Biofuel
Research Journal

Review Paper

Boosting plant oil yields: the role of genetic engineering in industrial applications

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HIGHLIGHTS

➢ Plant oil-based products have emerged as eco-friendly alternatives to petroleum counterparts.
➢ Plant oils are versatile, with applications in cooking, lubrication, cosmetics, polymers, and medicine.
➢ Non-edible plant oils present new opportunities for biodiesel and bioproduct production.
➢ Genetic engineering can enhance both the yield and quality of plant oils for bio-based industries.

GRAPHICAL ABSTRACT
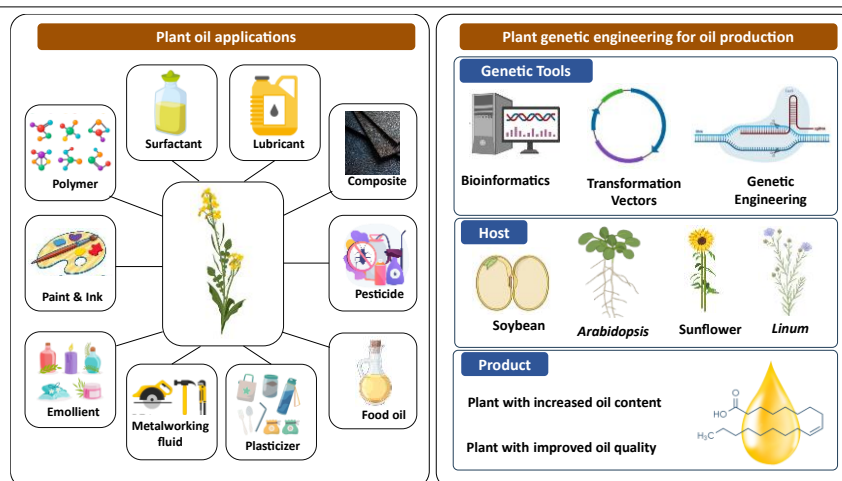
ARTICLE INFO

ABSTRACT

As climate change intensifies and the need to reduce human-caused emissions becomes more urgent, transitioning to a bio-based economy is essential. This paper explores the diverse industrial applications of plant oils as sustainable alternatives to petroleum-based products, including their use in food, polymers, lubricants, surfactants, pesticides, emollients, and biofuels. This review delves into biosynthetic pathways, detailing the key enzymes and processes involved in the synthesis of triacylglycerol. It thoroughly discusses how genetic and metabolic engineering can not only increase oil yields but also modify fatty acid compositions to better meet industrial requirements. By understanding genetics and utilizing advanced biotechnologies, the oil content and quality of plant sources can be significantly enhanced, aligning with both sustainability goals and industrial demands. This paper provides a comprehensive overview of the current uses and genetic engineering of plant oil production, proposing innovative strategies such as utilizing oils from biomass or cultivating non-edible oil crops. These approaches aim to establish a sustainable industrial system, reduce reliance on fossil fuels, and promote the growth of an environmentally responsible bio-based economy. Additionally, the review highlights future directions, examining the economic implications and environmental benefits of adopting plant oils across various sectors and positioning them as pivotal to achieving an eco-friendly, bio-based economy.

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Abbreviations

ABA	Abscisic acid	G3PDH	Glycerol-3-phosphate dehydrogenase
ACCase	Acetyl-CoA carboxylase	GAPDH	Glyceraldehyde 3-phosphate dehydrogenase
AP2	Apetala2	GPAT	Glycerol-3-phosphate acyltransferase
ARF2	Auxin Response Factor 2	LPAAT	Lysophosphatidic acid acyltransferase
CAGR	Compound annual growth rate	MWFs	Metalworking fluids
CPT	Choline phosphotransferase	PC	Phosphatidylcholine
CRISPR	Clustered regularly interspaced short palindromic repeats	PDAT	Phospholipid: diacylglycerol acyltransferase
DGAT	Diacylglycerol acyltransferase	PVC	Polyvinyl chloride
ER	Endoplasmic reticulum	PXA1	Peroxisomal ABC transporter 1
ESBO	Epoxidized soybean oil	SDP1	SUGAR-DEPENDENT1
FA	Fatty Acids	TAG	Triacylglycerol
FAD2	Fatty acid desaturase 2	TFs	Multiple transcription factors
FAR	Fatty Acid Reductases	TP	Triose-phosphates
G3P	Glycerol-3-phosphate	TTG2	Transparent Testa Glabra 2

1. Introduction

Climate change and its adverse impacts on various aspects of human health were recently projected in the latest global report released by the Lancet Countdown: Tracking Progress on Health and Climate Change (Watts et al., 2021). Among the reported findings was an increased rate of exposure to heatwaves globally between 2000 and 2016, affecting an additional 125 million medically vulnerable adults. The widespread use of petroleum-derived products has been linked to rising atmospheric CO_2 levels, which are associated with the frequency of heatwaves (Verma et al., 2019; Rej et al., 2022). These findings highlight the need to decrease anthropogenic greenhouse gas (GHG) emissions through strategies such as transitioning towards a bio-based economy (Bergfreund et al., 2021; Hajinajaf et al., 2022c; Hajinajaf et al., 2024). Replacing petroleum-derived products with eco-friendly alternatives is a key feature of this transition (De Vrieze et al., 2020).

