.

OB	Origin	FA				Total TOH (ppm)			Total sterol (ppm)			ref
		PA	OA	LA	FA*	αTOH	γTOH	Other TOH**	campesterol	stigmasterol	β sitosterol	
		(%)				Relative (%)			Relative (%)			
<i>Arachis hypogaea</i> Peanut	China	14	41	35	SA 4	–	–	–	–	–	–	[85]
	China	–	45	30	–	≈260 77	γTOH 23	γT3 –	632 17	stigmasterol 10	β sitosterol 72	[86]
<i>Argania spinosa</i> Argan	Morocco	10	45	32	SA 10	597.75 αTOH 50	γTOH 580	δTOH 50	–	–	–	[87]
<i>Carya illinoensis</i> Pecan nuts	China	6	73	17	ALA 0.24	–	–	–	–	–	–	[63]
<i>Crescentia alata</i> Jicaro (milk)	Nicaragua	–	–	–	–	175	–	–	–	–	–	[88]
<i>Cocos nucifera</i> L. Coconuts	Tonga	7	4	1	Lau 52 MA 17	–	–	–	150	–	β sitosterol 100	[78]
<i>Eschium plantaginium</i> Purple viper's-bugloss	–	8	18	13	ALA 34 SDA 14	563 αTOH 3	γTOH 93	δTOH 4	–	–	–	[71]
<i>Gevuina avellana</i>	Chili	2	26	10	PIA 26	–	–	–	–	–	–	[62]
<i>Hippophae rhamnoides</i> L. Sea buckthorn	Poland	7	13	36	PIA 36	686–1147 αTOH 89	γTOH 2	βTOH 6	9304–16129 campesterol 1	stigmasterol –	βsitosterol 43–57	[89]
<i>Madia sativa</i>	Chili	13	9	70	–	–	–	–	–	–	–	[62]
<i>Persea americana</i> Mil. Avocado	Mexico	37–39	41–43	16–21	–	–	–	–	–	–	–	[73]
<i>Sesbania rostrata</i>	Philippine	15	17	38	ALA 6	–	–	–	–	–	–	[90]

FA\*: other fatty acid; SA: stearic acid; ALA: Linolenic acid; Lau: lauric acid, MA, myristic acid, RA: ricinoleic acid, SDA: stearidonic acid, PIA: palmitoleic acid; PuA: punicilic acid, ricinoleic acid; RiA.  
TOH\*\*: T3: tocotrienol.

Beta-sitosterol is always the predominant form, except perhaps for *Eschium plantaginium* with a higher amount of campesterol (68–72 %).

To our knowledge, information on phospholipid content and composition are rarely indicated in OB from non-temperate sources, but phosphatidylcholine (PC) emerges as the predominant phospholipid in almost all the documented species, such as *Arachis hypogaea* or *Eschium plantaginium* (60.8 %, 52.4 %, respectively) [66,72] (Table 6). In *Arachis hypogaea*, the high percentage of phosphatidylserine (PS) is to be underlined [66], this phospholipid being generally quite rare in

vegetables but plays an important role in cognitive faculties [111].

In conclusion, the biochemical composition of OB from non-temperate crops is similar than OB from major crops with fatty acid compositions, TOH contents of interest.

As OB are natural reservoirs concentrating of valuable FA, phospholipids, TOH, phytosterols but also, perhaps vitamins, investigating these aspects in promising plants from developing countries could holds the potential to develop valorization strategies.

