# Lipid Metabolism and Improvement in Oilseed Crops

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Contributor: Mengjia Bu , Wei Fan , Ruonan Li , Bing He , Peng Cui

Oilseed crops are rich in plant lipids that not only provide essential fatty acids for the human diet but also play important roles as major sources of biofuels and indispensable raw materials for the chemical industry. The regulation of lipid metabolism genes is a major factor affecting oil production.

oilseed crops lipid metabolism seed oil content

## 1. Introduction

### Function of Lipids

Lipids play many roles in plant cells. For example, polar glycerides are the major components of cell membranes, where they act as protective barriers against external damage and initiate signaling [1].

Lipid composition varies widely among different species and tissues [2]. For example, plants accumulate large amounts of lipids in their seeds or fruits to provide the energy needed for germinating seeds, maintaining moisture, and preventing cold cracking and frostbite in the seeds. Lipids play essential roles in cell signal transduction between flowers, leaves, stems, and other tissues [3] and are deposited as waxes on the plant surface to decrease non-stomatal plant water loss or ultraviolet (UV) damage, thus increasing plant tolerance to abiotic stress [4].

### Classification of Plant Lipids

Lipids are widely distributed in all plant tissues and can be divided into eight types according to their chemical composition: FAs, glycerol lipids, glycerophospholipids, sphingolipids, sterol lipids, allyl alcohol lipids, glycolipids, and polyketides [5][6] (**Figure 1**). FAs are the building blocks of many of the more complex lipids. About 40 FAs serve as the major components of natural lipids, among over 10,000 known fatty acyl molecules (https://www.lipidmaps.org) accessed on 22 September 2018 [5][7]. When supplied with sufficient oxygen, FAs can be oxidized and broken down into $CO_2$ and $H_2O$, releasing large amounts of energy, thus making them a major source of energy. FAs can be further divided into saturated fatty acids (SFAs) and unsaturated fatty acids (UFAs) based on the absence or presence of double bonds. In most plants, the major SFAs are palmitic acid (16:0, 16 is the number of carbon atoms, 0 represents the number of double bonds) and stearic acid (18:0), and the major UFAs are monounsaturated FAs (MUFAs), such as oleic acid (18:1), and polyunsaturated FAs (PUFAs), such as linoleic acid (LA, 18:2) and α-linolenic acid (α-ALA, 18:3) [8]. These five FAs account for approximately 90% of the lipids in commercial vegetable oils on the market [9].

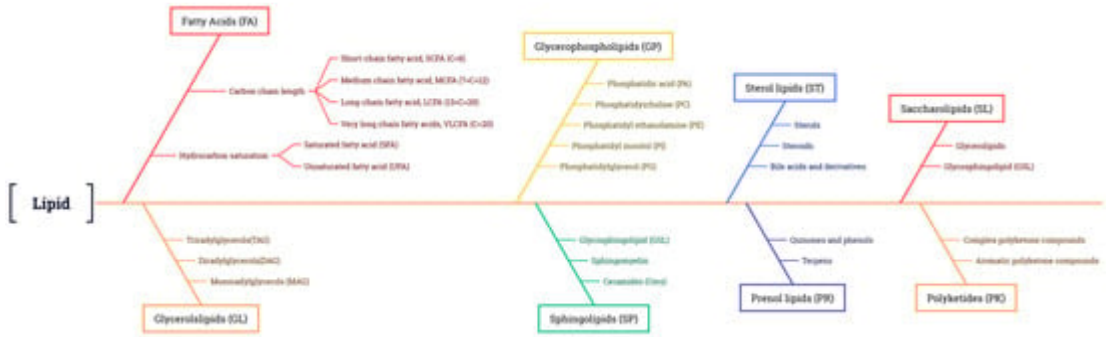


**Figure 1.** Classification of lipids.

## Lipid Accumulation and Storage in Plants

In oilseed crops, the first step in FA biosynthesis is the conversion of acetyl-CoA produced via sucrose glycolysis to malonyl-CoA by acetyl-CoA carboxylase (ACCase). ACCase is a type I biotin-containing enzyme and there are two main forms of ACCase in plants: Heteromeric ACCaseI and Homomeric ACCaseII. ACCase is composed of four subunits: biotin carboxylase (BC), biotin carboxyl carrier protein (BCCP), α-carboxyltransferase (α-CT), and β-carboxyltransferase (β-CT). It has three functional domains, namely the BC functional domain, the BCCP functional domain, and the CT functional domain, respectively [10][11]. After its biosynthesis, malonyl-CoA is transferred to the ACP component of the fatty acid synthase (FAS) complex by malonyl-CoA:ACP malonyltransacylase (MCMT). In plants, FAS is a multi-component type-II enzyme located in the plastids, consisting of 3-β-ketoacyl-ACP synthase III (KASIII), β-ketoacyl-ACP synthase (KASI), ketoacyl-ACP reductase (KAR), hydroxyacyl-ACP reductase (HAD), and enoyl-ACP reductase (ENR). FAS uses acetyl-CoA as the starting unit for a condensation reaction. Each elongation cycle is supplied with a two-carbon unit by malonyl-ACP to produce 16:0-ACP and 18:0-ACP after seven or eight cycles, respectively, at which point 18:0-ACP passes through Δ9 stearoyl-ACP desaturase to form 18:1-ACP, making phosphatidic acid (PA) (16:0) and oleic acid (18:1) the major products of FA biosynthesis in most plant plastids [12].

In most oilseed crops, such as soybean (*Glycine max*) and rapeseed (*Brassica napus*), TAGs are stored in seeds as an energy source for germination and aid in seed dispersal [13]. TAG consists of a glycerol backbone and three FA molecules chemically linked by ester bonds, providing a carbon skeleton and energy source. TAG biosynthesis and accumulation occur through a complex network of reactions taking place in the plastid, cytoplasm, and ER. Depending on the plant species, TAG can accumulate in different organs, mainly in embryonic tissues (rapeseed) or endosperm tissues (castor bean). In oilseeds that store oil in the embryo, the main storage tissue is the cotyledons, but substantial seed oil can also accumulate in the hypocotyl, radicle, and surrounding endosperm/aleurone layers [14]. After acyl-CoA is transported from the plastid to the ER, the most common pathway for TAG biosynthesis is the acyl-CoA-dependent Kennedy pathway [15]. In this pathway, acyl-CoA is incorporated into glycerol-3-phosphate (G3P) by acyl-CoA:glycerol-3-phosphate acyltransferase (GPAT) and lysophosphatidic acid acyltransferase (LPAT) at the sn-1 and sn-2 positions of G3P, respectively, to form PA.

