

1 Plant Physiology Review

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3 Title:

4 **Born of frustration: the emergence of *Camelina sativa* as a platform for lipid**
5 **biotechnology.**

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12 **Abstract**

13 The emerging crop *Camelina sativa* (L.) Crantz (camelina) is a Brassicaceae oilseed with a
14 rapidly growing reputation for the deployment of advanced lipid biotechnology and metabolic
15 engineering. Camelina is recognised by agronomists for its traits including yield, oil/protein
16 content, drought tolerance, limited input requirements, plasticity and resilience. Its utility as a
17 platform for metabolic engineering was then quickly recognised, and biotechnologists have
18 benefited from its short life cycle and facile genetic transformation, producing numerous
19 transgenic interventions to modify seed lipid content and generate novel products. The
20 desire to work with a plant that is both a model and crop has driven the expansion of
21 research resources for camelina, including increased availability of genome and other “-
22 omics” data sets. Collectively the expansion of these resources has established camelina as
23 an ideal plant to study the regulation of lipid metabolism and genetic improvement.
24 Furthermore, the unique characteristics of camelina enables the design-build-test-learn cycle
25 to be transitioned from the controlled environment to the field. Complex metabolic
26 engineering to synthesize and accumulate high levels of novel fatty acids and modified oils
27 in seeds, can be deployed, tested and undergo rounds of iteration in agronomically relevant
28 environments. Engineered camelina oils are now increasingly being developed and used to
29 sustainably supply, improved nutrition, feed, biofuels and fossil fuel replacements for high-
30 value chemical products. In this review, we provide a summary of seed fatty acid synthesis
31 and oil assembly in camelina, highlighting how discovery research in camelina supports the
32 advance of metabolic engineering towards the predictive manipulation of metabolism to
33 produce desirable bio-based products. Further examples of innovation in camelina seed lipid
34 engineering and crop improvement are then provided, describing how technologies (e.g.,
35 genetic modification (GM), gene editing (GE), RNAi, alongside GM and GE stacking) can be
36 applied to produce new products and denude undesirable traits. Focusing on the production
37 of long chain polyunsaturated omega-3 fatty acids in camelina, we describe how lipid
38 biotechnology can transition from discovery to a commercial prototype. The prospects to
39 produce structured triacylglycerol with fatty acids in specified stereospecific positions are
40 also discussed, alongside the future outlook for the agronomic uptake of camelina lipid
41 biotechnology.

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44 Introduction

45 Over recent years the annual oilseed crop *Camelina sativa* L. Crantz (camelina) has
46 received renewed interest from multiple communities including researchers, growers,
47 processors, and policy makers. Each of these groups is attracted by the potential of
48 camelina to address the challenges of agricultural sustainability, sourcing renewable biofuels
49 and bio-based materials, and increasing climate resilience in our cropping systems.
50 Camelina is a member of the Brassicaceae, native to Europe and found on farms across a
51 huge range of geographical locations (e.g., Alaska to Argentina; Weiss et al. 2024). Recent
52 reviews have captured the potential of camelina, namely it has: (1) remarkable agronomic
53 versatility, metabolic plasticity, and environmental adaptability, (2) low-input requirements, (3)
54 resistance to pests and diseases, and (4) multiple uses in food, feed, and biobased
55 applications (Berti et al. 2016; Boutet et al. 2022, Zanetti et al. 2024). The agronomic
56 adaptability of camelina (both spring and winter biotypes have been identified) has made it
57 an attractive crop for integration into farming systems as an intermediate/cover/cash crop via
58 intercropping, double cropping, or use on marginal lands. It is important to recognise that
59 camelina is an oilseed crop, with seed oil yields typically comparable to that of *Brassica*
60 *juncea* and *Brassica rapa*, and higher than that of soya bean. Camelina may yet not match
61 the oil yield of canola, but the costs of production (camelina has lower fertilizer requirements)
62 can be less than half that of *Brassica napus* (canola/rapeseed). Camelina can therefore
63 provide a route to profitability for agricultural regions with limited economic opportunities
64 (Zanetti et al. 2024) and efforts are now underway using conventional breeding programs to
65 develop new camelina varieties with improved agronomic traits (e.g., Ghidoli et al. 2024).
66 Typically, camelina seeds contain approximately 38 to 42% oil predominantly in the form of
67 triacylglycerol (TAG), which consists of three fatty acids esterified to a glycerol backbone.
68 Camelina shows remarkable morphological plasticity (Zanetti et al. 2021) and any variations
69 in camelina seed oil and fatty acid composition typically reflect genetics, environmental
70 conditions, and genotype-by-environment interactions (Brock et al. 2020). Camelina oil has a
71 nutritionally beneficial profile rich in unsaturated fatty acids ($n-6/n-3$ ratio 0.6) e.g., oleic,
72 (18:1^{Δ9} (total carbons:desaturations), 14–16%), linoleic (LA), (18:2^{Δ9,12} 15–23%), α-linolenic
73 (ALA), (18:3^{Δ9,12,15} 31–40%), and eicosenoic (20:1^{Δ9} 12–15%) acid. Other minor fatty acids
74 include palmitic (C16:0), stearic (C18:0), and erucic (22:1^{Δ13}) acid. The accumulation of
75 erucic acid and glucosinolates (defensive secondary metabolites commonly found in
76 *Brassica* species) in camelina seeds is relatively low but can be a challenge for the use of
77 this oil in some food and feed applications. Addressing these issues had been a task for both
78 breeders and metabolic engineers alike.