**Table 5**  
FA composition, TOH and sterol content of oil.

	Origin	FA				Total TOH (ppm)			Total sterol (ppm)			ref
		PA	OA	LA	FA	$\alpha$ TOH	$\gamma$ TOH	Other TOH**	campesterol	stigmasterol	$\beta$ sitosterol	
Oil		(%)				Relative (%)			Relative (%)			
<i>Carya illinoensis</i> Pecan nuts	Turkey	4	41	50	ALA 1	182			1965			[91]
						$\alpha$ TOH 7	$\gamma$ TOH 93	–	campesterol 3	stigmasterol 17	$\beta$ sitosterol 81	
<i>Mauritia flexuosa</i> L.f. Buriti	+	17	70	7	ALA 1	1041.4			–			[92]
<i>Persea americana</i> Mil. Avocado	Indonesia	22–36	22–56	14–21	ALA 1–2	32.78–49.8			–			[93]
						$\alpha$ TOH 88–99	$\gamma$ TOH 1–8	–				
<i>Pistacia vera</i> L. Pistachios	Turkey	8–9	57–72	14–19	–							[94]
	Brazil	7	58	30	–	291			5586			[91]
						$\alpha$ TOH 5	$\gamma$ TOH 95	–	campesterol 4	stigmasterol 12	$\beta$ sitosterol 83	
<i>Ricinus communis</i> Castor bean	Saudi Arabia	3	7–8	9	RiA 65–74	110.2–129.7			2370–2481			[95]
<i>Sesamum indicum</i> L. Sesame	Turkey	9	37	46	ALA 1	5291.7			7184			[96]
						$\alpha$ TOH 1	$\gamma$ TOH 99	–	campesterol 18	stigmasterol 8	$\beta$ -sitosterol 57.6	
<i>Anacardium occidentale</i> Cashew	ND	10	57	21		60.8			1990			[91]
						$\alpha$ TOH 6	$\gamma$ TOH 94	–	campesterol 5	stigmasterol 6	B sitosterol 88	
<i>Crescentia alata</i> Jicaro	Nicaragua	15	55	20	ALA 2	12.36			–			[97]
						$\alpha$ TOH –	$\gamma$ TOH 91	$\beta/\delta$ TOH 9				
<i>Coix lacryma-jobi</i> Job's Tears	Taiwan	13	43–49	34–40	ALA 0.5–1	31–39			462–626			[98]
						$\alpha$ TOH 5	$\gamma$ TOH 46	$\gamma$ T3 43	campesterol 15	stigmasterol 24	$\beta$ sitosterol 60	
<i>Eschium plantaginium</i> Purple viper's-bugloss	–	–	38–51	30–38	–	–			–			[99]
		15–16	12.9–14	11	ALA 28	782.24			1911–2330			[100]
					SDA 13							
<i>Gevuina avellana</i>		2	39	6	PLA 23	133.3						[101]
						$\alpha$ TOH 1	$\gamma$ TOH 1	$\gamma$ T3 98				
<i>Hippophae rhamnoides</i> Sea buckthorn	Poland	7	13–14	35–36	ALA 36–37	2736–4303			6161–7724			[102]
						$\alpha$ TOH 44–51	$\gamma$ TOH 41–47	–	campesterol 3	stigmasterol –	$\beta$ sitosterol 97	
<i>Madia sativa</i>	–					768–856			3000			[103]
						$\alpha$ TOH 74–96	$\gamma$ TOH 1–6	$\gamma$ T3 0–5.1	campesterol 14–17	stigmasterol 11–15	B-sitosterol 60–70	
<i>Punica granatum</i> Pomegranate	Spain	3–4	3–6	4–5	PuA 79–84	1350–5250			4000–5500			[104]
						$\alpha$ TOH 2.7–5	$\gamma$ TOH 73–99		campesterol 7–8	stigmasterol 3–4	$\beta$ -sitosterol 60–65	

## 1.2. Impact of climate on OB composition

Another reason of the interest of OB is that a reciprocity of action is found between climate and their composition. As previously mentioned, while these structures provide protection for lipids against stressful climates, environmental factors can induce changes in lipid composition. However, it is often really hard to differentiate variability coming from genotype modification and phenotype change related to climate only as other environmental factor can also modify the crop properties (soil, agricultural practices, etc.).

### 1.2.1. Chia seeds

Various studies have tried to determine the differences in seeds of the same species and variety cultivated in distinct climates and between seeds from temperate regions and those from other climates. One intriguing seed attracting considerable attention is the chia seed (*Salvia hispanica*), renowned for its high ALA content (between 50 and 67 %) [113,114]. Originating from Central America, chia seeds seem to come from a diversity of climates according to Köppen climate classification (Fig. 4). Referring to the Köppen climate classification, four non-temperate climates, i.e. Tropical, Arid, Continental and Polar, can

be distinguished [115].

Chia being sensitive to frost has a limited possible expansion (10–35 °C) and is not generally found in arid, continental and polar climates but is already present in diverse latitudes and longitudes [116]. The typical FA compositions of chia seeds of different species cultivated in Europe, Africa and South of America are presented in Table 7. The OA and ALA contents varied from 10 to 5 and 49–65 % for Kenya and France, respectively. The quality of chia seeds from five Northwestern location in Argentina was analysed [117]. The authors highlighted the ALA content (ranging from 52 to 63 % for Yuto (345 m) and Metan (859 m), respectively) did not solely depend on altitude. In contrast, opposite altitudes had similar levels of ALA (61 and 62.7 % for Yuto (306 m) and Rosario de Lerma (1332 m), respectively) indicating that others factors such as rainfall and temperature, also played a role. In another work, the same authors demonstrated that chia seeds cultivated in different climatic conditions of South America seemed to show an inverse correlation between linoleic acid and ALA contents with temperature [118]. The same tendency was observed for soybean [119]. However, other factors such as, soil types, available nutrients and light also contributed to the composition of chia seeds attributes cultivated in different climatic conditions of South America [118].