Cytoplasmic lipid droplets (LDs) are organelles that store non-polar lipids such as TAGs and sterol esters [16]. In mature seeds, LDs are distributed in the central region of storage cells and are mostly oval or irregular in shape

[17]. The primary LD structure consists of a phospholipid monolayer coated with various proteins. The current general model of LD biogenesis is that non-poplar lipids such as TAGs are first produced by membrane-associated enzymes in the ER and then accumulate in the form of a lens between lobes of the ER membrane, culminating with LD formation on the cytoplasmic side of the ER membrane [18]. Two important proteins have recently been shown to be involved in LD formation: SEIPIN [19][20] and lipid-droplet-associated protein in Arabidopsis (*Arabidopsis thaliana*) [21].

Oil accumulation in seeds involves a dynamic balancing act between lipid biosynthesis and degradation. Due to lipid degradation, the oil content of rapeseed decreases by about 10% during the final stages of seed development, resulting in an estimated loss of approximately 20 million tons of vegetable oil per year [22]. The two types of enzymes responsible for lipid degradation are lipases and lipoxygenases [23]. Lipid degradation via lipases produces glycerol and NEFAs [24]. FAs are transported to the mitochondria and glyoxylate cycle bodies for β-oxidation and then the glyoxylate cycle. β-Oxidation allows NEFAs to be converted to acetyl-CoA, and complete oxidation of acetyl-CoA occurs via the tricarboxylic acid cycle [25][26] (**Figure 2**).

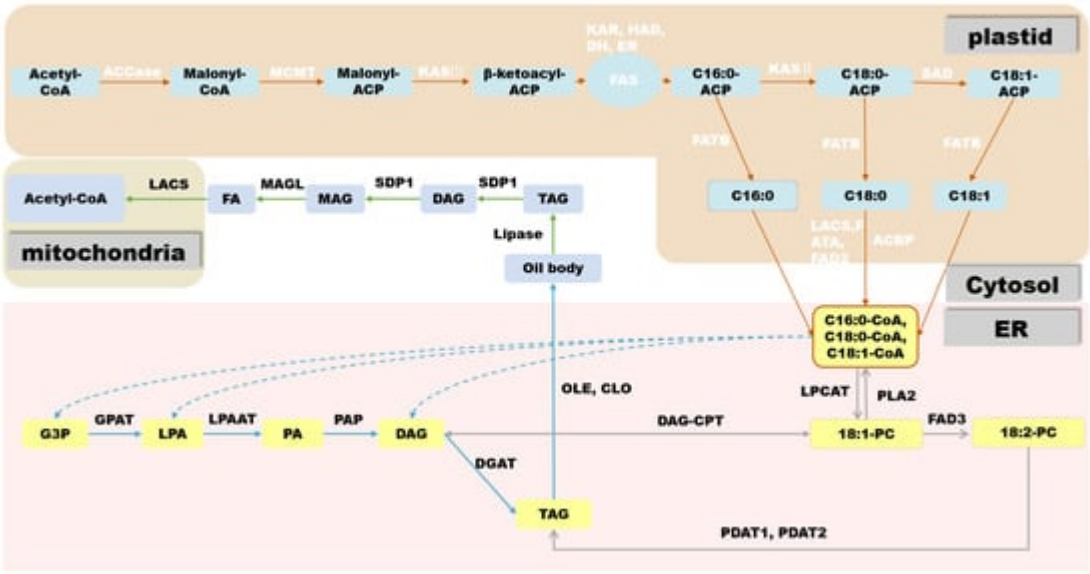


**Figure 2.** General overview of fatty acid biosynthesis in oilseed crops. ACCase: Acetyl-CoA Carboxylase; MCMT: Monoacylglycerol acyltransferase; KASIII: β-ketoacyl-ACP; KAR: β-ketoacyl-ACP reductase; HAD: β-hydroxyacyl-ACP dehydrogenase; DH: enoyl-ACP dehydratase; ER: enoyl-ACP reductase; KASII: 3-ketoacyl-ACP synthase II; SAD: stearoyl-ACP desaturase; FATB: Fatty Acid Thioesterase B; LACS: Long-chain acyl-CoA synthetase; FATA: Fatty Acid Thioesterase A; FAD2: Fatty acid desaturase 2; ACBP: Acyl-CoA binding protein; LPCAT: Lysophosphatidylcholine acyltransferase; PLA2: Phospholipase A2; FAD3: Delta-15 desaturase; DAG-CPT: Diacylglycerol cholinephosphotransferase; PDAT: Phospholipid: Diacylglycerol Acyltransferase; OLE: Oleate desaturase; CLO: Linoleate desaturase; SDP1: sn-glycerol-3-phosphate dehydrogenase; MAGL: Monoacylglycerol lipase; DGAT: Diacylglycerol acyltransferase; PAP: Phosphatidate phosphatase; LPAAT: Lysophosphatidic acid acyltransferase; GPAT: Glycerol-3-phosphate acyltransferase.

# 2. Progress in the Identification of Key Genes behind Lipid Metabolism in Plants

## 2.1. Identification and Functional Characterization of Key Genes

As mentioned above, FATB is a key enzyme in FA biosynthesis that catalyzes the removal of ACP from 16:0-ACP and 18:1-ACP to generate NEFAs. The knockdown of *GmFATB1* expression decreases UFA content in soybean seeds [27]. Similarly, the expression of *BnFATB* in rapeseed appears to be highly and positively correlated with seed oil content (SOC), as evidenced by an analysis integrating quantitative trait loci (QTLs) from nine different populations [28].

LPAT is one of the key enzymes in the Kennedy pathway that converts acyl-CoA to PA. The heterologous expression of a yeast (*Saccharomyces cerevisiae*) sn-2 acyltransferase gene in rapeseed resulted in increased FA content by 8–22% [29]. Cloning and spatiotemporal expression of *AhLPAT2* from peanut (*Arachis hypogaea*) showed that increased expression of this gene was closely related to seed oil content; moreover, heterologous expression of *AhLPAT2* in Arabidopsis from a seed-specific promoter significantly increased SOC [30].

DGAT is a key enzyme that acylates DAG at the sn-3 position. Seed-specific overexpression of Arabidopsis *DGAT* in wild-type plants resulted in an increase in SOC and seed weight from 29% to 35%, along with an increase in the average thousand-seed weight from 19 mg in non-transgenic plants to 23 mg in the overexpression lines [31], which was consistent with the results of heterologous expression of *DGAT1* from sesame (*Sesamum indicum*) in Arabidopsis [32].