There are growing concerns about the future availability of petroleum-derived products (Siracusa and Blanco, 2020). Utilizing renewable raw materials for daily life products seems crucial for sustainable development (Bergfreund et al., 2021; Hajinajaf et al., 2022b). **Figure 1a** shows the share of different sources in the global primary energy supply. Using renewable materials can reduce CO_2 emissions and offer additional advantages
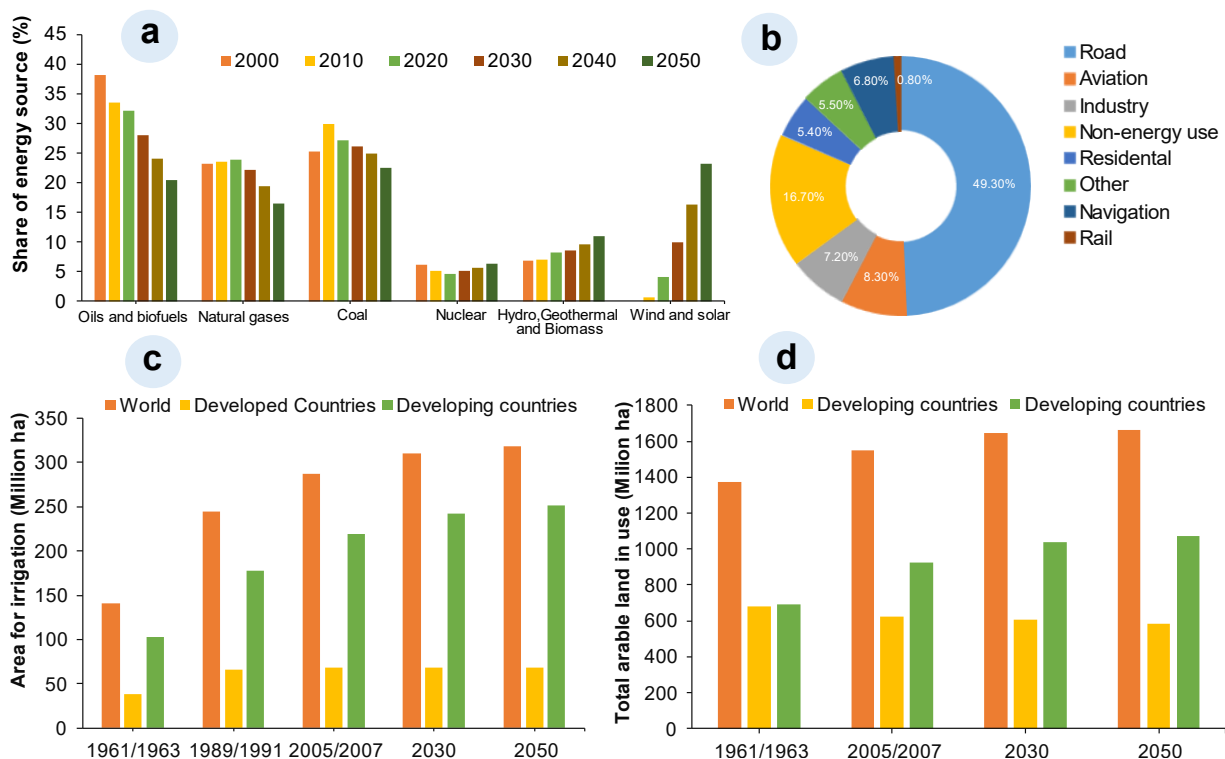
Fig. 1. a) Share (%) of different sources in global primary energy supply (Kan et al., 2019); **b)** Shares of world oil consumption in various sectors and industries in the year 2018 (IEA., 2018). The "Other" category encompasses agriculture, commercial and public services, non-specified other, pipeline, and non-specified transport; **c)** Area equipped for irrigation (OECD, 2012); **d)** Total arable land in use (FAO, 2011).

associated with green chemistry, such as biodegradability and lower toxicity (Fallahi et al., 2021; Hajinajaf et al., 2021).

One of the most important needs of various industries, including the food industry, is industrial oils, ranging from lubricating to hydraulic and cutting oils. Currently, a significant portion of industrial oil resources used even in the food industry are derived from petroleum, leading to substantial oleochemical pollution (Metzger and Hüttermann, 2009; Hayes, 2021; Fayyazbakhsh et al., 2022). **Figure 1b** shows the distribution of global oil consumption across different sectors and industries in 2018 (IEA., 2018).

Plant oils are considered ideal environmentally friendly, renewable, and sustainable feedstocks that could potentially replace petroleum-derived oil in the mentioned industries (El-Dalatony et al., 2022; Yaashikaa et al., 2022). With a market cap comparable to that of fossil-based fuels (Hoang et al., 2021), industrial oil is a key sector for transitioning from petroleum-based to plant-based oils. However, since over 85% of the plant oils produced globally are used for human nutrition, it is unrealistic to fully replace fossil oils with plant oils in industry and transportation (Hajjari et al., 2017). It has been highlighted that replacing just 40% of the fossil oils in these industries would require global plant oil production to triple by 2030 (Carlsson et al., 2011). The increasing scarcity of renewable water resources (as highlighted in **Figure 1c** and detailed in **Table 1**), along with the diminishing availability of arable land (as shown in **Fig. 1d**), adds significant complexity to this endeavor. This challenge is particularly pronounced when we depend on existing oil crops with stabilized yields and oil content. **Table 2** shows the yield and oil content of various plant oil feedstocks.

In addition to yield and oil content, challenges associated with existing plant oils extend to unfavorable fatty acid profiles in certain feedstocks, leading to bio-oil properties unsuitable for specific industrial applications. Moreover, the presence of toxic or allergenic compounds further complicates the utilization of these oils (Baskar et al., 2019; Nomanbhay et al., 2018). Therefore, it is critical to develop innovative and promising industrial plant oil platforms to tackle these challenges. However, it is equally crucial to ensure that these platforms do not intensify competition with food crops, thereby safeguarding global food security. This importance is highlighted by global plant oil production statistics, which forecast an increase from 149 million tonnes in 2005 to 282 million tonnes in 2050, aimed at meeting the demands of a growing world population (Alexandratos and Bruinsma, 2012). **Table 3** provides an overview of global plant oil production, current demands, and projected demands beyond 2050.