**Table 6**

Mass percentage composition of phospholipids of OB from major crops. PC: phosphatidylcholine, PE: phosphatidylethanolamine, PI: phosphatidylinositol, PS: phosphatidylserine.

	PC	PE	PI	PS	ref
<i>Arachis hypogaea</i> Peanut	61.6	5.0	8.4	25.0	[55]
<i>Brassica napus</i> Rapeseed	59.9	5.9	14.0	20.2	[55]
<i>Brassica nigra</i> Mustard	53.1	15.5	13.1	18.3	[55]
<i>Eschium plantaginium</i> purple viper's- bugloss	52.4	12.3	4.2	32.6	[72]
<i>Glycine max</i> Soybean	58.0	15.0	14.0	(-)	[112]
<i>Gossypium hirsutum</i> L. Cotton seed	58.6	4.6	18.1	18.7	[55]
<i>Helianthus annuus</i> Sunflower	81	13	5	(-)	[60]
<i>Linum usitatissimum</i> Linseed	57.2	2.8	6.9	33.1	[55]
<i>Sesamum indicum</i> L. Sesame	41.2	15.8	20.9	22.1	[55]
<i>Zea mays</i> Maize	64.1	8.1	7.6	20.2	[55]

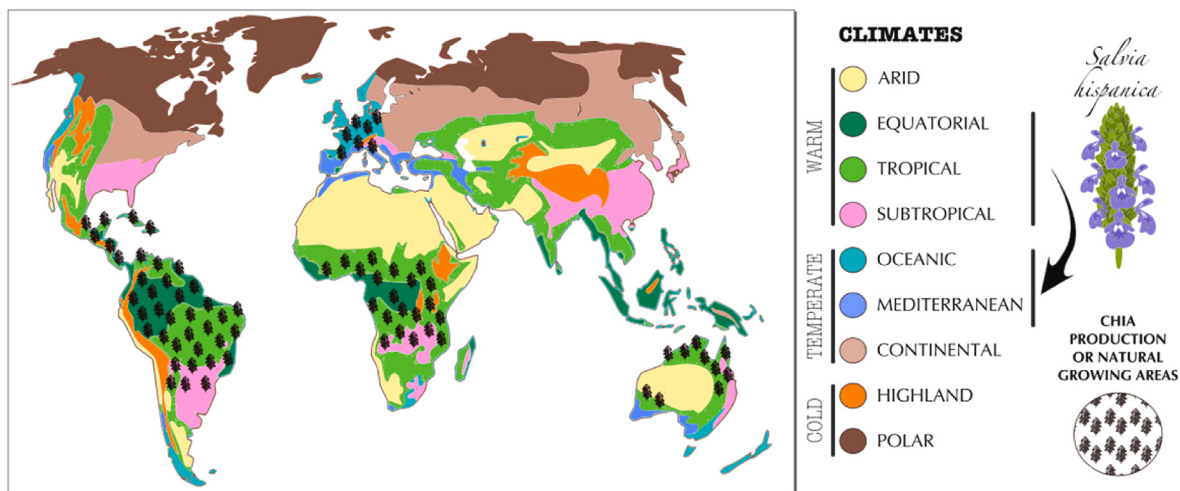
On the other hand, drawing a correlation between climate and the FA composition of chia seeds in several countries poses challenges, as differences arising from seed maturation and genotypes can be as significant as those attributable to climate. For instance, in a study conducted in Germany with three genotypes, two years of cultivation and two locations, the most influent parameters were the year of cultivation,

followed by the location and the genotype [122]. Here, the effects of the year and location seem to be linked to the different temperatures offered to chia plant cycle. The year with the lowest temperatures gave the best results. Low temperature would give more time to synthesize PUFA. In this study, the oil yields and ALA contents were equivalent or surpassed the values obtained for chia cultivated in central or south of America (30.9–33.7 % and 46.7–67.2 %, respectively).

**1.2.2. Genotype/environment interaction**

Apart from the case of chia, there are few well-documented examples of seed domestication from temperate climates to arid conditions [123]. Most seeds consumed in Africa, despite sometimes having high oleic or linoleic acid content, tend to be low in linolenic fatty acid. For example, sorghum contains only 1.0–2.0 % (relative) [124], millet (2.15 %) [125], chickpea (2.7–3.1 %) [126], pigeon pea (5.6 %) [127]. Cowpea, however, has shown higher percentages, ranging from 18 to 30 % of total lipid (w/w) in studies on genetic and environmental variability [128] with an even broader range of 9.6–30.9 % reported [129]. However, this must be considered alongside its naturally low-fat content. One successful example of plant domestication across diverse climatic conditions is maize, which has undergone extensive selection, allowing it to thrive in various environments [130]. Maize OB have demonstrated microbiological and oxidative stability in emulsions [131,132], further highlighting its adaptability. Studying different climate change scenarios can help identify maize varieties best suited to future conditions [133]. Similarly, sunflower has long been studied for its ability to grow in diverse regions, but given the high demand for sunflower OB, improving its adaptability to climate change remains a priority [134].