GDSL esterase is a type of hydrolase that is widely involved in various physiological activities in plants and is important in oil metabolism. The name of the enzyme derives from its conserved domain (GDSL), where G, D, and S represent glycine (Gly), aspartate (Asp), and serine (Ser), respectively [33]. Arabidopsis has five GDSL-like lipase genes (also called *SEED FATTY ACID REDUCER* [*SFAR*] genes) that decrease SOC by acting downstream of the gibberellin signaling (GA) pathway since GA may affect the seed FA content via SFARs [34]. The overexpression or knockout of each *SFAR* gene significantly lowered or increased SOC, respectively, and altered FA composition. The heterologous expression of a *GDSL* gene from oil palm (*Elaeis guineensis*) in Arabidopsis resulted in a 9.5% increase in total FA content compared to the wild type.

In addition to these important pathway enzymes and their encoding genes directly involved in de novo FA biosynthesis and TAG assembly, recent studies have identified several genes annotated as participating in carbon source provisioning and photosynthetic pathways that may also be involved in regulating SOC [35]. For instance, trehalose-6-phosphate (T6P), a metabolic precursor of sucrose and a key signaling molecule for plants to respond to carbon availability and regulate growth and development, also regulates FA biosynthesis by inhibiting sucrose non-fermenting 1-related kinase 1 (SnRK1). Indeed, incubation of rapeseed suspension cells in T6P-containing medium or heterologous expression of *T6P synthase* from *Escherichia coli* in *Nicotiana benthamiana* significantly increased FA biosynthesis rates [36]. CALCINEURIN B-LIKE PROTEIN-INTERACTING PROTEIN KINASEs

(CIPKs) are a family of energy-signaling protein kinases in plants. Relative to non-transgenic plants, the overexpression of *BnCIPK9* during seed development in transgenic rapeseed lowered oil biosynthesis [37].

## 2.2. Transcription Factors Involved in Regulation

Looking for transcription factors (TFs) that regulate the expression of multiple genes is also an effective method to increase SOC [38]. Currently, well-studied TFs in plants mainly include WRINKLED1 (WRI1), LEAFY COTYLEDON1 (LEC1), LEC2, LEC1-LIKE (LIL), FUSCA3 (FUS3), and ABSCISIC ACID INSENSITIVE3 (ABI3).

WRI1 is an APETALA2 (AP2)/ETHYLENE-RESPONSIVE ELEMENT BINDING PROTEIN (EREBP) that regulates genes involved in glycolysis and sucrose entry into TAG [39]. WRI1 was discovered in Arabidopsis in 1998 as a mutant affecting seed storage accumulation. Compared with the wild type, the mutant was unable to convert glucose and sucrose into precursors for fatty acid synthesis during seed development and reduced the activity of several glycolytic enzymes such as hexokinase and phosphofructokinase, resulting in an 80% reduction in SOC [40]. The oil content of *N. benthamiana* leaves expressing *WRI1* from castor bean showed a 4.3–4.8 times increase compared to the control group. The Arabidopsis *wri1* loss-of-function mutant was almost completely rescued by the strong expression of castor bean *WRI1* from a seed-specific promoter, resulting in a total FA content close to that of non-transgenic seeds [41]. LEC1 is a member of the nuclear factor-YB (NF-YB) family of TFs, and the individual overexpression of Arabidopsis *LEC1* or *L1L*, or the overexpression of their homologous genes *BnLEC1* or *BnL1L* from rapeseed, resulted in significantly increased FA levels in transgenic Arabidopsis [42][43].

FUS3, another member of the plant-specific B3 domain family, plays an important role in recognizing and binding to the RY element CATGCA, which is found in the promoters of many genes. *fus3* mutants in rapeseed showed a lower total SOC than the wild type [44]. Inducible expression of Arabidopsis *FUS3* increased the oil content of Arabidopsis seedlings to 6% of dry weight, which was more than 50-fold higher than that of non-transgenic seeds. Similarly, the inducible expression of *FUS3* in *Nicotiana tabacum* L. cv Bright Yellow2 (BY2) cells increased TAG accumulation, and the co-expression of *FUS3* and *DGAT1* further increased the TAG levels to 4% of the dry weight.

ABI3 is also a member of the B3 domain TF family. The heterologous expression of *GmABI3* from soybean in Arabidopsis significantly increased TAG content and altered the FA composition of seeds. In addition, *GmABI3* expression successfully complemented the phenotype and oil content of Arabidopsis *abi3* mutant seeds [45]. In another study, tobacco leaf protoplasts were prepared for transfection with effector constructs overexpressing *WRI1* and/or *DGAT1* alone or together with one of the master regulators *ABI3*, *FUS3*, *LEC1*, or *LEC2.* The co-expression of *FUS3* and *ABI3* with *WRI1* and *DGAT1* significantly increased the content of total non-polar lipids of the protoplasts. Notably, the expression of *ABI3* overexpression alone resulted in the highest accumulation of total non-polar lipid in protoplasts. Furthermore, in contrast to *LEC2*, the co-expression of *ABI3* further increased the lipid content of protoplasts transiently expressing *WRI1* and *DGAT1* [46].

MYB TFs comprise one of the largest gene families in plants and are associated with the regulation of plant growth and development, metabolism, morphology, and cellular patterning [47]. MYB92 can directly bind to the promoter of and activate the transcription of *Biotin carboxyl carrier protein 2* (*BCCP2*), which encodes a component of the FA biosynthetic pathway. The overexpression of Arabidopsis *MYB92* in *N. benthamiana* induced the expression of FA biosynthesis genes, resulting in the accumulation of various types of lipids [48]. DECREASE WAX BIOSYNTHESIS 2 (DEWAX2) is a member of the AP2-EREBP TF family in Arabidopsis and negatively regulates epidermal wax deposition by directly binding to the promoters of *LACS1*, *LACS2*, *KCSII*, and *ECERIFERUM1* (*CER1*) to inhibit their expression [4].

*Growth-regulating factor 2a* (*BnRGF2a*) was identified in rapeseed based on its differential expression between two rapeseed lines with differing seed oil production. Arabidopsis lines overexpressing *BnGRF2* showed improved seed quality and oil content. In addition, transcriptome analysis revealed that some genes related to cell proliferation, photosynthesis, and oil biosynthesis were upregulated in these overexpression lines, suggesting that cell number and photosynthesis are linked to the observed increase in seed weight and oil content [49].

## 2.3. Advances in Multi-Omics Studies of Oilseed Crops

With the abundance of high-throughput sequencing information, the mining of large amounts of biological data is becoming increasingly popular and feasible. The availability of genomic, transcriptomic, and other multi-omics data provides a powerful avenue to unravel the detailed regulation of lipid metabolism [50][51]. From an omics perspective, the following aspects of lipid metabolism in oilseed crops are currently of interest (**Figure 3**).