79 Following the publication of genomes for the camelina doubled haploid DH55 accession
80 (Kagle et al. 2014; see updated version <http://cruciferseq.ca>) and the spring biotype
81 'Suneson' (Fang et al. 2023, Brock et al. 2024), efforts to improve camelina have been
82 underpinned by the increasing number and diversity of genomic resources available e.g.,
83 Bird et al. (2024) recently sequenced, assembled, and annotated twelve complete,
84 chromosome-scale genomes of camelina. Camelina genomics resources are part of the
85 Brassica database BRAD (<http://brassicadb.org>) and they are accessible via the JGI
86 Phytozome BAP project and camelina pangenome sequencing effort ([https://phytozome-](https://phytozome-next.jgi.doe.gov/info/CsativaJoelle_v1_1)
87 [next.jgi.doe.gov/info/CsativaJoelle_v1_1](https://phytozome-next.jgi.doe.gov/info/CsativaJoelle_v1_1)). Furthermore, camelina gene expression data can
88 be examined in several different ways e.g., The University of Toronto has developed an
89 image expression browser (Kagale et al. 2016; <http://bar.utoronto.ca/>) for camelina,
90 representing expression data from a large developmental set. In addition, the Camelina
91 Genomic Resources (camelinagenome.org) contains embryo transcript data on protein and
92 lipids. Whilst the Camelina Gene Regulation Database (Gomez-Cano et al. 2020;
93 <http://camregbase.org/>), provides a resource for aspects related to camelina gene regulation,
94 including tissue-specific gene expression visualization and gene co-expression analyses.
95 The re-analysis of published gene expression data has identified evidence for genome
96 dominance in camelina, with the third subgenome dominant over the other two (Chaudhary
97 et al. 2020; Mandáková et al. 2019). However, this is now thought to be largely restricted to
98 floral and fruit organs (Brock et al. 2024), which has significance for seed lipid engineering
99 approaches that depend on endogenous metabolism. Collectively these resources make
100 camelina an excellent chassis for biotechnology. Metabolic engineers can make use of its
101 simple 'floral dip' transformation protocol (Lu and Kang 2008) and short life cycle to make
102 rapid progress from the laboratory to the field. More broadly, discoveries in camelina are
103 often directly transferable to staple commodity oilseed crops e.g., canola, and are highly
104 informative for other dicot oilseeds, including soybean.

105 **Seed Lipid Metabolism in Camelina**

106 Seed oil biosynthesis requires a supply of carbon. When exposed to light, oil producing
107 green seeds convert maternally supplied sugars and amino acids into storage products
108 (starch, oil, and protein). Seed oil triacylglycerols (TAG) are composed of fatty acids
109 generated by combining 2-carbon acetyl groups derived from 3-carbon pyruvate and
110 requires energy (ATP) and reducing power (NADPH and NADH). The decarboxylation of
111 pyruvate to acetyl coenzyme A results in 33% of the carbon being converted to CO₂. Seeds
112 also respire carbon through the tricarboxylic acid (TCA) cycle to produce adenosine
113 triphosphate and carbon skeletons for amino acids used in protein biosynthesis. CO₂
114 produced in green seeds can be refixed by ribulose bisphosphate oxygenase carboxylase

115 (RUBISCO). However, camelina has a low carbon conversion efficiency (CCE) (32 to 40%;
116 Carey et al. 2020) compared to other green oilseeds and is characterised by a highly active
117 oxidative pentose phosphate pathway (OPPP), which produces excessive NADPH (used in
118 fatty acid synthesis or dissipated by alternative oxidase AOX1). Latterly research in camelina
119 has demonstrated a role for pod walls to fix CO₂ photosynthetically and contribute to seed
120 biomass, enable seed filling and maximise the number of viable seeds. In the absence of
121 leaves, photosynthesis in pod walls has the capacity to contribute ~79% of seed biomass
122 (Koley et al. 2022).

123 Camelina shares many features of fatty acid synthesis with other oilseeds and the
124 complexities of lipid synthesis and oil assembly have been reviewed elsewhere (see Li-
125 Beisson et al. 2013, Bates 2016 and Yang et al. 2022; camelina pathway descriptions in Xu
126 et al 2024; www.fatplants.net/). Briefly, fatty acids are generated in the plastid, whereas TAG
127 assembly occurs outside the plastid in the endoplasmic reticulum (ER) and the TAG is
128 packaged into oil bodies (see Fig1A for summary). The first committed step in the pathway is
129 catalysed by plastidial acetyl-CoA carboxylase (ACCase). Assembly of fatty acids occurs on
130 an acyl carrier protein (ACP) via a cycle of reactions that elongate the carbon chain by two
131 carbons. After seven cycles, the saturated 16 carbon acyl-ACP can either be hydrolyzed by
132 the FATB acyl-ACP thioesterase or further elongated by beta-ketoacyl-ACP synthase II
133 (KASII) to 18:0-ACP, which is then desaturated (Δ^9 -18:0-ACP desaturase (SAD)) to 18:1-
134 ACP and hydrolyzed by the FATA thioesterase to produce C16:0 and C18:1, with their
135 relative proportions determined by the activities of FATA, FATB, SAD and KASII.
136 Polyunsaturated fatty acids are synthesized by one of two parallel pathways commonly
137 referred to as the prokaryotic and eukaryotic pathways located in the plastid and
138 endoplasmic reticulum, respectively. Fatty acids are esterified to different lipids in the two
139 compartments, phosphatidylcholine (PC) in the ER and glycosylglycerides in the plastid.
140 Conversion of C18:1 to C18:2 is mediated by FATTY ACID DESATURASE 2 (FAD2) in the
141 ER and by FAD6 in the plastids, and conversion of C18:2 to C18:3 mediated by FAD3 in the
142 ER and by either FAD7 or FAD8 in the plastid. The synthesis of very long chain fatty acids
143 (VLCFA) e.g. C22:1 is by the FA elongation enzyme complex located at the ER membrane.
144 The complex sequentially adds two carbon units to C18:1, growing the acyl chain using four
145 core enzymes, namely multigene family 3-ketoacyl-CoA synthase (KCS), 3-ketoacyl-CoA
146 reductase (KCR), 3-hydroxyacyl-CoA dehydratase (HCD), and trans-2,3-enoyl-CoA
147 reductase (ECR). FATTY ACID ELONGASE1 (FAE1)-encoded β -ketoacyl-CoA synthase is a
148 specific member of the KCS family and is a rate-limiting enzyme directing the longation of
149 C18:1; therefore, KCS/FAE1 is an important regulatory target for altering VLCFA content
150 through metabolic engineering.