Genotype, perhaps even more than environmental factors, plays a crucial role in FA composition and can enable a plant to grow in a new



**Fig. 4.** Köppen climate classification and chia production or natural growing area.

**Table 7**

Some examples of protein yield, lipid yield and fatty acid compositions of chia seeds of different species cultivated from 8 countries.

Country of production	Protein yield (%)	Oil Yield (%)	Main FA* (%)					ref
			PA	SA	OA	LA	ALA	
France	19.6–19.8	30.4–32.9	6.9–7.3	3–3.5	5.3–5.9	17.7–18	66.1–64.7	[113]
Argentina	16.0–24.2	25.9–32.2	6.4–8.1	2.4–4.3	6.5–9.3	17.7–22.5	60.0–64.7	[120]
	18.8–20.7	28.5–32.5	6.6–7.4	2.8–3.0	7.2–6.9	20.1–21.1	61.7–62.2	[118]
Columbia	18.8–20.3	28.8–31.1	7.3–7.7	3.4–3.6	3.4–13.3	18.0–20.5	54.2–63.2	
Peru	23.1	32.4	7.2	3.0	6.9	18.4	64.2	
Bolivia	n/a	32.7	7.4	2.7	7.1	18.7	63.6	
Mexico	18.5–22.3	21.5–32.7	6.0–7.1	2.8–5.2	7.1–8.7	18.9–20.1	59.9–62.8	[121]
Kenya	20.1–21.9	25.6–31.2	6.2–7.5	4.3–5.4	7.2–10.8	18–20.3	51–57	[114]
Uganda	20.5–20.6	27.6–33.1	7.2–8.5	2.9–4.8	6.9–11.6	15.9–16.6	45.3–49.1	

FA\*: PA: palmitic acid; SA: stearic acid; OA: oleic acid; LA: linolenic acid; ALA: α-Linolenic acid.

environment. When comparing the composition of oilseeds from different countries, it is rarely the same genotype that dominates, suggesting adaptation to local climatic conditions. This is how chia was successfully introduced to France through long-term variety selection, leading to the development of the Oruro© variety, well suited to the French climate [135]. However, maintaining high levels of unsaturated FA requires either low oxidative conditions or antioxidant mechanisms, both of which vary among plant species [136,137].

### 1.3. OB of non-temperate minor crops not yet exploited but of interest due to a biochemical specificity

The use of new sources of OB would be one of the ways to respond to current and future societal challenges (such as improvement of food security, health, economic growth).

Enhancing the value of the raw materials present in each climate zones and exploiting them industrially, limiting their transformation in order to exploit their characteristics would make it possible to reduce different global sustainability impacts, decreasing malnutrition for some plants rich in high value nutrients, promoting social conditions for the local communities exploiting them, reducing environmental impacts by lowering soil erosion, creating shades with trees in the case of agroforestry (Table 8.) draws up some potential non-temperate sources of OB. The oils were selected on the basis of their lipid/protein content and their lipid compositions (Table 9.).

To comment this table, some examples according to their FA specificity are detailed.

#### 1.3.1. PUFA

**1.3.1.1. Rich sources of omega-3.** The interest of studies on omega 3 FA is constantly growing due to their numerous medicinal and pharmacological properties. The contribution of omega 3 via the diet has repeatedly shown its benefits on health. In temperate area, the intake of omega 3 comes from both oily fish (with eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) and plant sources like flaxseed oil or walnuts (39–60 % and 8–14 % of ALA, respectively) [163,164]. ALA has also applications in coatings, inks, mainly by its drying oil properties [165–167].

Tropical or nontemperate plant sources also possess high ALA content like *Kigelia africana* or *Echium amoenum*. *Kigelia africana*, also called sausage tree due to the long fruit, is a tree from the family Bignoniaceae. *Kigelia africana* is already known for their many pharmacological and medicinal properties [140]. *Kigelia africana* seeds might be a good candidate for the study of OB due to its both crude protein and lipid content of (357 and 492 g/kg DM, respectively) [139,150]. Moreover, high alpha ALA content (54.29 %) is very attractive. *Echium amoenum* is an endemic plant from the family of Boraginaceae native of oriental area. *Echium amoenum* is used in traditional medicine application because the presence of many biologically active substances like rosmarinic acid or polyphenols [168]. Whereas no protein content was analysed in our knowledge, the lipid content were measured and comprised between 6 and 33 % [169]. ALA is the predominant fatty acid (40–50 %), but another omega-3 fatty acid, stearidonic acid, is present in proportion of 1–8 %. Chia seed or flaxseed oil are occidental sources which possess an equivalent ALA content as *Kigelia africana* (64 vs. 40–60 %, respectively), but these two oils are not commonly consumed [170].