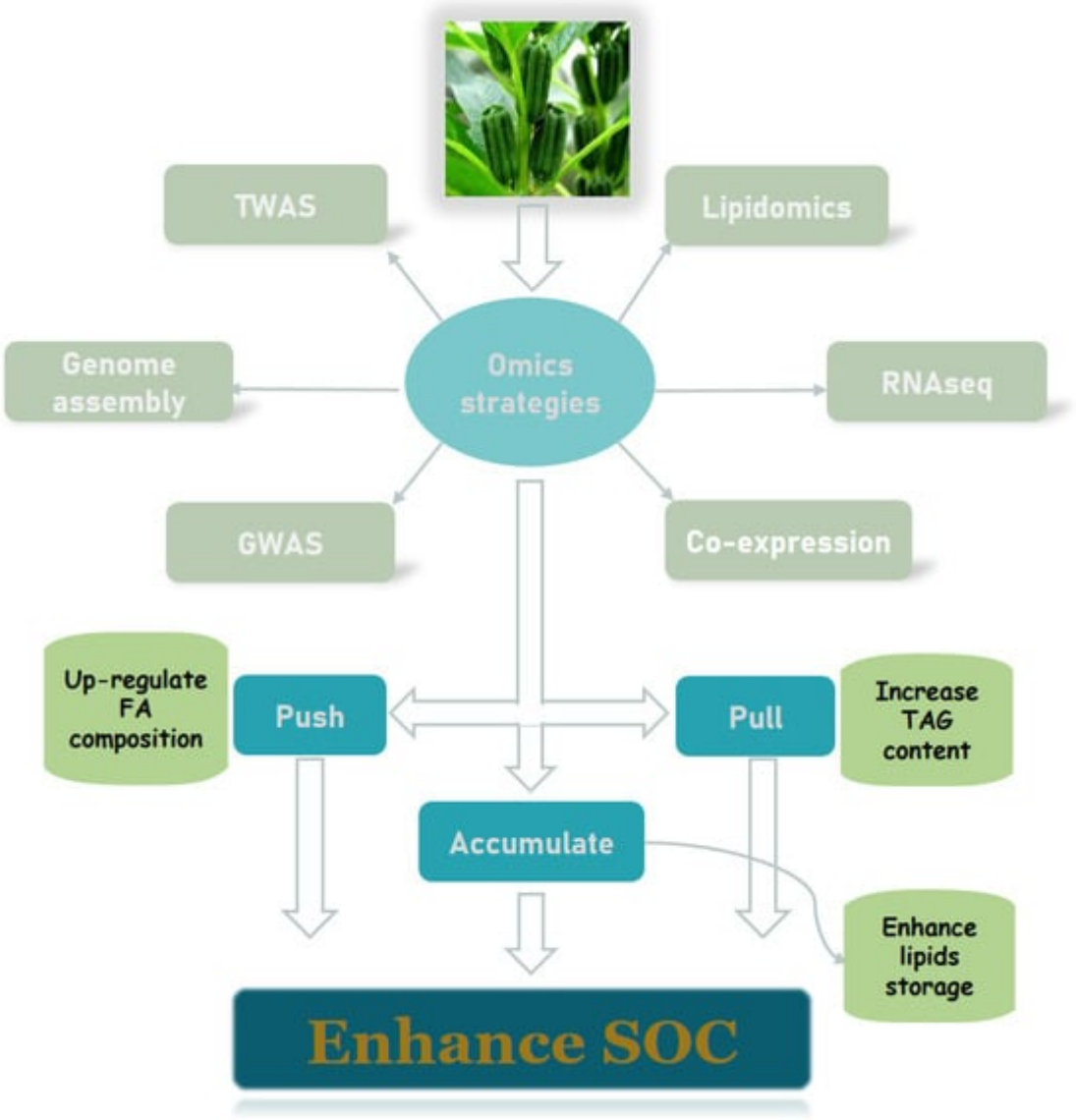


**Figure 3.** Multiple strategies to identify lipid metabolism related genes to increase SOC based on multi-omics approaches.

### 2.3.1. De Novo Genome Sequencing and Annotation

Genomic information plays a fundamental role in crop improvement programs, and large-scale population genomic analyses based on a range of genetic resources provide accurate information for identifying genomic variation underlying the selection of desirable traits [52]. In recent years, several new technologies have greatly improved existing reference genomes, including single-molecule real-time sequencing (SMRT) [53] and high-throughput chromosome conformation capture (Hi-C) technologies [54]. Continuous improvement of genome quality has greatly facilitated gene identification and deepened the understanding of crop breeding.

Taking representative oilseed genomes as an example, the first published rapeseed genome was for the winter-type European rapeseed cultivar '*Darmor-bzh*', with 1097 and 1132 lipid biosynthesis genes annotated in its An and Cn subgenomes, respectively. Most of the lipid biosynthesis genes present in the genome of the rapeseed

ancestor are conserved in modern-day cultivars, with the exception of 18 acyl–lipid homologs. The subgenomes An and Cn have undergone subtle structural, functional, and epigenetic cross-talk with abundant homoeologous exchanges. In addition, the selection of different rapeseed cultivars may have accelerated the loss of glucosinolate biosynthetic genes and maintained the expansion of oil biosynthesis genes [55].

Using SMRT sequencing in combination with BioNano and Hi-C, the genome of peanut var. '*Shitouqi*' was assembled, and the functional annotation of genes involved in seed size evolution, SOC, disease resistance, and symbiotic nitrogen fixation was performed. A total of 1944 acyl–lipid orthologs were identified in peanut, grouped into 727 gene families [56].

Pan-genomic analyses have aided the identification of candidate genes associated with agronomic traits by revealing many genetic variations that would not have been detected in a single genome, including large structural variants and gene fusion events [57]. In soybean, 26 representative lines from 2898 deeply sequenced varieties were selected and de novo assembled. Together with three previously reported genomes, these 26 varieties were used to construct a map-based pan-genome, followed by linking structural variants with changes in the expression of candidate genes responsible for important traits [58].

### 2.3.2. Identification of Differentially Expressed Genes

The mining of differentially expressed genes (DEGs) is a widely used strategy to study many developmental programs, including lipid metabolism [59][60][61]. Through functional enrichment analysis of DEGs between the two high-oil peanut varieties '*W191*' and '*YH15*' and the low-oil variety '*JT1*', 57 DEGs involved in oil biosynthesis were identified, including three genes encoding ACCase, one gene encoding KASIII, one gene encoding HAD, and one gene encoding EAR. There were 11 TFs related to lipid biosynthesis.