151 Overall production of fatty acids is regulated by both the transcription factor WRINKLED 1
152 (WRI1; Cernac and Benning 2004) and the complex biochemical network of control
153 surrounding ACCase e.g., phosphorylation, redox status, PII interactions, and feedback
154 regulation by 18:1-ACP (reviewed in Conrado et al. 2024). Several additional genes have
155 been identified in Arabidopsis to regulate seed fatty acids synthesis and oil accumulation e.g.
156 LEAFY COTYLEDON 2 (LEC2), ABSCISIC ACID INSENSITIVE 3 (ABI3), and FUSCA3
157 (FUS3) (Miray et al. 2021). However, aspects of seed lipid metabolism in camelina are
158 unique and Gomez-Cano et al. (2022) identified CsaMYB1, CsaABI3AVP1-2, CsaHB1,
159 CsaNAC2, CsaMYB3, and CsaNAC1 as regulators likely involved in the control of seed fatty
160 acid elongation, and CsaABI3AVP1-2 and CsaZIP1 as potential regulators of the synthesis
161 and degradation of triacylglycerols (TAGs). After export, long-chain acyl-CoA synthetase
162 (LACS) converts free fatty acids to acyl-CoA for the assembly of TAG. Glycerol-3-phosphate
163 and acyl-CoAs are synthesised into TAG via the Kennedy pathway (Fig 1A), a series of
164 activities including two acylations of G3P by sn-1 glycerol-3-phosphate acyltransferase
165 (GPAT) and lysophosphatidic acid acyltransferase (LPAAT), followed by phosphatidic acid
166 phosphatase (PAP), and a third acylation by diacylglycerol acyltransferase (DGAT).
167 Alternatively, newly synthesized FAs can enter the PC pool via acyl-
168 CoA:lysophosphatidylcholine acyltransferase (LPCAT). PC plays a central role in TAG
169 synthesis through acyl editing where further desaturation or modification can occur before
170 release back into the acyl-CoA pool for participation in TAG synthesis, direct transfer of fatty
171 acids to Diacylglycerol (DAG) producing TAG via phospholipid:diacylglycerol acyltransferase
172 (PDAT) and utilisation of PC-derived DAG as a substrate for TAG synthesis. Analysis of
173 camelina seed total DAG identified a predominance of linoleic and linolenic acids (e.g., 36:5
174 18:2/18:3, 36:6 18:3/18:3 and 36:4 18:2/18:2; 55% of total DAG), alongside other DAG
175 molecular species containing VLCFA e.g. 38:4 (20:1/18:3) and 38:3 (20:1/18:2) at 11 % and
176 7 %, respectively (Rodríguez-Rodríguez et al. 2021). Studies of TAG biosynthesis kinetics
177 using [¹⁴C]glycerol labelling demonstrated a role for the PC-derived DAG pathway in
178 camelina, but identified a significantly greater flux through the Kennedy pathway relative to
179 other oilseeds such as Arabidopsis or soybean (Bates et al. 2014).

180 In developing camelina embryos, the maximum rate of oil synthesis is at mid-maturation i.e.,
181 between 14–20 days post-anthesis (DPA), while the mid-point for oil deposition is around
182 17–18 DPA. A striking feature of seed maturation in camelina is the late-stage surge and
183 then abrupt cessation in C18:3 deposition. The rate of C18:1 deposition also dips during
184 mid-maturation, consistent with its role as precursor for C18:2, C18:3 and C20:1
185 biosynthesis. Synthesized by FAE1, C20:1 is first detected at 11 DPA and the production of
186 other minor VLCFAs, such as eicosanoic acid (C20:0) and erucic acid (C22:1), closely

187 parallels that of C20:1. Also, in late seed maturation, C18:0 accumulation is greatly reduced
188 relative to C16:0 (see detailed description provided in Pollard et al. 2015 and developmental
189 changes in lipid biosynthesis transcripts illustrated in Fig 1B). Camelina seed TAG fatty acid
190 composition characteristically reflects the total lipid profile and ESI-MS analysis identifies
191 abundant 52:3 - 52:6, 54:2 – 54:9, 56:2 - 56:9 and 58:2 - 58:7 molecular species; alongside
192 some minor 60:x, 62:x and 64:x species. The leaf fatty acid 16:3 and odd chain fatty acids
193 are rarely found in seed TAG. Seed TAG content and composition is not fixed, indeed a
194 small family of triacylglycerol lipase genes in Brassicas (Eastmond 2006), consisting of
195 SUGAR-DEPENDENT1 (SDP1) and SDP1-LIKE (SDP1L), are responsible for a decline in
196 seed oil content (~10%) in maturing oilseeds. The suppression of SDP1 in *Brassica napus*
197 during seed development resulted in an 8% gain in seed oil yield and is recognised by
198 researchers as a route to enhance oil yield in seeds (Kelly et al. 2013). A further TAG lipase
199 (TAGL) has been identified (Horn et al. 2016) in seeds from the Brassicaceae *Physaria*
200 *fendleri* and its upregulation during seed development in camelina engineered to produce
201 novel hydroxy fatty acids has been observed. Lipase (TAGL) activity has now been shown to
202 have a role in TAG remodelling, enabling the accumulation of unusual fatty acids in multiple
203 positions in the glycerol backbone of TAG demonstrating that TAG should be considered not
204 as a metabolic endpoint but a dynamic pool (Bhandari and Bates 2021; Parchuri et al. 2024),
205 as previously proposed in the 1990s.

206 Aside from TAG other lipid species contribute to the camelina seed total lipids. This includes
207 contributions from plastid localised lipids e.g., monoglactosyldiacylglycerol (MGDG),
208 phosphatidylglycerol (PG), diglactosyldiacylglycerol (DGDG) and
209 sulfoquinovosyldiacylglycerol (SQDG). The synthesis of these plastid lipids peaks at
210 approximately 16 DPA and then continues to decline through seed maturity. The other major
211 membrane glycerolipids are PC, phosphatidylethanolamine (PE) and phosphatidylinositol
212 (PI). The PC pool is central to seed lipid metabolism and oil synthesis, it provides substrates
213 for desaturation, acyl editing and TAG synthesis; however, the composition of PC is dynamic
214 and changes during seed maturation reflecting the production of C18:3 and C20:1 relative to
215 C18:1 and C18:2. Analysis of seeds from the Brassicaceae, including camelina, has shown
216 that the embryo typically provides 85 to 90% of the seed oil content (Li et al. 2006), but the
217 embryo has a complexity of cell types and differentiated lipid metabolism. Over recent years
218 this complexity has been addressed using mass spectrometry imaging of seed sections to
219 provide a detailed analysis of TAG (product) and PC (precursor) tissue-specific lipid
220 distributions (Horn and Chapman 2024). This approach identified unexpected heterogeneity
221 in camelina seed lipid distributions, with PC and TAG species enriched in C18:2
222 preferentially localized to the embryonic axis and lipid classes enriched in C20:1

223 preferentially localized to the cotyledons (Horn et al. 2013). This asymmetric distribution has
224 identified the potential for tissue-specific biosynthetic pathways (Fig 2B). TAG production in
225 seeds reflects the precursor specificity of the acyltransferases PDAT and DGAT; DGAT has a
226 higher selectivity for C20:1 and PDAT is more likely to incorporate C18:2 into TAG. The lack
227 of tri-18:2 in the cotyledon suggests DGAT predominates in cotyledons and PDAT is more
228 significant in the embryonic axis (a distribution supported by a PDAT and DGAT knock-down
229 study in camelina; Marmon et al. 2017). The further identification of PC species containing
230 C18:3 in the outer cotyledon indicated not only a developmental regulation of FAD3, but also
231 the possibility of tissue-specific expression.