Besides increasing plant oil production yield per hectare, one of the main approaches to meeting industrial demand for plant oils is developing new oil crops that can utilize marginal or non-agricultural lands and waters. In alignment with these goals, this review aims to comprehensively explore the diverse applications of plant oils across various industries while addressing the associated challenges. It also delves into plant metabolic pathways for oil production and the use of genetic engineering to enhance oil quantity and quality. Additionally, the review critically examines innovative alternative strategies, such as biomass-derived oils. **Table 4** summarizes the various aspects of plant oils, their applications, and related research covered in this review, comparing them to discussions in review articles published from 2017 to 2023.

2. Industrial applications of plant oil and the challenges faced

Major oil crops on which global oil production depends include palm, soybean, rapeseed (also known as canola), corn, sunflower, cottonseed, olive, and peanut. Minor oil feedstocks include safflower, coconut, sesame, and linseed (**Table 2**) (Alexandratos and Bruinsma, 2012; Wan et al., 2017b). While the majority of global oil production over the last decade has been directed toward food/feed applications, approximately one-fifth has been used for industrial and bioenergy applications, and this proportion is expected to increase (Scarlat et al., 2015). In other words, the ratio between food, feed, and industrial/bioenergy applications of global oil production generally stands at 80:6:14 (Quispe et al., 2013). However, with growing biodiesel production, this ratio has shifted to 74:6:20 (Biermann et al., 2011). These proportions are still anticipated to change further in favor of non-food applications, including bioenergy and industrial plant-based oil production (Rathour et al., 2023). Therefore, the main challenge is increasing the quantity of global plant oil production to meet these growing

Table 1.
Annual renewable water resources and irrigation water withdrawal.

	Precipitation (mm/annum)	Renewable Water Resources (km^3)	Water Use Efficiency Ratio (%)		Irrigation Water Withdrawal (km^3)		Pressure on Water Resources due to Irrigation (%) *	
			2005/2007	2050	2005/2007	2050	2005/2007	2050
World	800	4200	44	46	2620	2906	6	7
Developed Countries	540	14000	42	43	505	493	4	4
Developing Countries	990	28000	44	47	2115	2413	8	9

*Water withdrawal for irrigation as a percentage of total annual renewable water resources.
Sources: Bruinsma (2009); Nachtergaele et al. (2023); http://www.fao.org/nr/solaw/thematic-reports/en/.

Table 2.
Different plant oil feedstocks, their production parameters, and commercial applications. Source: Wan et al. (2017b).

Oil Crop	Oil Content (wt%)	kg oil/ha	L oil/ha	Global Cultivation Area (million ha) in 2016	Global Seed Production (million tonnes) in 2016	Global Oil Production (million tonnes) in 2016	Commercial Uses (non-food uses in Bold)
Soybean (*Glycine max*)	15-20	375	446	120.41	345.97	54.47	Food, biodiesel, inks, plasticizers, crayons, paints, and soy candles
Rapeseed (*Brassica napus* L.)	38-46	1000	1190	34.05	68.52	27.31	Food, biodiesel
Sunflower (*Helianthus annuus*)	25-35	800	952	23.36	45.36	17.11	Food, coatings
Olive (*Olea europaea*)	10-30	1019	1212	9.7	2.700	2.854 2.713	Food, lubricants, inks
Peanut (*Arachis hypogaea*)	45-55	890	1059	24.77	42.28	5.78	Medicine, biodiesel, cosmetics, massage oils and soaps, confectionery and bakery industries
Cotton seed (*Gossypium hirsutum*)	18-25	273	325	29.58	38.88	5.09	Food and feed, margarine, salad dressings, medicine
Palm (*Arecaceae*)	30-60	5000	5950	-	Palm kernel 17.09	7.58 kernel 63.86 palm	Food, margarine, shortening, cooking oil, confectionary, soaps, sauces, fat substitutes, biodiesel
Safflower (*Carthamus tinctorius* L.)	20-45	655	779	<1	0.8	-	Food, margarine, painting, skin moisturizer, and creams for softening and smoothing the skin
Corn (*Zea mays*)	3.3-15.9	145	172	35	1608.62	0.523	Food, biodiesel, carrier for drug molecules in pharmaceutical preparations, soap, salve, inks and paint, and textile industries
Sesame (*Sesamum indicum*)	52-63	585	696	8	4.4	1.926	Food, wholesome tonic, medicine, hair treatment, body massage, worship
Coconut (*Cocos nucifera*)	63-65	2260	2689	-	61.44	3.44	Food, medicine, healtcare, fuel
Mustard (*Brassica alba*)	25-30	481	572	-	8.6	-	Food, medicine, soap production, beverages, pharmaceuticals
Rice bran (*Oryza sativa* L.)	12.1-25 16-32	696	828	-	63	1.8	Food, margarine, medicinal
Tung fruit (*Aleurites fordii*)	14-22	790	940	-	-	-	Enamels, varnishes, resins, coatings
Avocado (*Persea americana*)	11.23-18.8	2217	2638	-	8.9	-	-
Jatropha (*Jatropha curcas* L.)	35-40	1590	1892	-	-	0.015	-
Karanja (*Pongamia pinnata*)	27-39	-	-	-	-	0.055	-
Castor (*Ricinus communis*)	53 37-60	1188	1413	-	1.8	0.73	Plasticizers, lubricants, medicine, adhesives, cosmetics, hair oils, food containers, fuel additives, insulation, nylon, synthetic resins, fibers, paints, varnishes, plastics, inks, textiles, drying oils, fungus-growth-inhibiting compounds, embalming fluid, soaps, dyeing aids, cleaning products, detergents, personal care products, styling gel, and adhesive remover
Camelina (*Camelina sativa*)	30-40	490	583	-	-	-	-
Jojoba (*Simmondsia chinensis*)	44-59	1528	1818	-	-	-	-
Linseed (*Linum usitatissimum*)	38 -44	402	478	-	3.9	0.8	Medicine, feeds, sealants, caulking compounds, linoleum, earthen floors, adobe, textiles, fixative, rust inhibitor, lubricant, leather treatment, polishes, varnishes, oil paints, composition ornament for molded decoration, animal care products, wood preservation, industrial lubricant

Table 2.
continued.