The transcriptomes of seeds and carpels at different developmental stages were determined for three sesame cultivars differing in their oil content, representing 22 datasets. A comparison of transcriptomes between sesame seeds with low and high oil content revealed more DEGs upregulated during seed development in the variety with high oil content, suggesting that seed oil plays a key role in lipid biosynthesis at later stages. Key homologous lipid genes involved in TAG biosynthesis, including those encoding GPAT, DGAT, and phospholipid:diacylglycerol acyltransferase (PDAT) at different stages of asynchronously enhanced lipid transfer protein (*LTP*) genes SIN_1019175, SIN_1019172, and SIN_1010009, are usually prominent in sesame seeds with high oil content.

SOC accumulation rates and gene expression levels change dynamically during soybean seed development. Through the integration of DEGs and gene co-expression analysis in soybean, 124 potential genes related to oil biosynthesis were identified. Among these was *FAD2*, encoding an enzyme that catalyzes the conversion from 18:1-CoA to 18:2-PC; three other candidate genes (*GmABI3b*, *GmNFYA*, and *GmFAD2-1B*) were determined to control SOC [62]. DEG analysis was performed on seven transcriptome datasets from a pair of *Brassica rapa* accessions with different seed size, color, and oil content at different developmental stages.

### 2.3.3. Construction of Oil Co-Expression Networks

Co-expression networks are another common strategy for studying the transcriptional regulation of lipid metabolism based on multi-omics data, among which weighted gene co-expression network analysis (WGCNA) is the most widely used method [63][64]. Co-expression gene networks have been widely applied in several species [62][65][66][67].

A multi-level approach was implemented in oil palm combining WGCNA, quantification of allele-specific gene expression, and joint multivariate analysis of the transcriptome and lipidome to an interspecific backcross population between the African oil palm and the American oil palm, which have contrasting oil contents and FA compositions. The resulting gene co-expression network revealed a close transcriptional coordination of FAS in plastid with sugar sensing, plastid glycolysis, transient starch storage, and carbon recovery pathways [68].

### 2.3.4. Genome-Wide Association Studies to Map Oil Content–Related Loci

Genome-wide association studies (GWASs) analyze the association between traits of interest and markers or candidate genes based on linkage disequilibrium between loci within a population, providing a new research strategy for mining genomic regions of importance [69]. A GWAS-based analysis using whole-genome resequencing of 418 rapeseed varieties identified 628 candidate genes related to 56 important agronomic traits, including SOC.

A resequencing effort with 302 soybean accessions facilitated a GWAS that revealed associations between 10 selected regions and nine domestication traits and identified 13 new loci associated with agronomic traits, including SOC. When integrated with previous QTL information, the GWAS established that, of the 230 detected selective sweeps, 96 correlated with previously reported oil-related QTLs. Importantly, 21 of the mapping intervals for these QTLs contained FA biosynthesis genes.

### 2.3.5. Lipidomics for Oil Structure and Quality Identification

Lipidomics is now considered a systematic research pattern based on high-throughput liquid chromatography–tandem mass spectrometry (LC-MS/MS) analysis, which can be used to determine the composition and changes in the abundance of the lipidome in organisms [70]. Lipidomic analysis of developing rapeseed seeds showed that initial lipid deposition begins in the aleurone layer and endosperm. As the seed develops, lipid accumulation in the embryo increases significantly and the distribution of molecular species changes significantly from early (20 DAF) to intermediate (27 DAF) stages of lipid accumulation [71].

To investigate the effect of host carbon supply on nodulation and nitrogen fixation in the interaction between symbiotic rhizobia and legumes, researchers performed lipidomic and transcriptomic analyses on soybean roots and nodules at six different developmental stages. The lipidomic data revealed adaptive changes in lipid metabolism during nodule formation that affect rhizobial proliferation, growth, and differentiation and demonstrated that the biosynthesis and transport of FAs, monoacylglycerol (2-MAG), and membrane lipids may be a prerequisite for symbiotic success [72]. The advantage of lipidomic analysis lies in its ability to accurately quantify and identify lipids; despite certain advances in food component characterization and quality identification, lipidomics as a new emerging discipline started relatively late compared to other omics fields [73][74][75][76].

## References


1. Jorge, N.; Goncalves, L.A.G.; Dobarganes, M.C. Influence of fatty acid composition on the formation of polar glycerides and polar fatty acids in sunflower oils heated at frying temperatures. Grasas Aceites 1997, 48, 17–24.
2. De Carvalho, C.; Caramujo, M. The Various Roles of Fatty Acids. Molecules 2018, 23, 2583.
3. Slocombe, S.P.; Cornah, J.; Pinfield-Wells, H.; Soady, K.; Zhang, Q.Y.; Gilday, A.; Dyer, J.M.; Graham, I.A. Oil accumulation in leaves directed by modification of fatty acid breakdown and lipid synthesis pathways. Plant Biotechnol. J. 2009, 7, 694–703.
4. Lewandowska, M.; Keyl, A.; Feussner, I. Wax biosynthesis in response to danger: Its regulation upon abiotic and biotic stress. New Phytol. 2020, 227, 698–713.
5. Sud, M.; Fahy, E.; Cotter, D.; Brown, A.; Dennis, E.; Glass, C.; Merrill, A.H.; Murphy, R.; Raetz, C.; Russell, D.; et al. LMSD: LIPID MAPS structure database. Nucleic Acids Res. 2007, 35, D527–D532.
6. Fahy, E.; Subramaniam, S.; Brown, H.A.; Glass, C.K.; Merrill, A.H., Jr.; Murphy, R.C.; Raetz, C.R.; Russell, D.W.; Seyama, Y.; Shaw, W.; et al. A comprehensive classification system for lipids. J. Lipid Res. 2005, 46, 839–861.
7. Ohlrogge, J.; Thrower, N.; Mhaske, V.; Stymne, S.; Baxter, M.; Yang, W.; Liu, J.; Shaw, K.; Shorrosh, B.; Zhang, M.; et al. PlantFAdb: A resource for exploring hundreds of plant fatty acid structures synthesized by thousands of plants and their phylogenetic relationships. Plant J. 2018, 96, 1299–1308.
8. Harwood, J.L. Fatty Acid Metabolism. Annu. Rev. Plant Physiol. Plant Mol. Biol. 1988, 39, 101–138.
9. Lunn, D.; Wallis, J.G.; Browse, J. A multigene approach secures hydroxy fatty acid production in Arabidopsis. J. Exp. Bot. 2021, 73, 2875–2888.
10. Alban, C.; Baldet, P.; Douce, R. Localization and characterization of 2 structurally different forms of acetyl-coa carboxylase in young pea leaves, of which one is sensitive to aryloxyphenoxypropionate herbicides. Biochem. J. 1994, 300, 557–565.
11. Kozaki, A.K.; Mayumi, K.; Sasaki, Y. Thiol-disulfide exchange between nuclear-encoded and chloroplast-encoded subunits of pea acetyl-CoA carboxylase. J. Biol. Chem. 2001, 276, 39919–39925.
12. Bates, P.D. Understanding the control of acyl flux through the lipid metabolic network of plant oil biosynthesis. Biochim. Biophys. Acta (BBA) Mol. Cell Biol. Lipids 2016, 1861, 1214–1225.