**1.3.1.2. Rich sources of omega 6.** Another west African OB source is *Telfairia occidentalis* (another name fluted pumpkin). This tropical climbing plant of the Cucurbitaceae family is also native from central Africa and is very exploited. *Telfairia occidentalis* is mainly used to leafy vegetable in food application but has high antioxidant properties that enhance medical and pharmaceutical applications [171]. Proportion of

**Table 8**

Some potential non-temperate sources of OB. Botanical name, specificity and their exploitation for nutritive, pharmaceutical, medicine or chemical applications.

Botanical name and specificity Tree/plant Seeds/kernel/ leaf/nut	Sources	Origin	Use	ref
Asteraceae Seed	<i>Carthamus dentatus</i>	Turkish	Pharmaceutical Industrial application	[138]
Bignoniaceae Tree/Seeds	<i>Kigelia africana</i> (Sausage tree)	South, central and west Africa (sub)	Pharmaceutical Medicine	[139,140]
Bombacaceae Tree/Nut	<i>Bombacopsis glabra</i>	Tropical of America (and Europe), Africa (Nigeria)	Pharmaceutical	[141]
Boraginaceae Seeds/Leaf/ Stem	<i>Echium amoenum</i> (Red feather)	Asia	Medicine	[142]
Brassicaceae Plant/Seed	<i>Descurainia sophia</i> <i>Eruca sativa</i> <i>Cardaria draba</i> <i>Rapistrum rugosum</i>	Turkish	Food Industrial application	[138]
Cucurbitaceae Tropical grape vine/ Seeds	<i>Telfairia occidentalis</i> <i>Hook.f.</i>	West Africa	Food Pharmaceutical Medicine	[143,144]
Euphorbiaceae Plant/Seeds	<i>Cnidioscolus tubulosus</i> ( <i>Jatropha tubulosa</i> ) <i>Jatropha excisa</i>	Centre and south of America	Biodiesel	[145]
Euphorbiaceae Tree/Seeds/ Kernels	<i>Ricinodendron heudelotii</i> (Djansan, Akpi, Wama) <i>Tetracarpidium conophorum</i>	Humid tropical zones in Africa (Congo)	Food Thickening agent	[146]
Fabaceae Tree/Seeds/ Fruits	<i>Geoffroea decorticans</i> (Chañar)	Africa	–	[147]
Irvingiaceae Tree/ Kernel/ Seeds	<i>Irvingia gabonensis</i> (African mango)	South America	Food	[148]
Lamiaceae Plant/Seeds	<i>Perilla frutescens</i> (Bhanjira)	Africa (Nigeria)	Food Medicine	[149,150]
Moraceae Tree/Seeds	<i>Treculia africana</i>	Oriental Asia	Food	[151–153]
Moringaceae Tree/Seeds	<i>Moringa oleifera</i>	Swim areas and riverine forests of tropical Africa (Nigeria)	Food Cosmetic Pharmaceutical	[149]
Olacaceae Tree/Seeds	<i>Coula edulis</i> (African walnut)	Asia (India)	Food Artisanal culture	[154]
Tiliaceae Tree/Seeds	<i>Grewia asiatica</i> <i>L. (Phalsa)</i>	Sub-Saharan Africa (Cameroon, Nigeria)	–	[155–157]
		Southeast Asia (Pakistan)		[158]

(continued on next page)

Table 8 (continued)

Botanical name and specificity Tree/plant Seeds/kernel/ leaf/nut	Sources	Origin	Use	ref
Sapiendaceae Tree/Seeds/ Kernel	<i>Nephelium lappaceum</i> (Ramboutan)	Malaysia-Indonesia Mexico, Congo, Thailande	Food Industrial application	[159,160]
Sapotaceae Tree/Seed	<i>Mimusops zeyheri</i> (Red Milkwood)	Sub-Saharan Africa	Food	[161]

protein-lipid is interesting since the contents from both are 30 and 47 %, respectively [172]. The ratio between unsaturated and saturated FA is also promising for industrial applications as for biodiesel and bio-lubricant [173]. Linoleic acid (LA) is the major fatty acid of the seed of the *Telfairia occidentalis* with 64 % of fatty acid composition. Linoleic acid is an essential FA. LA is transformed into different family of indispensable molecules for the organism as phospholipids, cholesterol esters, ceramides. It is then a very important part of food intakes and can have also clinical uses to treat notably skin diseases linked to its deficiencies [174].