232

233 **Demonstrating the Efficacy of Camelina as a Platform for Metabolic Engineering**

234 Historically, manipulation of camelina seed for oil content and composition has included
235 identifying natural (Vollmann et al. 2007) and induced (ethyl methanesulfonate (EMS); e.g.,
236 Büchenschütz-Nothdurft et al. 1998) variation. The key target genes for manipulation have
237 included genes for fatty acid desaturases that control polyunsaturated fatty acid production
238 e.g., FAD2 that forms C18:2 by Δ 12 desaturation, FAD3 for C18:3 production, and FAE1 that
239 elongates C18:1 to C20:1 and C22:1 respectively. By screening EMS camelina lines
240 Neumann et al. (2021) were able to identify mutants in *FAE1*, *FAD2* and *FAD3*, and
241 successfully stack these traits into one line to produce a camelina line with mid-oleic acid oil.
242 However, opportunities for innovation have prompted the application of biotechnological
243 strategies for trait improvement in camelina. Predominantly many of these approaches have
244 focused on seed traits e.g., yield (seed size and number), oil content and composition (Supp.
245 Table 1). Metabolic engineering of these traits can be a challenge given the complexity of
246 endogenous seed lipid metabolism (discussed above; Fig 1), and the polyploid genome of
247 camelina with multiple copies of each gene (one for each sub-genome). Overcoming these
248 challenges researchers have successfully demonstrated how metabolic engineering can be
249 used to improve oilseed crops and create sustainable solutions. The examples of metabolic
250 engineering detailed in Supp. Table 1 are not exhaustive but provide demonstrations of how
251 biotechnology has been applied for crop improvement in camelina. Examples include the
252 utilisation of different approaches (RNAi, gene editing; GE, and genetic modification; GM)
253 and interventions to change seed oil composition. This includes RNA interference (RNAi)-
254 mediated suppression of chlorophyll b assembly for improved photosynthesis and field
255 performance (Friedland et al. 2019), the production of high-oleate lines generated by RNAi-
256 mediated suppression of *FAD2* and *FAE1*, producing high-linoleate lines (C18:2), effectively
257 reducing the production of C18:3 and C20:1 in the seed (Horn et al. 2013, Nguyen et al.

258 2013). Reducing the production of VLCFA, including the undesirable erucic acid (C22:1), and
259 increasing the production of eighteen carbon fatty acids, has led to metabolic engineers
260 targeting *FAE1* using RNAi (Bashiri et al 2023), and gene editing methods (Ozseyhan et al.
261 2018).

262 Gene editing has been extensively applied in camelina for crop improvement. For example,
263 to reduce *FAE1* expression and lower seed VLCFAs (60% reduction; Ozseyhan et al. 2018),
264 generate *FAD2* knock outs with decreased 18:2 and 18:3 producing seeds with increased
265 MUFA content (Jiang et al. 2017; Lee et al. 2021), compositional changes resulting from the
266 knock down of *DGAT1* & 2 (Lee et al. 2024), and disruption of the Transparent Testa 8 (*TT8*)
267 transcription factor, increasing seed total fatty acid, TAG content, and producing heavier
268 seed weights (Cai et al. 2024). Furthermore, efficient multiplex gene editing has been
269 demonstrated in the hexaploid camelina (see Bellec et al. 2022), producing early-flowering
270 biotypes suitable for summer cropping by targeting flowering repressor genes (*FLOWERING*
271 *LOCUS C*, *SHORT VEGETATIVE PHASE*, *LIKE HETEROCHROMATIN PROTEIN 1*,
272 *TERMINAL FLOWER 1* and *EARLY FLOWERING LOCUS 3*). Titration of the induced
273 combinatorial mutations identified early-flowering phenotypes stable for five generations.
274 Other iterations include the use of gene editing to address potential adverse properties of
275 camelina seeds e.g., glucosinolates, that can represent a limitation on the use of Brassica
276 species in livestock feed. Cas9 endonuclease-based targeted mutagenesis of the
277 glucosinolate transporters *CsGTR1* and *CsGTR2* caused a strong decrease in glucosinolate
278 amounts, whilst mutagenesis of each glucosinolate biosynthesis transcription factor
279 (*CsMYB28* and *CsMYB29*) homeolog resulted in the complete loss of glucosinolates,
280 representing the first glucosinolate-free Brassicaceae crop (Hölzl et al. 2023). As illustrated
281 in Supp. Table 1, increasing seed oil content has been addressed by several different
282 approaches to manipulate seed fatty acid production and lipid assembly pathways including
283 the expression of: the transcription factor *WRI1* (An et al. 2015); fatty acid transporters *FAX1*
284 and members of the ATP-binding cassette transporter subfamily A9 (Cai et al. 2021); oil
285 biosynthesis enzymes *PDAT* (Abdullah et al. 2024) and *DGAT1* (Kim et al. 2016); *DGAT1*
286 and a yeast cytosolic glycerol-3-phosphate dehydrogenase (*GPD1*) (Chhikara et al. 2018);
287 overexpression of the *ACC*ase subunit α -CT (Wang et al. 2022); vacuolar sugar transporter
288 *TST1* (Okoooboh et al. 2022), and fatty acid exchange via a non-specific phospholipase *C6*
289 (Cai et al. 2020). Improving the performance (flower fertility, yield, oil content and plant
290 architecture) of camelina has also received attention through expression of *CYP78A* genes
291 of the P450 monooxygenase family previously demonstrated to be involved in regulating
292 seed development in *Arabidopsis* (*AtCYP78A6* or *AtCYP78A5*; Hölzl et al. (2021) and via
293 improved CO₂ use efficiency (expression of the *E.coli* chloroplast glycolate dehydrogenase,

294 glyoxylate carboxylase, and tartronic semialdehyde reductase; Dalal et al. (2015)) enhancing
295 growth of transgenic camelina plants, with larger capsules and seeds. These are just some
296 highlighted examples of biotechnological crop improvement in camelina – additional
297 examples are described by Yu et al. (2018).