13. Fahy, E.; Subramaniam, S.; Murphy, R.C.; Nishijima, M.; Raetz, C.R.; Shimizu, T.; Spener, F.; van Meer, G.; Wakelam, M.J.; Dennis, E.A. Update of the LIPID MAPS comprehensive classification system for lipids. J. Lipid Res. 2009, 50, S9–S14.
14. Lu, S.; Sturtevant, D.; Aziz, M.; Jin, C.; Li, Q.; Chapman, K.D.; Guo, L. Spatial analysis of lipid metabolites and expressed genes reveals tissue-specific heterogeneity of lipid metabolism in high- and low-oil Brassica napus L. seeds. Plant J. 2018, 94, 915–932.
15. Kennedy, E.P. Biosynthesis of complex lipids. Fed. Proc. 1961, 20, 934–940.
16. Ischebeck, T.; Krawczyk, H.E.; Mullen, R.T.; Dyer, J.M.; Chapman, K.D. Lipid droplets in plants and algae: Distribution, formation, turnover and function. Semin. Cell Dev. Biol. 2020, 108, 82–93.
17. Yin, D.; Wang, Y.; Zhang, X.; Li, H.; Lu, X.; Zhang, J.; Zhang, W.; Chen, S. De Novo Assembly of the Peanut (Arachis hypogaea L.) Seed Transcriptome Revealed Candidate Unigenes for Oil Accumulation Pathways. PLoS ONE 2013, 8, e73767.
18. Thiam, A.R.; Ikonen, E. Lipid Droplet Nucleation. Trends Cell Biol. 2021, 31, 108–118.
19. Taurino, M.; Costantini, S.; De Domenico, S.; Stefanelli, F.; Ruano, G.; Delgadillo, M.O.; Sanchez-Serrano, J.J.; Sanmartin, M.; Santino, A.; Rojo, E. SEIPIN Proteins Mediate Lipid Droplet Biogenesis to Promote Pollen Transmission and Reduce Seed Dormancy. Plant Physiol. 2018, 176, 1531–1546.
20. Kelly, A.; Shaw, E.; Powers, S.; Kurup, S.; Eastmond, P. Suppression of the SUGAR-DEPENDENT1 triacylglycerol lipase family during seed development enhances oil yield in oilseed rape (Brassica napus L.). Plant Biotechnol J. 2013, 11, 355–361.
21. Pyc, M.; Gidda, S.K.; Seay, D.; Esnay, N.; Kretzschmar, F.K.; Cai, Y.Q.; Doner, N.M.; Greer, M.S.; Hull, J.J.; Coulon, D.; et al. LDIP cooperates with SEIPIN and LDAP to facilitate lipid droplet biogenesis in Arabidopsis. Plant Cell 2021, 33, 3076–3103.
22. Chia, T.Y.P.; Pike, M.J.; Rawsthorne, S. Storage oil breakdown during embryo development of Brassica napus (L.). J. Exp. Bot. 2005, 56, 1285–1296.
23. Chiofalo, B.; Lo Presti, V. 404-Sampling Techniques for the Determination of Volatile Components in Food of Animal Origin. In Comprehensive Sampling Sample Preparation; Pawliszyn, J., Ed.; Academic Press: Oxford, UK, 2012; pp. 61–85.
24. Huang, A.H.C. Oleosins and oil bodies in seeds and other organs. Plant Physiol. 1996, 110, 1055–1061.
25. Goepfert, S.; Poirier, Y. Beta-oxidation in fatty acid degradation and beyond. Curr. Opin. Plant Biol. 2007, 10, 245–251.
26. Gupta, R.; Gupta, N. Lipid Biosynthesis and Degradation; Springer: Singapore, 2021; pp. 491–523.

27. Ma, J.; Sun, S.; Whelan, J.; Shou, H. CRISPR/Cas9-Mediated Knockout of GmFATB1 Significantly Reduced the Amount of Saturated Fatty Acids in Soybean Seeds. Int. J. Mol. Sci. 2021, 22, 3877.
28. Raboanatahiry, N.; Chao, H.; Guo, L.; Gan, J.; Xiang, J.; Yan, M.; Zhang, L.; Yu, L.; Li, M. Synteny analysis of genes and distribution of loci controlling oil content and fatty acid profile based on QTL alignment map in Brassica napus. BMC Genom. 2017, 18, 776.
29. Zou, J.; Katavic, V.; Giblin, E.M.; Barton, D.L.; Mackenzie, S.L.; Keller, W.A.; Hu, X.; Taylor, D.C. Modification of seed oil content and acyl composition in the brassicaceae by expression of a yeast sn-2 acyltransferase gene. Plant Cell 1997, 9, 909–923.
30. Chen, S.L.; Lei, Y.; Xu, X.; Huang, J.Q.; Jiang, H.F.; Wang, J.; Cheng, Z.S.; Zhang, J.A.; Song, Y.H.; Liao, B.S.; et al. The Peanut (Arachis hypogaea L.) Gene AhLPAT2 Increases the Lipid Content of Transgenic Arabidopsis Seeds. PLoS ONE 2015, 10, e0136170.
31. Jako, C.; Kumar, A.; Wei, Y.; Zou, J.; Barton, D.L.; Giblin, E.M.; Covello, P.S.; Taylor, D.C. Seed-Specific Over-Expression of an Arabidopsis cDNA Encoding a Diacylglycerol Acyltransferase Enhances Seed Oil Content and Seed Weight. Plant Physiol. 2001, 126, 861–874.
32. Wang, Z.K.; Huang, W.J.; Chang, J.M.; Sebastian, A.; Li, Y.G.; Li, H.Y.; Wu, X.X.; Zhang, B.B.; Meng, F.L.; Li, W.B. Overexpression of SiDGAT1, a gene encoding acyl-CoA:diacylglycerol acyltransferase from Sesamum indicum L. increases oil content in transgenic Arabidopsis and soybean. Plant Cell Tissue Organ Cult. 2014, 119, 399–410.
33. Akoh, C.C.; Lee, G.C.; Liaw, Y.C.; Huang, T.H.; Shaw, J.F. GDSL family of serine esterases/lipases. Prog. Lipid Res. 2004, 43, 534–552.
34. Chen, M.X.; Du, X.; Zhu, Y.; Wang, Z.; Hua, S.J.; Li, Z.L.; Guo, W.L.; Zhang, G.P.; Peng, J.R.; Jiang, L.X. Seed Fatty Acid Reducer acts downstream of gibberellin signalling pathway to lower seed fatty acid storage in Arabidopsis. Plant Cell Environ. 2012, 35, 2155–2169.
35. Brocard-Gifford, I.M.; Lynch, T.J.; Finkelstein, R.R. Regulatory networks in seeds integrating developmental, abscisic acid, sugar, and light signaling. Plant Physiol. 2003, 131, 78–92.
36. Zhai, Z.Y.; Keereetaweep, J.; Liu, H.; Feil, R.; Lunn, J.E.; Shanklin, J. Trehalose 6-Phosphate Positively Regulates Fatty Acid Synthesis by Stabilizing WRINKLED1. Plant Cell 2018, 30, 2616–2627.
37. Guo, Y.; Huang, Y.; Gao, J.; Pu, Y.; Wang, N.; Shen, W.; Wen, J.; Yi, B.; Ma, C.; Tu, J.; et al. CIPK9 is involved in seed oil regulation in Brassica napus L. and Arabidopsis thaliana (L.) Heynh. Biotechnol. Biofuels 2018, 11, 124.
38. Zafar, S.; Li, Y.-L.; Li, N.-N.; Zhu, K.-M.; Tan, X.-L. Recent advances in enhancement of oil content in oilseed crops. J. Biotechnol. 2019, 301, 35–44.