Oil Crop	Oil Content (wt%)	kg oil/ha	L oil/ha	Global Cultivation Area (million ha) in 2016	Global Seed Production (million tonnes) in 2016	Global Oil Production (million tonnes) in 2016	Commercial Uses (non-food uses in Bold)
Coca (Cacao)	40-45	863	1026	-	5.8	-	-
Hazelnut	50-55	405	482	-	-	-	Food, chocolates, bakery, confectionery, mixed nuts, medicine

Table 3.
Global plant oil production; current demands and envisioned demands beyond 2050 (Alexandratos and Bruinsma, 2012).

Key Variables	2005/2007	2050	2080	2100
Population (million) UN 2010 Revision	6584	9306	9969	10125
Oil crops (oil equivalent), food (kg/capita)	12.1	16.2	16.9	-
Oil crops (oil equivalent), all uses (kg/capita)	21.9	30.5	33.8	-
Arable land area	1592	1661	1630	-
Oil crop production (million tonnes)	149	282	367	-
Oil crops (for biofuel) (million tonne)	7	29	-	-
Oil crops (for biofuel) (% total uses)	4.8	10.3	-	-

industrial and bioenergy demands (Haregu et al., 2023). The various industrial uses of plant oils and their derivatives, such as oleochemicals, fatty acids (FA), fatty alcohols, and glycerin across different industries, are presented in **Figure 2**. Moreover, industrial applications and the market size of plant oil are discussed in the subsequent sections (**Fig. 3**).

2.1. Polymers

Over the last few decades, commercially available polymers have been derived from non-renewable fossil resources. The global annual consumption of polymers is approximately 300 million tonnes, with an annual growth rate of 5% (Halden, 2010). This significant quantity, along with the resultant waste streams often disposed of into various ecosystems

Table 4.
Comparative analysis of plant oil applications and research topics in recently published review articles.

Reference	Applications			Genetic Engineering			Global Market	Oil-seed Production	Policy and Practical Implications
	Industrial Applications	Energy	Biosynthetic Pathway	Oil Content	Oil Composition	Oil in Biomass			
Afonso et al. (2023)	√	×	×	×	×	×	×	×	×
Xu et al. (2018)	×	√	√	×	×	√	√	×	×
Sagun et al. (2023)	×	×	√	√	√	√	×	√	×
Zhou et al. (2023)	×	×	√	√	√	×	×	×	×
Wan et al. (2017b)	×	√	√	√	√	√	×	√	×
Rauf et al. (2023)	×	×	√	√	√	√	×	√	×
Qi et al. (2020)	√	×	√	√	√	√	×	×	×
Salehi Jouzani et al. (2018)	×	√	√	√	√	×	×	×	×
Msanne et al. (2020)	×	×	√	√	√	×	×	√	×
Present Review	√	√	√	√	√	√	√	√	√

without treatment in many parts of the world, has led to growing environmental and health concerns, particularly regarding the use of petrochemical-based polymers. Conversely, this situation has sparked a surge in interest in biobased polymers (Desroches et al., 2012). These polymers are not only renewable but also biodegradable and eco-friendly (Adekunle and Okolie, 2015; Hajinajaf et al., 2022a). Biobased polymers can be synthesized from polysaccharides, fibers, polylactic acid, and other materials, with triacylglycerol (TAG) oils and FA also serving as reliable starting materials during the production process (Acquavia et al., 2021; Zubair et al., 2021). In 2019, the total production volume of biobased polymers reached 3.8 million tonnes (https://www.bioplasticsmagazine.com/en/).

Plant oil-based polymers can undergo fabrication using various copolymerization techniques, such as cationic, free radical, and thermal methods, which involve combining plant oils with a variety of petroleum-based co-monomers (Gogoi et al., 2022; Zhu et al., 2023). However, it is important to note that most plant oils require modifications at their naturally occurring reactive sites, such as ester groups and carbon-carbon double

bonds, before they can be utilized in biopolymer production (Ike et al., 2021; Ruiz-Rico and Barat, 2021). Therefore, these reactive sites, including the carbon-carbon double bonds found in fatty acid chains, play a crucial role during polymerization (Biermann et al., 2021; Rajput et al., 2023). In simpler terms, these double bonds act as excellent starting points for biopolymer production.