298 The most striking examples of biotechnology for crop improvement in camelina occur when
299 GM approaches are used to redesign seed metabolism to produce higher value food and
300 non-food products. A demonstration of this is the diversion of sinapine precursors to produce
301 a value-added co-product e.g., 4-vinyl phenols. Sinapine is an antinutritional compound
302 found in Brassica species that reduces the suitability of protein-rich seed meal for use in
303 animal feed, whilst 4-vinyl phenols have utility in a range of industrial applications. Rather
304 than using a genetic intervention to reduce sinapine levels, Menard et al. (2022) expressed a
305 modified bacterial phenolic acid decarboxylase (PAD) in developing camelina to redirect
306 phenylpropanoid pathway flux from sinapine biosynthesis to the production of 4-vinyl
307 phenols, providing a non-petrochemical source of this class of industrial chemicals.
308 Metabolic engineers have successfully utilised camelina for the sustainable production of
309 many valuable biobased products (reviewed in Bansal and Durrett 2016, Yuan and Li 2020,
310 Ghidoli et al. 2023). Several demonstrations of these approaches are provided in Supp.
311 Table 1 and include the production, via metabolic engineering, of novel fatty acids e.g.
312 hydroxyl fatty acids (Snapp et al. 2014, Aryal et al. 2018), 3-acetyl-1,2-diacyl-sn-glycerols
313 (acetyl-TAGs) with medium-chain fatty acids (Liu et al. 2015; Bansal et al. 2018, Alkotami et
314 al. 2024), production of nervonic acid (C24:1 Δ 15; Huai et al. 2015), ω -7 fatty acids (Nguyen
315 et al., 2015; Rodríguez-Rodríguez et al. 2021), precursors for sustainable aviation fuel
316 including capric and myristic fatty acid production (Kim et al. 2015), and cyclopropane fatty
317 acid accumulation (Yu et al. 2019). Metabolic engineering in camelina has further validated
318 routes to the production of industrial lubricants (waxes; Zhu et al., 2016; Iven et al. 2016 and
319 Ruiz-Lopez et al. 2017) and replacements for the chemical feedstocks used to create
320 plastics and polymers (Malik et al. 2015, 2023). These approaches support the transition
321 from our dependence on fossil fuels, providing a biobased alternative in an existing oilseed
322 cropping system.

323 **The Transition from Proof of Concept to Prototype: Nutritional Enhancement of** 324 **Camelina**

325 The application of biotechnological approaches in camelina has enabled researchers to
326 develop metabolic engineering strategies to improve the nutritional quality of oilseeds (e.g.,
327 increased production of tocopherols; Konda et al. 2023, and carotenoids; He et al. 2022),
328 and produce new supplies of finite resources. This is particularly true for aquaculture, which

329 relies on marine extraction for key feed ingredients including omega-3 long chain
330 polyunsaturated fatty acids (omega-3 LC-PUFAs; eicosapentaenoic acid (EPA;
331 20:5^{Δ5,8,11,14,17}) and docosahexaenoic acid (DHA; 22:6^{Δ4,7,10,13,16,19})), which are present only in
332 marine food webs. Healthy diets depend on key nutrients such as omega-3 LC-PUFAs and
333 their sustainable supply is a challenge for our existing food systems. The production of these
334 novel fatty acids in oilseeds is not straightforward and required the reconstruction and co-
335 ordination of a complex seed-specific biosynthetic pathway in camelina comprising a series
336 of enzymatic reactions that convert endogenous C18 fatty acids to C20+ LC-PUFAs
337 (reviewed in Napier and Betancor 2023, Venegas-Caleron and Napier 2023). The successful
338 reconstitution of this pathway involved extensive iteration to define the optimal gene
339 combinations that effectively combined with endogenous camelina seed lipid metabolism to
340 produce a terrestrial seed oil with EPA and DHA levels matching that found in commercial
341 fish oil (Ruiz-Lopez et al. 2013; Ruiz-Lopez et al. 2014). Using the same approach a tailored
342 camelina oil was generated accumulating EPA and the related omega-3 LC-PUFA
343 eicosatetraenoic acid (ETA, 20:4^{Δ8,11,14,17}) (Ruiz-Lopez et al. 2015). Seed oils such as these
344 represented an additional source of EPA, and an entirely new source of the bona fide fish oil
345 ETA. At this point camelina EPA+DHA oil was a proof of concept (Fig 2A & C), like many of
346 the demonstrations illustrated in Supp. Table 1. To achieve the successful translation of this
347 biotechnology to a prototype required further validation steps. Firstly, oils derived from
348 omega-3 (EPA+DHA) rich camelina were successfully trialled as substitutes for fish oil in
349 feed diets used in aquaculture. The trials showed that fish fed the GM-derived oils had
350 enhanced levels of n-3 LC-PUFA in their flesh compared to either a commercial diet control
351 or a feed containing wild-type camelina. Indeed, in some cases salmon fed a diet containing
352 high omega-3 LC-PUFA camelina oil accumulated almost double the amount of these health
353 beneficial fatty acids as salmon fed a fish oil diet (Betancor et al. 2017, Napier et al. 2020).
354 Secondly, the stability of the camelina seed EPA+DHA trait had to be confirmed in field
355 situations, effectively incorporating field trialling into the engineering biology 'design-build-
356 test-learn' cycle. Therefore, the transgene-directed accumulation of non-native omega-3 long
357 chain polyunsaturated fatty acids in the seed oil of camelina was evaluated in distinct
358 geographical and regulatory locations (UK, USA and Canada; Han et al. 2020). The
359 accumulation of EPA+DHA in seeds was found to be consistent with controlled environment
360 experiments irrespective of the agricultural environment, demonstrating the stability and
361 robust nature of the omega-3 trait (and camelina as a host for enhanced lipid metabolism).
362 Additional examination of field grown non-seed tissues for the unintended accumulation of
363 EPA and DHA failed to identify their presence, further confirming the seed-specific
364 accumulation of these novel fatty acids (Han et al. 2022b). The asymmetric distribution of
365 camelina oil assembly pathways noted in earlier sections (predominant DGAT activity in