39. Fei, W.J.; Yang, S.Q.; Hu, J.; Yang, F.; Qu, G.Y.; Peng, D.; Zhou, B. Research advances of WRINKLED1 (WRI1) in plants. Funct. Plant Biol. 2020, 47, 185–194.
40. Benning, N.F.a.C. wrinkled1: A Novel, Low-Seed-Oil Mutant of Arabidopsis with a Deficiency in the Seed-Specific Regulation of Carbohydrate Metabolism. Plant Physiol. 1998, 118, 91–101.
41. Ji, X.-J.; Mao, X.; Hao, Q.-T.; Liu, B.-L.; Xue, J.-A.; Li, R.-Z. Splice Variants of the Castor WRI1 Gene Upregulate Fatty Acid and Oil Biosynthesis When Expressed in Tobacco Leaves. Int. J. Mol. Sci. 2018, 19, 146.
42. Mu, J.Y.; Tan, H.L.; Zheng, Q.; Fu, F.Y.; Liang, Y.; Zhang, J.; Yang, X.H.; Wang, T.; Chong, K.; Wang, X.J.; et al. LEAFY COTYLEDON1 is a key regulator of fatty acid biosynthesis in Arabidopsis. Plant Physiol. 2008, 148, 1042–1054.
43. Tan, H.; Yang, X.; Zhang, F.; Zheng, X.; Qu, C.; Mu, J.; Fu, F.; Li, J.; Guan, R.; Zhang, H.; et al. Enhanced seed oil production in canola by conditional expression of Brassica napus LEAFY COTYLEDON1 and LEC1-LIKE in developing seeds. Plant Physiol. 2011, 156, 1577–1588.
44. Elahi, N.; Duncan, R.W.; Stasolla, C. Decreased seed oil production in FUSCA3 Brassica napus mutant plants. Plant Physiol. Biochem. 2015, 96, 222–230.
45. Manan, S.; Zhao, J. Role of Glycine max ABSCISIC ACID INSENSITIVE 3 (GmABI3) in lipid biosynthesis and stress tolerance in soybean. Funct. Plant Biol. 2021, 48, 171.
46. Pouvreau, B.; Blundell, C.; Vohra, H.; Zwart, A.B.; Arndell, T.; Singh, S.; Vanhercke, T. A Versatile High Throughput Screening Platform for Plant Metabolic Engineering Highlights the Major Role of ABI3 in Lipid Metabolism Regulation. Front. Plant Sci. 2020, 11, 288.
47. Chen, Y.H.; Yang, X.Y.; He, K.; Liu, M.H.; Li, J.G.; Gao, Z.F.; Lin, Z.Q.; Zhang, Y.F.; Wang, X.X.; Qiu, X.M.; et al. The MYB transcription factor superfamily of arabidopsis: Expression analysis and phylogenetic comparison with the rice MYB family. Plant Mol. Biol. 2006, 60, 107–124.
48. To, A.; Joubes, J.; Thueux, J.; Kazaz, S.; Lepiniec, L.; Baud, S. AtMYB92 enhances fatty acid synthesis and suberin deposition in leaves of Nicotiana benthamiana. Plant J. 2020, 103, 660–676.
49. Liu, J.; Hua, W.; Yang, H.L.; Zhan, G.M.; Li, R.J.; Deng, L.B.; Wang, X.F.; Liu, G.H.; Wang, H.Z. The BnGRF2 gene (GRF2-like gene from Brassica napus) enhances seed oil production through regulating cell number and plant photosynthesis. J. Exp. Bot. 2012, 63, 3727–3740.
50. Libault, M.; Farmer, A.; Joshi, T.; Takahashi, K.; Langley, R.J.; Franklin, L.D.; He, J.; Xu, D.; May, G.; Stacey, G. An integrated transcriptome atlas of the crop model Glycine max, and its use in comparative analyses in plants. Plant J. 2010, 63, 86–99.
51. Severin, A.J.; Woody, J.L.; Bolon, Y.-T.; Joseph, B.; Diers, B.W.; Farmer, A.D.; Muehlbauer, G.J.; Nelson, R.T.; Grant, D.; Specht, J.E.; et al. RNA-Seq Atlas of Glycine max: A guide to the soybean

transcriptome. BMC Plant Biol. 2010, 10, 160.