Other plants rich in linoleic acid may also be of interest, such as *Striga asiatica*, also known as "Asiatic witchweed". This is a hemiparasitic plant belonging to the *Orobanchaceae* family. *Striga asiatica* is an agricultural pest that reduces the yield of many crops, such as sorghum, rice, and corn [175]. To our knowledge, there is very little data on the protein and lipid composition of this plant [176]. studied the variations in total polar lipids and TAG during the different stages of germination, as well as the changes in FA content of the total polar lipids. They found that the proportion of TAG decreased from 94 % to 82 %, while that of polar lipids increased from 6.4 % to 17.9 %. Additionally, they observed that the amount of LA increased from 25 to 90  $\mu\text{mol FA/g}$  dry weight after 22 days of incubation. New studies could highlight other properties of *Striga asiatica* that would allow this pest to be valued.

**1.3.1.3. Rich sources of omega 9.** Considering unsaturated FA, *Coula edulis* and *Moringa oleifera* have high concentration of monounsaturated acids (95 and 73 %, respectively). Only *Coula edulis* is detailed here. *Coula edulis* called also African Walnut is a tree of the *Oleaceae* family native to Sub-Saharan Africa (Nigeria, Cameroun, etc.) [177]. The production is artisanal and the nuts are consumed in the local market. The lipid content is 34 %, the protein content is not yet mentioned (the amount of protein in the cake is between 12 % and 17 %) [155,178]. *Coula edulis* is already a source of income for some populations such as in Gabon [179]. The high oleic acid content could enhance the potential of its OB in pharmacology application but also, for example, as an excipient or as an emulsifying agent in food application. Among seeds adapted to temperate climate that could correspond to such high levels of oleic acid content, a developed variety of sunflower can be mentioned, this high content in oleic acid being challenging to cope with different climates as effect of temperature on this content could be minimized with the development of adapted genotypes [180,181]. Oleic acid can also have industrial applications as biofuels after esterification [182] or to produce shorter chain fatty acids acid through oxidative scission, as palargonic acid broadly used as a weedkiller [183].

**1.3.1.4. Conjugated fatty acids.** Conjugated fatty acids (CFA) are other particular fatty acid tropical sources. Due to their many attractive properties, such as lipid reduction, antidiabetic effects, anticancer, antioxidants, etc, conjugated fatty acids has become much popular in recent years [184]. However, harmful effects are also identified on

toxicity, insulin resistance but no toxicity, allergenicity were showed [185] The main CFA are CLA and CLnA with a higher interest for the last one [186].

**1.3.1.4.1. Conjugated linoleic acid isomers (CLA).** A lot of studies indicate that conjugated linoleic acids (CLA) has a lot of medicine and pharmacology applications [187,188]. The main sources of CLA are meats and dairy of ruminants, but some vegetable sources possess also like the *Punica granatum*. *Punica granatum* seed oil may have a beneficial effect for the treatment of multiple-sclerosis, but also could help preventing of treating obesity and diabetes [189].

**1.3.1.4.2. Conjugated linolenic acid isomers (CLnA).** *Ricinodendron heudelotii* is a tree of the *Euphorbiaceae* family found in sub-Saharan Africa. The tree is also known as Njansang, musodo eimado, corkwood essessang and its fruit as akpi. The seeds can be found on most western market stalls in Africa [146]. One of the distinguishing features of this seed is that the main fatty acid contained in its oil is  $\alpha$ -eleostearic acid (50–60 %), followed by linoleic acid (23–30 %). Seeds are already used in food and their fatty acids composition opens the way to chemistry and pharmacological applications. For example, various polymers such as epoxy or alkyd resins could be derived from  $\alpha$ -eleostearic acid (ALE) [190–192]. The  $\alpha$ -eleostearic acid is not the only CLnA that can be found in the oil of these seeds, as the latter tends to isomerize in the light to form two other CLnA,  $\beta$ -eleostearic acid (C18:3 9t,11t113t) and catalpic acid (C18:3 9t, 11t, 13c) [193]. Enriching *Ricinodendron heudelotii* oil with one or other of these CLnA's using an eco-fractionation process opens up a wide range of technological uses [194]. The possibility of the future emergence of an *R. heudelotii* value chain in Ivory Coast will make it possible to develop outlets for the kernels and the oil they contain [195]. It will also enable product quality to be improved and controlled, and seed crushing and oil extraction methods to be modernized, all of which are essential conditions for increasing production and structuring and expanding the market.