366 cotyledons and significant PDAT activity within the embryonic axis) impacted EPA+DHA
367 biosynthesis and accumulation in seeds; MSI approaches found that novel fatty acids
368 preferentially accumulated in the embryonic axis of glasshouse and field grown material
369 (Usher et al. 2017), demonstrating how tissue-specific endogenous oil biosynthesis
370 influences the accumulation of novel fatty acids in seeds (Fig 2B). Combining transgene-
371 derived seed-specific synthesis of omega-3 LC-PUFAs with CRISPR-Cas9 gene editing to
372 inactivate the FAE1 pathway in a 'GM+GE stack' and evaluating this iteration in a field
373 environment further demonstrated that the accumulation of EPA+DHA can be increased by
374 augmenting the α -linolenic acid precursor pool and shutting off the carbon shunt into 20:1 ^{Δ 11}
375 and 22:1 ^{Δ 13} (Han et al. 2022a) Finally, if omega-3 (EPA+DHA) camelina oil is to be a means
376 of provisioning the human population with an alternative supply of EPA and DHA, studies
377 were required to test if EPA and DHA consumed as oil from transgenic camelina are
378 incorporated after a meal into blood lipids at least as well as when consumed as fish oil. A
379 double blind, postprandial cross-over trial concluded there were no significant differences
380 between test oils or sexes in EPA and DHA incorporation into plasma TAG and PC over the
381 duration of the trial. The incorporation into blood lipids of EPA and DHA consumed as
382 camelina EPA+DHA oil was equivalent to commercial blended fish oil, and the efficacy of
383 transgenic camelina derived oils as a suitable dietary source of EPA and DHA in humans
384 was demonstrated (West et al. 2019; West et al. 2020). Producing omega-3 LC-PUFAs in
385 camelina seeds and validating the derived oils confirmed the stability and utility of this oil in
386 both indirect and direct human nutrition, effectively derisked the biotechnology, and provided
387 the impetus for its commercialisation via public-private partnership. Collectively these
388 discovery and development efforts have established a road map for the translation of
389 camelina biotechnology. The production of EPA+DHA in camelina and other oilseeds e.g.,
390 Canola (Event NS-B50027-4; Petri et al. 2020; Event BPS-BFLFK-2; Andre et al. 2019) has
391 been a huge effort across the lipid community and represents some of the most complex
392 engineering in plants to date.

393 **Prospects for Engineering New types of Nutritional Lipids in Camelina seed TAG**

394 The successful development of oils rich in omega-3 LC-PUFAs provides a road map for
395 engineering production of other dietary lipids in camelina, such as sustainable alternatives to
396 animal fats. The TAGs found in meat and milk differ from those of plants in both the types of
397 FAs that are esterified to the glycerol backbone and their stereospecific positions (sn-1, 2 or
398 3) (Michalski et al. 2013). These differences not only affect the physicochemical properties of
399 the TAGs but also their digestion, absorption, and metabolic fate (Michalski et al. 2013). For
400 example, more than 70% of the C16:0 found in human milk fat is esterified to the sn-2
401 position on the glycerol backbone and 1,3-dioleoyl-2-palmitoylglycerol (OPO) is the

402 predominant TAG species (Wei et al. 2019). Harboring C16:0 in this specific TAG
403 stereoisomer is known to be beneficial for lipid and calcium absorption in the infant gut
404 (Béghin et al. 2018). Dietary TAGs are hydrolysed in the duodenum by pancreatic lipase,
405 which is sn-1/3 specific. The 2-monoacylglycerol (2-MAG) and free fatty acids that are
406 released are absorbed by intestinal mucosal cells. However, saturated long chain fatty acids,
407 such as C16:0, are absorbed less efficiently than unsaturated fatty acids because they form
408 insoluble soaps with calcium and magnesium ions, whereas 2-MAGs are absorbed well
409 regardless of their fatty acyl group (Wei et al. 2019). Vegetable fats are used in most infant
410 formulas, but plants only esterify C16:0 to the sn-1/3 position and not to sn-2 (van Erp et al.
411 2019). *Arabidopsis thaliana* seeds have been engineered to alter the stereospecific position
412 of C16:0 to sn-2 (van Erp et al. 2019) and ultimately to produce TAG with a similar level of
413 OPO to human milk fat (van Erp et al. 2021). This engineering strategy could potentially be
414 applied to camelina. It is noteworthy that animal fats generally harbour considerably more
415 C16:0 in the sn-2 position than do plant fats (Michalski et al. 2013). Dairy milk fat additionally
416 contains a range of short and medium chain saturated FA, with short chain, predominantly
417 butyrate (C4:0), found only at the sn-3 position (Michalski et al. 2013).

418 **Conclusion and Perspectives**

419 The renaissance of camelina over recent years reflects its potential contribution to some of
420 society's most significant challenges, including nutritional security and the supply of
421 sustainable feedstocks and products, all enshrined in the UN Sustainable Development
422 Goals. The challenge of food production in a changing climate, alongside the transition from
423 fossil fuels, is driving research and innovation in non-staple crops like camelina. As
424 illustrated here, the successful exploration and application of metabolic engineering can
425 provide solutions. Although the solutions described above may have associated regulatory
426 burdens, they have the advantage of utilising the pre-existing infrastructure and know-how
427 which underpin modern agriculture, allowing rapid scaling and incorporation into production
428 cycles. The future of camelina will involve continued iterative advancement; developing new
429 traits e.g., improved protein content and composition (Supp. Table 1) and stacking trait
430 combinations together to develop new biotypes that incorporate climate-resilience and novel
431 products. Expanding our use of plant-derived feed and foodstuffs will be essential for
432 operating within planetary boundaries (Walter et al. 2019) and collectively we need to
433 embrace a different approach – enabling plant biotechnology to play a key role by supporting
434 both the discovery *and validation* of metabolic engineering approaches.