For instance, converting double bonds in FA into hydroxyl groups, followed by their reaction with isocyanate, could result in the formation of polyurethanes (Dyer et al., 2008). Additionally, other polymerization techniques, such as acyclic metathesis polymerization (Piccini et al., 2021; Quirino et al., 2021) and ring-opening metathesis polymerization (ROMP) (Ganewatta et al., 2021; Yarolimek et al., 2021), have been employed to synthesize plant oil-based polymers (Garrison et al., 2016). Neves et al. (2018) also demonstrated that modified vegetable oils containing acrylic double bonds exhibit high reactivity and form thermosetting biopolymers through free radical polymerization. **Table 5** provides examples of commercially available plant oil-based polymers and their real-world applications.
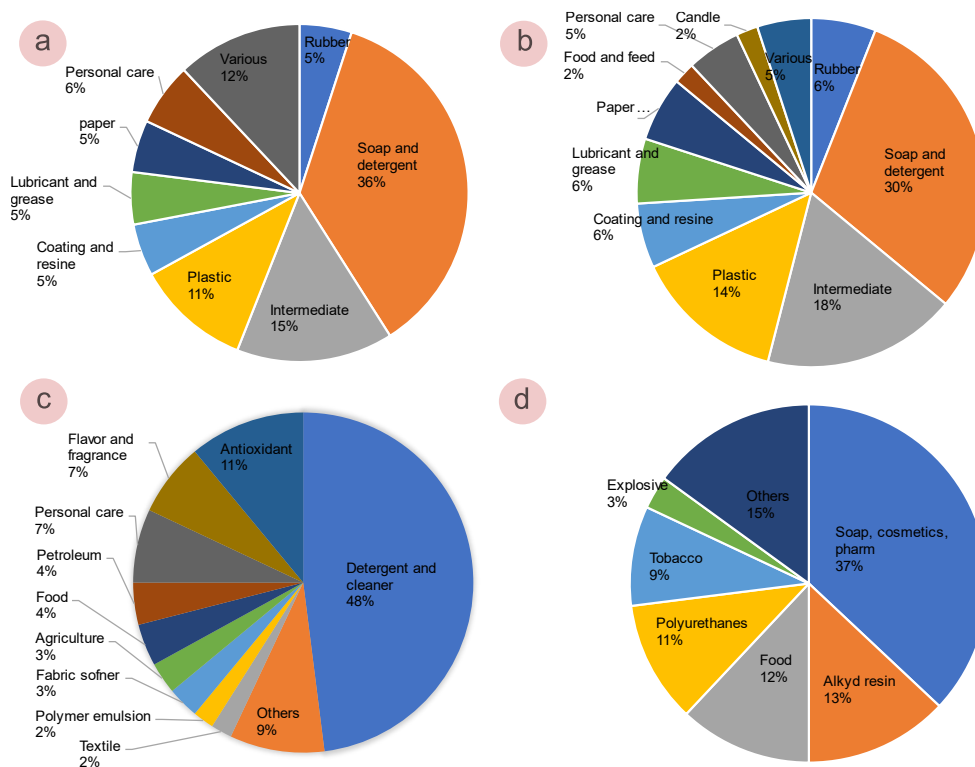
Fig. 2. Global market break-up of **(a)** oleochemical, **(b)** fatty acids, **(c)** fatty alcohols, and **(d)** glycerin by different industries.
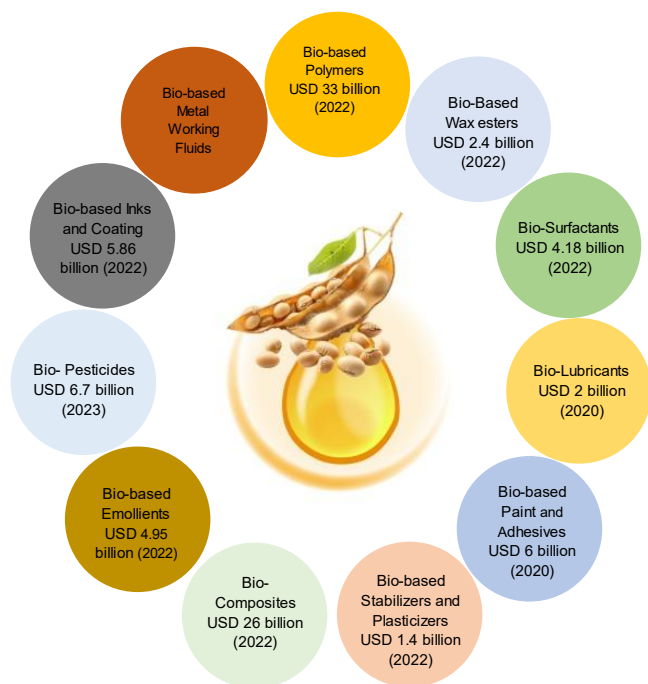

Fig. 3. Industrial applications of plant oils and their market size (Zhou et al., 2020; https://www.marketsandmarkets.com; and https://www.statista.com).

2.2. Surfactants

Surfactants are amphipathic compounds that influence the surface or interfacial energy of materials (Bergfreund et al., 2021). They constitute a widely used class of chemicals predominantly sourced from petroleum (Nagtode et al., 2023). Typically, surfactants comprise a hydrophilic group linked to a hydrophobic moiety (Polarz et al., 2018; Lamch et al., 2020). The hydrophilic groups vary depending on whether the surfactants are anionic or cationic. Anionic surfactants encompass carboxylate, sulfate, sulfonate, or phosphate groups, while cationic surfactants comprise amine or ammonium groups (Rocky et al., 2023). Surfactants find application in both edible and non-edible products, ranging from soaps and detergents to food emulsifiers and cosmetics (Bergfreund et al., 2021; De Luca et al., 2021; Mohammed and Ikiensikimama, 2023). As illustrated in **Table 6**, surfactants derived from petrochemicals have raised significant health and environmental concerns due to their toxicological properties. Consequently, safer alternatives, known as biosurfactants, have garnered considerable attention, particularly in the food and cosmetics industries.