52. Huang, X.; Han, B. Natural Variations and Genome-Wide Association Studies in Crop Plants. Annu. Rev. Plant Biol. 2014, 65, 531–551.
53. Ardui, S.; Ameur, A.; Vermeesch, J.R.; Hestand, M.S. Single molecule real-time (SMRT) sequencing comes of age: Applications and utilities for medical diagnostics. Nucleic Acids Res. 2018, 46, 2159–2168.
54. Lieberman-Aiden, E.; Van Berkum, N.L.; Williams, L.; Imakaev, M.; Ragoczy, T.; Telling, A.; Amit, I.; Lajoie, B.R.; Sabo, P.J.; Dorschner, M.O.; et al. Comprehensive Mapping of Long-Range Interactions Reveals Folding Principles of the Human Genome. Science 2009, 326, 289–293.
55. Chalhoub, B.; Denoeud, F.; Liu, S.; Parkin, I.A.P.; Tang, H.; Wang, X.; Chiquet, J.; Belcram, H.; Tong, C.; Samans, B.; et al. Early allopolyploid evolution in the post-Neolithic Brassica napus oilseed genome. Science 2014, 345, 950–953.
56. Zhuang, W.; Chen, H.; Yang, M.; Wang, J.; Pandey, M.K.; Zhang, C.; Chang, W.-C.; Zhang, L.; Zhang, X.; Tang, R.; et al. The genome of cultivated peanut provides insight into legume karyotypes, polyploid evolution and crop domestication. Nat. Genet. 2019, 51, 865–876.
57. Li, Y.-H.; Zhou, G.; Ma, J.; Jiang, W.; Jin, L.-G.; Zhang, Z.; Guo, Y.; Zhang, J.; Sui, Y.; Zheng, L.; et al. De novo assembly of soybean wild relatives for pan-genome analysis of diversity and agronomic traits. Nat. Biotechnol. 2014, 32, 1045–1052.
58. Liu, Y.C.; Du, H.L.; Li, P.C.; Shen, Y.T.; Peng, H.; Liu, S.L.; Zhou, G.A.; Zhang, H.K.; Liu, Z.; Shi, M.; et al. Pan-Genome of Wild and Cultivated Soybeans. Cell 2020, 182, 162–176.
59. Zhang, L.; Wang, S.-B.; Li, Q.-G.; Song, J.; Hao, Y.-Q.; Zhou, L.; Zheng, H.-Q.; Dunwell, J.M.; Zhang, Y.-M. An Integrated Bioinformatics Analysis Reveals Divergent Evolutionary Pattern of Oil Biosynthesis in High- and Low-Oil Plants. PLoS ONE 2016, 11, e0154882.
60. Wang, J.; Singh, S.K.; Du, C.; Li, C.; Fan, J.; Pattanaik, S.; Yuan, L. Comparative Transcriptomic Analysis of Two Brassica napus Near-Isogenic Lines Reveals a Network of Genes That Influences Seed Oil Accumulation. Front. Plant Sci. 2016, 7, 1498.
61. O'Rourke, J.A.; Bolon, Y.T.; Bucciarelli, B.; Vance, C.P. Legume genomics: Understanding biology through DNA and RNA sequencing. Ann. Bot. 2014, 113, 1107–1120.
62. Yang, S.; Miao, L.; He, J.; Zhang, K.; Li, Y.; Gai, J. Dynamic Transcriptome Changes Related to Oil Accumulation in Developing Soybean Seeds. Int. J. Mol. Sci. 2019, 20, 2202.
63. Huang, R.; Zhou, Y.; Zhang, J.; Ji, F.; Jin, F.; Fan, W.; Pei, D. Transcriptome Analysis of Walnut (Juglans regia L.) Embryos Reveals Key Developmental Stages and Genes Involved in Lipid Biosynthesis and Polyunsaturated Fatty Acid Metabolism. J. Agric. Food Chem. 2021, 69, 377–396.

64. Liu, J.; Dong, L.; Duan, R.; Hu, L.; Zhao, Y.; Zhang, L.; Wang, X. Transcriptomic Analysis Reveals the Regulatory Networks and Hub Genes Controlling the Unsaturated Fatty Acid Contents of Developing Seed in Soybean. Front. Plant Sci. 2022, 13, 876371.
65. Niu, Y.; Wu, L.; Li, Y.; Huang, H.; Qian, M.; Sun, W.; Zhu, H.; Xu, Y.; Fan, Y.; Mahmood, U.; et al. Deciphering the transcriptional regulatory networks that control size, color, and oil content in Brassica rapa seeds. Biotechnol. Biofuels 2020, 13, 90.
66. Zhang, Z.; Dunwell, J.M.; Zhang, Y.M. An integrated omics analysis reveals molecular mechanisms that are associated with differences in seed oil content between Glycine max and Brassica napus. BMC Plant Biol. 2018, 18, 328.
67. Yao, M.; Guan, M.; Zhang, Z.; Zhang, Q.; Cui, Y.; Chen, H.; Liu, W.; Jan, H.U.; Voss-Fels, K.P.; Werner, C.R.; et al. GWAS and co-expression network combination uncovers multigenes with close linkage effects on the oleic acid content accumulation in Brassica napus. BMC Genom. 2020, 21, 320.
68. Guerin, C.; Joët, T.; Serret, J.; Lashermes, P.; Vaissayre, V.; Agbessi, M.D.T.; Beulé, T.; Severac, D.; Amblard, P.; Tregear, J.; et al. Gene coexpression network analysis of oil biosynthesis in an interspecific backcross of oil palm. Plant J. 2016, 87, 423–441.
69. Flint-Garcia, S.A.; Thuillet, A.-C.; Yu, J.; Pressoir, G.; Romero, S.M.; Mitchell, S.E.; Doebley, J.; Kresovich, S.; Goodman, M.M.; Buckler, E.S. Maize association population: A high-resolution platform for quantitative trait locus dissection. Plant J. 2005, 44, 1054–1064.
70. Wenk, M.R. The emerging field of lipidomics. Nat. Rev. Drug Discov. 2005, 4, 725.
71. Borisjuk, L.; Neuberger, T.; Schwender, J.; Heinzel, N.; Sunderhaus, S.; Fuchs, J.; Hay, J.O.; Tschiersch, H.; Braun, H.P.; Denolf, P.; et al. Seed architecture shapes embryo metabolism in oilseed rape. Plant Cell 2013, 25, 1625–1640.
72. Zhang, G.; Ahmad, M.Z.; Chen, B.; Manan, S.; Zhang, Y.; Jin, H.; Wang, X.; Zhao, J. Lipidomic and transcriptomic profiling of developing nodules reveals the essential roles of active glycolysis and fatty acid and membrane lipid biosynthesis in soybean nodulation. Plant J. 2020, 103, 1351–1371.
73. Zhang, D.; Guo, X.; Wang, Q.; Zhao, L.Y.; Sun, Q.C.; Duan, X.L.; Cao, Y.P.; Sun, H. Investigation on lipid profile of peanut oil and changes during roasting by lipidomic approach. Lwt-Food Sci. Technol. 2022, 154, 112594.
74. Shi, T.; Wu, G.; Jin, Q.; Wang, X. Detection of camellia oil adulteration using chemometrics based on fatty acids GC fingerprints and phytosterols GC-MS fingerprints. Food Chem. 2021, 352, 129422.
75. Huang, Y.; Ma, R.; Xu, Y.; Zhong, K.; Bu, Q.; Gao, H. A Comparison of Lipid Contents in Different Types of Peanut Cultivars Using UPLC-Q-TOF-MS-Based Lipidomic Study. Foods 2021, 11, 4.

76. Demiral, I.; Dogan, M.; Bastu, E.; Buyru, F. Genomic, proteomic and lipidomic evaluation of endometrial receptivity. Turk. J. Obstet. Gynecol. 2015, 12, 237–243.