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437 **Advances Box**

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- 450 • **Breakthrough techniques for lipid analysis:** The advent of affordable benchtop
451 mass spectrometry has enabled researchers to develop techniques (e.g., targeted
452 and untargeted liquid chromatography mass spectrometry, LC-MS, direct infusion;
453 hydrophobic interaction liquid chromatography, HILIC; multi reaction monitoring,
454 MRM; and high-resolution accurate mass, HR/AM), for the quantitative assessment
455 of individual lipid classes and molecular species (plant lipidomics). These
456 approaches, along with radiolabelled flux analysis, have enabled the complete
457 characterisation of seed lipid pools and the exchange of fatty acids between lipid
458 classes. In turn, this has permitted a greater understanding of complex lipid assembly
459 and the interaction of endogenous metabolism with novel activities (Bates et al.
460 2014).
 - 461 • **Spatially resolved seed lipid metabolism:** tissue-specific transcriptomics,
462 proteomics and lipidomics (combined analysis in multi-omic experiments) has revised
463 our (whole seed) understanding of seed lipid metabolism and its distribution of
464 activities. Mass spectrometry imaging has provided striking images of asymmetric
465 lipid molecular species distributions within seeds.
 - 466 • **Iterative metabolic engineering and the design-build-test-learn cycle:** the
467 straightforward reconstitution of novel metabolic pathways in seeds is rarely simple
468 and requires the careful optimisation of gene candidates and combinations before the
469 accumulation of desired products is achieved. Importantly, some plant metabolic
470 engineers are now incorporating field testing into the DBTL-cycle to ensure desired
471 outcomes are stable in real world environments.
 - 472 • **The utility of plant biotechnology to deliver to sustainability goals:** by definition,
473 plant biotechnology involves the use of genetic modification and/or gene editing,
474 Approaches that require researchers to secure regulatory, funding, and societal
475 acceptance. However, despite these hurdles, plant biotechnology provides a
476 significant opportunity to mitigate the impacts of climate change, transition away from
477 fossil fuels and support nutritional security.
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471 **Outstanding Questions Box**

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- How do we successfully design constructs, integrating regulatory elements and
- 474 multiple transgenes, to ensure strong stable tissue-specific expression?
- 475
- What determines the stability of transgene expression across multiple generations?
- 476
- What causes the yield drag (reduced seed oil content) often associated with seed
- 477 lipid metabolic engineering?
- 478
- Can we use ML/AI to improve our metabolic engineering, including predicting how
- 479 modified plants will perform in the environment?
- 480
- How do we increase genetic diversity in camelina and optimise camelina ideotypes to
- 481 specific pedoclimates?

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483

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490 **Author contributions**

491 The review was conceived by all the authors and written collectively.

492 **Data availability**

493 No new data were generated or analysed in support of this update.

494

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936 **Author notes**937 *Conflict of interest statement.* None declared.

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939 **Legends**940 **Figure 1. Camelina seed lipid biosynthesis.**941 **(A) An illustration of endogenous cellular lipid synthesis and assembly pathways**

942 including the following selected genes: fatty acid synthase, FAS; beta ketoacyl acyl carrier
 943 protein synthase II, KASII; stearyl-acyl carrier protein desaturase, SAD; fatty acid
 944 desaturase 2, FAD2; fatty acid desaturase 3, FAD3; fatty acid export 1, FAX1; long chain
 945 acyl—CoA synthetase 9, LACS9; fatty acid elongation 1, FAE1; lysophosphatidylcholine
 946 acyltransferase LPCAT; diacylglycerol acyltransferase, DGAT, phospholipid:diacylglycerol
 947 acyltransferase, PDAT, phospholipase C, PLC; phospholipase D, PLD; diacylglycerol
 948 cholinephosphotransferase, CPT; phosphatidylcholine diacylglycerol
 949 cholinephosphotransferase, PDCT; Glycerol-3-phosphate acyltransferase, GPAT;
 950 lysophosphatidyl acyltransferase, LPAAT; and phosphatidate phosphatase, PAP.

951 **(B) Heatmap showing the expression of selected *Camelina sativa* genes during seed
 952 development** generated using [https://github.com/richysix/bioinf-](https://github.com/richysix/bioinf-gen/blob/master/docs/gene_expr_heatmap/gene_expr_heatmap.md)

953 [gen/blob/master/docs/gene_expr_heatmap/gene_expr_heatmap.md](https://github.com/richysix/bioinf-gen/blob/master/docs/gene_expr_heatmap/gene_expr_heatmap.md) (B). The colour scale
 954 represents normalised counts calculated by DESeq2. RNA sequencing reads generated by
 955 Kagale et al. (2016) (accessions SRX472942, SRX472943, SRX472945 & SRX472946)
 956 were aligned to the *Camelina sativa* reference genome (Kagale et al., 2014) (accession
 957 JFZQ00000000) using TopHat and quantified at the gene level with HTSeq. Key to seed
 958 stages: Early seed development (ESD), Early mid seed development (EMSD), Late mid
 959 seed development (LMSD), and Late seed development (LSD).

960 **Figure 2. Camelina as a platform of metabolic engineering.** (A) Field grown camelina

961 seed engineered with a range of traits including omega-3 and ketocarotenoids (Seeds from
 962 modified camelina are shown (clockwise) 1. Wildtype; 2. RUBY (betaline); 3. Astaxanthin;
 963 and 4. tt2 mutant (MYB); (B) Representative MSI study (camelina seed section; colouring
 964 indicates abundance – red high & green low) highlighting the asymmetric accumulation (in
 965 the embryonic axis tip) of a selected PC molecular species containing novel fatty acids
 966 (C22:6/C22:6; see Usher et al. 2017); (C) Field testing (Rothamsted Research, UK) of
 967 Camelina sativa engineered for the production of omega-3 long chain polyunsaturated fatty
 968 acids (EPA & DHA).

969

970 **Supp. Table 1. Metabolic engineering in camelina.** Crop improvement and the
971 deployment of novel traits in camelina using metabolic engineering approaches.