Indeed, eco-friendly alternatives, like biosurfactants, offer comparable physicochemical properties (such as emulsification, de-emulsification, foaming, and wetting) to their petroleum-derived counterparts (Ahmadi-Ashtiani et al., 2020; Sarubbo et al., 2022). They also possess several advantages, including lower toxicity, biodegradability, and increased resistance across a broader range of pH, salinity, and temperature conditions (Abbot et al., 2022; Sarubbo et al., 2022). Oilseed crops are considered promising feedstocks for biosurfactant production. Specifically, the FA present in plant oils or their corresponding methyl esters can be reduced to produce fatty alcohols, which are then utilized in biosurfactant formulations (Van Renterghem et al., 2018).

Despite their favorable environmental attributes, biosurfactants still present less favorable economic characteristics compared to surfactants derived from petroleum (Gaur et al., 2022; Joshi et al., 2022). This issue is

Table 5.
Examples of commercially available plant oil-based polymers (Desroches et al., 2012; McKeon et al., 2016; Zhang et al., 2017).

Plant oil Sources	Products	Trade name	Company	Applications
Soybean oil	Polymerized Soybean Oil (polySOY)	-	-	-
	Acrylated Epoxidized Soybean Oil (AESO)	Ebecryl 860	UCB Chemicals Company, Advent International (Boston, MA, USA)	Surface coatings
	Maleic acid reacted AESO (MAESO) also "maleated acrylated epoxidized soy oil (MAESO)"	-	-	Sheet molding compound
	Soybean oil monoglyceride (SOMG), also "maleinated soybean oil monoglyceride"	-	-	-
	Thermosets prepared by the cationic copolymerization of soybean Oil	-	-	-
	Polymerized epoxidized soybean oil (ESO)	PlastiSoy™	CHS (USA), Makwell (India), The Chemical Company (USA), MultiPlus (Thailand), PolyMar Enterprises (USA), FMC (USA)	Rubbers, Resins, Coatings, Paints, Plasticizers, Adhesives, Polyols (polyurethanes), Thermosets
	Epoxidized Soybean Oil	Vikoflex®	Arkema (USA)	-
	Norbornenyl-functionalized fatty alcohols derived from soybean oil (NMSA)	-	-	-
	Polyurethanes	BiOH®	Cargill (USA)	-
		Agrol®	BioBased Technologies (USA)	Lubricants, Building Products, Printing Inks, Diesel Additives, Coatings, Furniture, Adhesives, Automotive, Agricultural Products
		Renuva®	Dow Chemical (USA)	Adhesive, Conventional Flexible Polyurethane Foam (FPF), Viscoelastic Foam, High Resilience Foam (HR), Molded Foam
		Sovermol® polyols	BASF (Cogins) Oleochemicals (Malesia)	Adhesives, Binders, Floor coatings, Castings, Electroplating
Linseed oil	Linseed Oil Monoglyceride (LOMG)	-	-	-
	Polymerized Linseed Oil (Linoleum)	Linoville, Marmoleum®, Forbo's Topshield™, NATURCote™,	Forbo (Switzerland), Armstrong (USA), Torlys (Newzeland)	Floor covering
	Polyurethane (Boiled Linseed Oil (BLO))	Crown® Boiled Linseed Oil	W. M. Barr, USA; Crown (USA)	Wood finisher
	Epoxidized linseed oil	HiBond®	Polar Industries (Canada)	Paints, plasticizers, adhesives, coatings, or any application for an epoxidized oil
		Vikoflex	Arkema (USA)	-
	Cyclopentadiene polymers	Diluline™	Cargill (USA)	Dring oil
		ML189	Archer Daniel Midland (USA)	Varnish, Enamel, Aluminum paint, Reinforced oil
Castor oil	Maleated alcoholized castor oils (MACOs)	-	-	-
	2-(Acryloyloxy) Ethyl Oleate (AEO)	Heloxy™ Flexibilizer	Momentive Specialty Chemicals (USA)	Epoxy Resin, Coating, Construction, Composites, Adhesives, Electrical castings, Electrical laminates and Fibers
	Estolides	Heloxy™ Modifiers48	Hexion (USA)	-
		ERISYS™GE-35H	Emerald Performance Materials (USA)	Concrete Patching Compounds, Floor Coatings, Adhesives, Bridge Decking Compounds, Joint Sealants
		Vorite®Polymerized Castor Oil	Vertellus (USA)	Elastomers, Adhesives, Coatings, Inks, Polyols, Sealants
		Zenigloss ®	Zenitech (Canada)	Emollient, Lip gloss agent, Personal care applications
		Polyglycerol polyricinoleate (PGPR)	Fraken Biochemical (China), Spell Organics (India)	Food emulsifier/texture and viscosity control (Chocolate)
	Polyamides	Rilsan®PA11, Rilsan®Fine Powder,	Arkema (USA, France)	Electrical cable, fuel line, fluid transfer, quick connectors, fasteners and clips, friction parts, pneumatic and hydraulic hose
		Ultramid® BALANCE	BASF (USA)	Automotive
	Polyurethane	Agrol Star™	BioBased Technologies (USA)	Inks and Coatings
		Lupranol® Balance 50	BASF (Germany)	Foam
		-	Jayant Agro Organics Limited (India)	-
	Polymer	Pebax Rnew®	Arkema (USA, France)	Sports, Medical, Packaging and Industrial applications
		EcoPaXX™	DSM	Automotive and Electrical markets

Table 6.
Toxicity of different surfactants against various organisms (Ivancovic and Hrenovic, 2010; Cowan-Ellsberry et al., 2014; Yuan et al., 2014; Theis et al., 2016; Badmus et al., 2021).