### 1.3.2. Saturated fatty acids

**1.3.2.1. Lauric and myristic acids.** *Irvingia gabonensis*, a tropical tree native to Africa, presents a valuable source rich in saturated fatty acids, particularly lauric and myristic acid (38 % and 51 %, respectively) within its kernels [150]. The fruit and kernels of *Irvingia gabonensis* are consumed, with the latter containing approximately 65 % fat and 10 % protein. Lauric acid, a major component, finds applications in various industries. It serves as an intermediate compound and a surface-active agent, playing a significant role in the production of soaps and cosmetics. Moreover, lauric acid exhibits antifungal, antibacterial, and antimicrobial properties [196], enhancing its significance in both industrial and health-related contexts. The short and medium-chain saturated fatty acids found in *Irvingia gabonensis* also play essential roles in food and energy metabolism [197]. The unique composition of *Irvingia gabonensis* makes it a promising resource with diverse applications across different sectors [198].

Myristic acid, functioning as an emulsifier, flavour adjuvant or a defoaming agent, can serve in various food, beverages, cosmetics applications [199]. It has been associated with health benefits related to the regulation of some cellular functions [200]. Additionally, myristic acid associated or not with other short or medium saturated acid is studied in the renewable energy sector, in particular for thermal energy storage [201]. The exploitation of *Irvingia gabonensis*, if conducted with adherence to sustainability criteria, has the potential to enhance the livelihoods of local populations [202,203]. Establishing a sustainable value chain for *Irvingia gabonensis* can contribute to economic prosperity in local communities while ensuring the responsible and ethical utilization of this valuable natural resource.

**1.3.2.2. Arachidic acid.** The potential of *Nephelium lappaceum* (Rambutan) as a source of OB is noteworthy, particularly due to its high

**Table 9**

Some potential non-temperate sources of OB. Protein and lipid concentration, FA composition, TOH and sterols contents were documented for these sources.

Sources	Lipids (%)	proteins (%)	FA				Total TOH (ppm)			Total Sterols (ppm)			ref
			PA	OA	LA	Other FA*	αTOH	γTOH	Other TOH	Campesterol	Stigmasterol	β sitosterol	
			Relative (%)				Relative (%)			Relative (%)			
<i>Bombacopsis glabra</i>			53	7	5	StA 25	–						[141, 162]
<i>Carthamus dentatus</i>	15.39	9.4	9	20	66	-	-		-				[138]
<i>Cnidioscolus tubulosus</i>	29	–	13	14	66	ALA 0.9	–		–				[145]
<i>Coula edulis</i>	34	–	3	97	1	–	–		–				[155]
	24.31	4.6					84.6						[156]
	33–36	–	0.2	95–97	0.4	–	–		–				[157]
<i>Descurainia sophia</i>	28	30	8	11	20	ALA 41	–		–				[138]
<i>Eruca sativa</i>	24	28	5	10	7	EuA 57							
<i>Echium amoenum</i>	6.2–33.8		6–29	8–17	11–27	ALA 40–50 GLA 5–8 SDA 1–8	–			–			[142]
<i>Geoffroea decorticans</i> (Chañar)	47	21–24		42	43	–	–			–			[148]
<i>Grewia asiatica</i> L.	11	17	12	16	60	ALA 3	6570			333.3			[158]
<i>Irvingia gabonensis</i>	72		5	2	–	MA 51	99	<1	βTOH <1	12	12	55	[150]
						Lau 38	trace	99	–	6	30	31	
	65	9	5	3	1	MA 41–49 Lau 40–47	41–46			–			[149]
							21–32	4–5	βTOH 63–74				
<i>Jatropha excisa</i>	39		13	18	66	–	–						[145]
<i>Kigelia africana</i>	49	36		18	13	ALA 54	0.09						[139]
<i>Mimusops zeyheri</i>	21	9	15	85	–	–	2						[161]
<i>Moringa oleifera</i>	37	31	6	73	0.7	C22 6	365.8			–			[154]
							45	15	δTOH 40	17	19	47	
<i>Nephelium lappaceum</i>	–	–	5	42	2	ARA 33	–			–			[159]
	37–39	12–14	–	–	–		108			294.6			[160]
							100	–	–	2.62	71.61	4.26	
<i>Perilla frutescens</i>	17–43		6–9	9–20	11–25	ALA 47–64	–			–			[153]
	42.2	25.4	6	16	15	ALA 61	390			3182			[151]
							11	84	δTOH 6	10	5	85	
<i>Ricinodendron heudelotii</i>	47	21	3.8–4.1	6.7–7.1	22.8–24	SDA 50–60	1350			4120			[146]
							4	92	δTOH 3	7	3	84	
<i>Telfairia occidentalis</i> Hook.f.	49	16	18	39	28	–	–			–			[144]
	–	–	20	13	64	EPA 2.43	–			–			[143]
<i>Tetracarpidium conophorum</i>	50	24	1	14	16	ALA 63	–			–			[147]
<i>Treculia africana</i>	10–13	13	21	23–26	29–31	ALA 1	189–196			–			[149]
							αTOH 60–63	γTOH 10–13	βTOH 24–29				