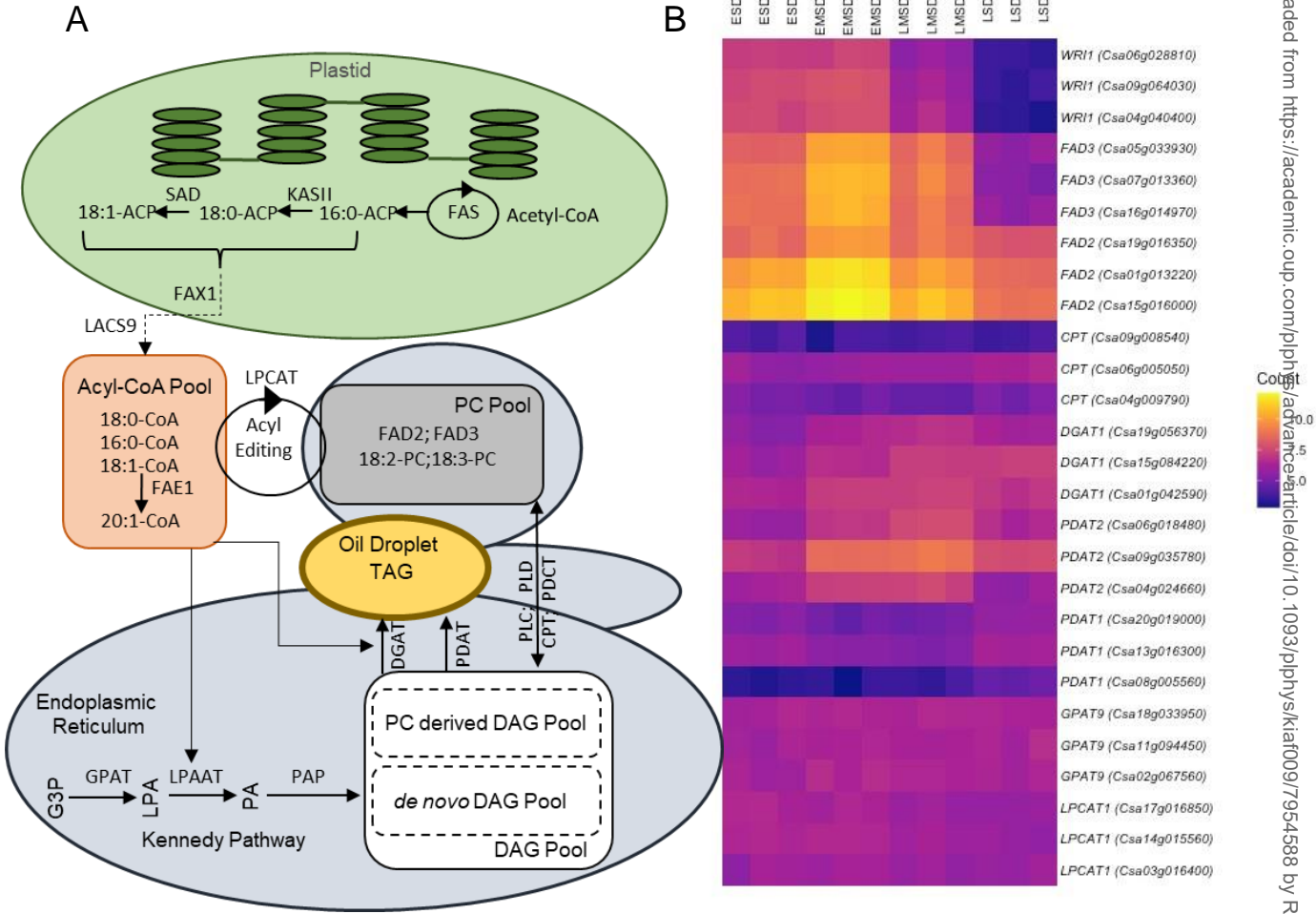


Figure 1. Lipid biosynthesis and assembly in camelina seeds.

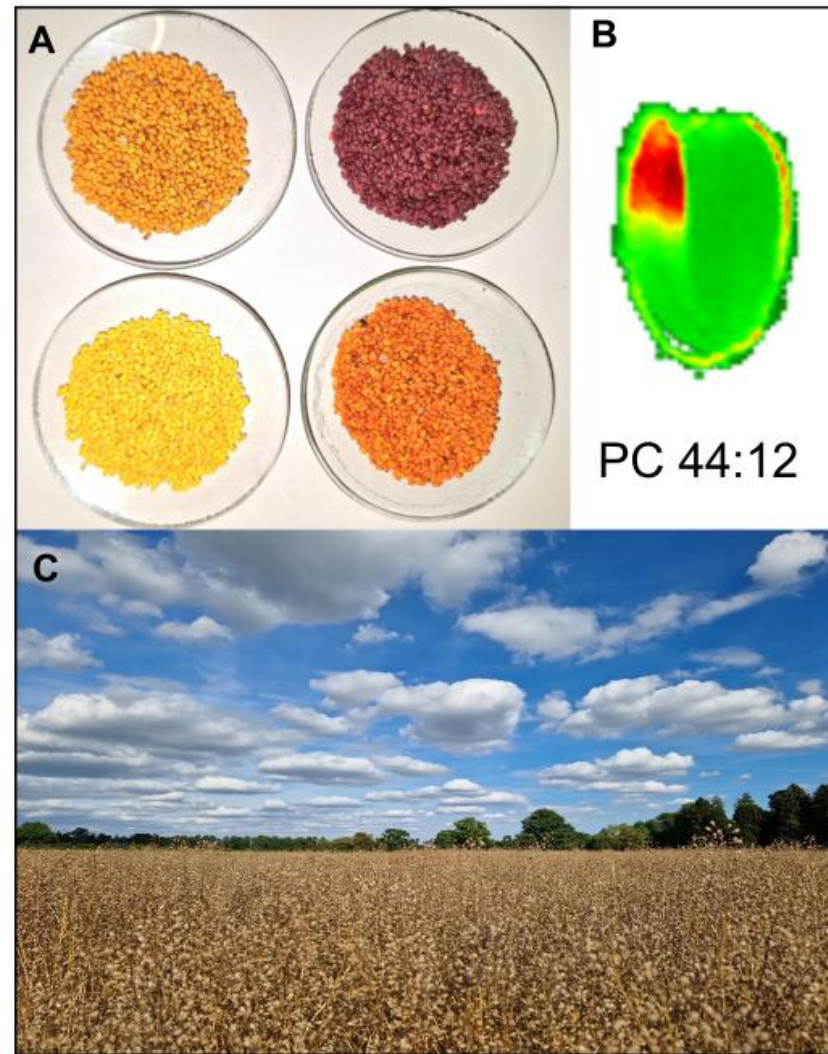


Figure 2. Camelina as a platform for metabolic engineering.

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Conflict of interest statement. None declared.