Surfactant Group	Petrochemical surfactants	Toxicological features of petrochemical surfactants	Plant oil-based alternatives	Application
Anionic	Linear alkylbenzene sulfonates (LAS)	**Bacteria:** *Vibrio fischer*i (EC$_{50}$-Luminescence 30 min: 2.6 mg/l) *Pseudomonase putida* (EC$_{50}$-Growth inhibition 16 h: 33.4 mg/l) **Algae:** *Dunaliella* sp (EC$_{50}$-24 h: 3.5 mg/l) **Crustaceans:** *Ceriodaphnia dubia* (EC$_{50}$- Immobilization 48 h: 5.96 mg/l) Daphnia magna LC50– 48 h, 13.9 mg/ LC50– 48 h, 8.1 mg/l LC50– 48 h, 1.22 mg/l **Fish:** *Carassius auratus* (EC$_{50}$- Immobilization 48 h: 5.1 mg/l) *Salmo gairdneri* (Immobilization EC$_{50}$– 48 h, 33.61 mg/l) *Gammbusia affinis* (mosquito fish) Immobilization EC$_{50}$-48 h, 40.15 mg/l *Carassius auratus* (goldfish) Immobilization EC$_{50}$-48 h, 38.04 mg/l **Plant:** Bush beans, radish and grasses: Yield and growth NOEC–76 days, 27 mg/kg Potato: Yield and growth NOEC–106 days, 16 mg/kg	Brand Name: Eurasol (Ammonium oleate, Potassium tallate, Mixed fatty acid salts, Potassium cocoate, Potassium palmate) EOC Co. Belgium Brand name: **SERVO® BRILLANT** (castor oil sulphonate) Elementis Co. The Netherlands	As detergents, foaming agents, emulsifiers, antistatic agents, dispersants, stabilizers in the family and chemical aspects of life, Cosmetic, Pharmaceutical and Petrochemical products
	Linear ether sulfate	-		
	Octylphenol polyoxyethylene sodium	-		
	Soaps	**Alga:** EC50: 10-50 mg/L		
	Sodium dodecyl sulphate (SDS)	**Bacteria:** *Vibrio fischeri* (EC50- Luminescence 15 min: 2.6 mg/L) **Algae:** *Raphidocelis subcapitata* (IC50 - Cell density 72 h: 36.58 mg/L) **Crustaceans:** *Artemia salina* (LC50 - Larvae mortality 24 h: 41.04 mg/L) **Gastropod:** *Physa acuta* (LC50 - Mortality 24 h: 27.2 mg/L) **Sea urchin:** *Paracentrotus lividus* (EC50- Fertilization rate: 3.2 mg/L) **Fish:** *Gammbusia affinis* (EC50- Immobilization 48 h: 13.64 mg/L) Salmo gairdneri (rainbow trout) Immobilization (EC50– 48 h, 10.84 mg/L) Carassius auratus (goldfish) Immobilization (EC50– 48 h, 12.35 mg/L)		
	Alkyl sulphate (AS)	-		
	Sodium lauryl sulphate (SLS)	-		
	Alkyl ethoxysulphate (AES)	**Algae:** *Pseudokirchneriella subcapitata* (EC50 - Cell density 72 h 3.5 mg/L) *Raphidocelis subcapitata* (IC50 - Cell density 72 h 2.18 mg/L) **Crustaceans:** *Artemia franciscana* (LC50- Nauplii mortality 72 h 23.92 mg/L) **Fish:** *Salmo gairdneri* (EC50- Immobilization 48 h 10.84 mg/L)		
	Secondary alkane sulphonates (SAS)	-		

Table 6.
continued.

Surfactant Group	Petrochemical surfactants	Toxicological features of petrochemical surfactants	Plant oil-based alternatives	Application
Non-ionic	Polyoxyethylenestearyl ether(20EO)	Water flea: EC50: 48 mg/L		
	Polyoxyethylenestearyl ether(10EO)	**Australian native frogs**: Full narcosis EC50– 48 h, 2.8– 3.8 mg/L **Fish:** Fathead minnow: LC50– 96 h, 4.6 mg/L	**Brand Name:** Eur Amid (cocamide diethanolamine, monoethanolamine); Euroxide (Cocamine oxide, Cocamidopropylamine Oxide, EOC Co. Belgium **Brand Name:** SERDOLAMIDE (coconut oil diethanol amide (Super-amide), oleic acid diethanol amide (Kritchevsky), soya oil diethanol amide in TEA/water (Super-amide)), SERDOX® (oleic acid monoethanol amide), ECOSURF™ SA Surfactants (Dow co, USA), EcoSense™ Surfactants (DOW company, USA)	Textile, paper, food, plastic, glass, fiber, medicines, pesticides, dyes, other industries, emulsifiers, wetting agents, and foam stabilisation agents, in various biotechnological processes, and to facilitate solubilisation and increase drug carrier stability
	Lauryl alcohol ethoxylates(7EO)	-		
	Nonylphenolethoxylates (9EO~11EO) (NPE)	**Crustaceans:** *Daphnia magna* LC50– 48 h, 14 mg/L **Fish:** Pimphales promelas (fathead minnow): LC50– 10 d, 2.7 mg/L Fathead minnow LC50– 96 h, 4.6 mg/L Effects on reproductive health of fish: NP induce the production of vitellogenin in male fish, a protein usually only found in sexually mature females under the influence of estrogens		
	Alkylphenol ethoxylate (APE)	-		
	Octyl phenol ethoxyales (OPE)	Effects on reproductive health of fish:OP induce the production of vitellogenin in male fish, a protein usually only found in sexually mature females under the influence of estrogens		
	Alcohol ethoxylate (AE)	**Bacteria:** *Microcystis aeruginosa (*Estimated EC10 - Cell density 0.154 mg/L) **Algae:** *Lemna minor* (Estimated EC10 - Frond count 0.101 mg/L) *Navicula pelliculosa* (Estimated EC10 - Cell density 0.140 mg/L) **Crustaceans:** *Ceriodaphnia dubia* (EC50 - Immobilization 48 h 0.39 mg/L) **Fish:** *Pimephales promelas* (NOEC - Survival 4.35 mg/L)		
	Fatty acid ethoxylate (FAE)	-		
Cationic	Cetyltrimethyl ammonium chloride	-	-	Sterilization, rust, corrosion, breaking, corrosion and mineral flotation, detergents, fabric softeners, and hair conditioners
	Quaternary ammonium compound (QAC)	QACs are toxic to mammalian cells and are not recommended for systemic application, damaging effects of cationic surfactants on human lymphocytes **Bacteria:** *Vibrio fischeri* (EC50- Luminescence 30 min 0.5 mg/L) *Pseudomonas putida (*EC50 - Growth inhibition 16 h 6.9 mg/L) **Algae:** *Dunaliella* sp. (EC50 - 24 h 0.79 mg/L) **Crustaceans:** *Daphnia magna* (EC50- Immobilization 24 h 0.38 mg/L) **Fish:** *Salmo gairdneri* (EC50- Immobilization 48 h 1.21 mg/L)		