FA\*: PA: Palmitic acid; OA: Oleic acid; LA: Linoleic acid; StA: Sterculic acid; ALA: α-Linolenic acid; EuA: Erucic acid; GLA: γ Linolenic acid; SDA: Stearidonic acid; MA: Myristic acid; Lau: Lauric acid; BEA: Behenic acid; ALE: α-Eleostearic acid; EPA: Eicosapentaenoic acid, ARA: arachidic acid.

arachidic acid content (33 %). *Nephelium lappaceum* fruits are not only consumed in local markets in various regions like Mexico, Congo or Thailand but also offer versatile uses for their seeds. The seeds, raw or roasted, are also edible and can be used in soap making and in the manufacture of candles due to their composition in fatty acids. Furthermore, the cooked kernels have narcotic and vermifuge

properties. Because its moisturizing, emulsifying and surfactant properties, arachidic acid is used in cosmetic [204]. This unique FA profile makes Rambutan seeds valuable for various applications, including those in the cosmetic industry.

For example, BASF company initiated a program for a sustainable use of Rambutan in mostly cosmetic applications [205]. Harvesting

Rambutan trees can contribute to CO<sub>2</sub> sequestration and raise the standard of living for Rambutan farmers, making it an interesting candidate for sustainable and multifaceted utilization [206].

### 1.3.3. Other relevant FA

Another interesting source of particular fatty acid is *Bombacopsis glabra* kernel, with around 25 % sterculic acid [141]. The tree is a pan-tropical, whose fruits can be eaten even if it remains health concerns about this use, especially due to the presence of this fatty acid. Sterculic acid applications are then more focused on pharmaceutical benefits, for example anti-cancer, or anti-inflammatory and anti-macular degeneration properties [207,208].

## 2. Conclusions and prospects

A vast field of research has been opened up on OB in non-temperate climates with their physico-chemical characterization, and their link with genotypes and cultivation conditions. In this way, the use of the extended diversity of OB and of their natural or technologically helped adaptative capacities to different climates should participate in the achievement of some sustainable development goals. The diversity of compositions found in oleaginous fruits or seeds from different climates, allied with conservation of important antioxidant, nutritive or nutraceutical properties in OB make these assemblies essential to formulate current and future food or industrial products which could benefit to the food security and health of local populations (SDG 2: zero hunger, SDG3: good health and well-being). Being naturally stabilized, they offer a real advantage over conventional oil formulations and avoid unsustainable seed processing and oil refining steps. However, to make these organelles fully exploitable, a better understanding on the activable levels for reaching a high resistance to coalescence should promote the development of more value-added compositions, sustain the possibility to cultivate polyunsaturated rich (as omega-3) seeds in non-temperate climates, especially arid ones, and improve the value chain of their production. The choice and development of some species and genotypes must yet be dependent on other factors than the sole chemical composition. Indeed, all the sustainability lifecycle assessment of the production of these seeds will be mandatory to assure that the exploitation of these seeds can profit to the three pillars of sustainability. Regarding the environment, cultivating these plants, attuned to challenging climates, supports sustainable practices. This is vital for preserving ecosystems and biodiversity (SDG 15: Life on land). The cultivation of the plants, trees or shrubs should give protection against soil erosion and/or provide shading to locally decrease the impacts of global warming (SDG 13: climate action). This is particularly crucial in areas susceptible to environmental degradation. However, these plants should in no way replace pre-existing species linked to traditional and profitable habits and life cycle assessment methods and/or comparative approaches should be chosen with this consideration (Bamber et al., 2023; Dekamin et al., 2018). Integrating the cultivation of these promising plants into agroecological systems should then allow them to coexist and interact synergistically with other plant species. This association can enhance overall agricultural productivity. The resilience of some of these plants in harsh conditions implies they may require fewer resources, contributing to sustainable agricultural practices, especially in regions facing resource scarcity. Regarding the economy and social aspects, the production must benefit primarily to the local communities whose work must allow substantial living conditions. Within this frame, the social conditions of the workers and local communities should be promoted (SDG 1: No poverty, SDG 5: gender equality, SDG 8: Decent growth and economic growth, SDG 11: Sustainable cities and communities). In conclusion, delving into the properties of OB in plants from developing countries not only provides economic opportunities but also aligns with sustainable and environmentally friendly practices. The diverse benefits, spanning resource efficiency to ecological preservation, underscore the potential positive impact of leveraging these plants for various

applications.

## CRediT authorship contribution statement

**Nathalie Barouh:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Conceptualization. **Eric Lacroix:** Writing – review & editing, Visualization, Validation, Conceptualization. **Romain Valentin:** Writing – review & editing, Validation. **Claire Bourlieu-Lacanal:** Writing – review & editing, Validation. **Jean-François Fabre:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

Data will be made available on request.

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