Table 6.
continued.

Surfactant Group	Petrochemical surfactants	Toxicological features of petrochemical surfactants	Plant oil-based alternatives	Application
Cationic	Benzalkonium chloride (BAC)	-		
	Cetylpyridinium bromide (CPB)	-		
	Cetylpyridinium chloride (CPC)	-		
	Hexadecyltrimethylammonium bromide (HDTMA)	-		
	Alkyl trimethyl ammonium halides (TMAC)	**Algae:** *Dunaliella* sp. (green alga): EC50– 24 h, 0.79 mg/L **Crustaceans:** *Daphnia magna* Immobilization (IC50– 24 h, 0.13– 0.38 mg/L)		
	Alkyl dimethyl ammonium halides (DMAC)	**Algae:** *Dunaliella* sp. (green alga): EC50– 24 h, 18 mg/L		
	Alkyl benzyl dimethyl ammonium halides (BDMAC)	**Algae:** *Dunaliella* sp. (green alga): EC50– 24 h, 1.3 mg/L **Crustaceans:** *Daphnia magna* Immobilization (IC50– 24 h, 0.13– 0.22 mg/L)		Sterilization, rust, corrosion, breaking, corrosion and mineral flotation, detergents, fabric softeners, and hair conditioners
	Dialkyl dimethyl ammonium halides (DADMAC)	-	-	
	Dihydrogenated tallow dimethyl ammonium chloride (DHTDMAC or DTDMAC)	**Crustaceans:** *Daphnia magna* LC50– 48 h, 0.49 mg/L NOEC–21 d, 0.38 mg/L **Fish:** *Salmo gairdneri* (rainbow trout) Immobilization (EC50– 48 h, 0.74 mg/L) *Gammbusia affinis* (mosquito fish) Immobilization (EC50– 48 h, 7.91 mg/L) *Carassius auratus* (goldfish) Immobilization (EC50– 48 h, 2.37 mg/L)		
	Ditallow trimethyl ammonium chloride (DTTMAC)	-		
	Diethyl ester dimethyl ammonium chloride (DEEDMAC)	**Crustaceans:** Daphnia magna Immobilization LC50– 24 h, 14.8 mg/l Growth NOEC– 21 days, 1 mg/l **Algae:** Selenastrum capricornutum (algae) Growth inhibition EC50– 96 h, 2.9 mg/l **Fish:** Pimphales promelas (fathead minnow) Growth NOEC– 35 days, 0.68 mg/l		
Amphoteric	Amine oxide	**Bacteria:** *Phosphobacterium phosphoreum* AO EC50 - Luminescence 15 min 2.4 mg/L **Crustaceans:** *Daphnia magna* AO EC50 - Immobilization 48 h 6.8 mg/L	**Brand Name:** Euroquat (Cocamidopropyl betaine), Euroglyc (Sodium cocoamphoacetate, Disodium cocoamphodiacetate, Disodium cocoamphodiacetate) EOC Co. Belgium	Personal protective equipment such as shampoo, shower gel, cosmetics, etc. and in industrial softeners and antistatic agents. foam boosters in dishwashing, in textile industry as anti-static agents, in rubber industry as foam stabilisers and polymerisation catalysts, and in deodorant bars as antibacterial agents
Specialty surfactants				Fire protection, textile, paper, mineral processing, leather, pesticides and chemical industries
Macromolecule surfactants	-	-	-	Thickener, gelling agent, fluidity-improving agent, emulsifier, dispersing agent and antistatic agent, petrochemical industry, emulsification, emulsion breaking, wetting, foaming, anti-static, textile, cosmetics, pharmaceutical, food, body washes, facial cleansers, liquid hand soaps and baby wipes

mainly due to the fact that more than half of the final production cost of biosurfactants is attributed to the cost of raw materials (Mohanty et al., 2021). However, given the increasing consumer preference for bio-based products and governmental initiatives supporting the use of renewable raw materials, various strategies have been widely considered to address this challenge (Bhardwaj, 2013). These strategies include the utilization of low-cost waste-oriented plant oils, such as waste oil generated during vegetable oil processing. Additionally, other wastes or by-products of triglyceride origins, such as biodiesel glycerol, have been utilized as feedstocks for biosurfactant production (Bhardwaj et al., 2013). A significant amount of glycerol, around 10% (v/v) of the total production volume, is generated during the biodiesel production process, also known as transesterification (Salaheldeen et al., 2021). Polymers of glycerol, like polyglyceryl laurates, have demonstrated efficacy as sources of biosurfactants (Salaheldeen et al., 2021).

Despite the economic challenges, the current and projected market for biosurfactants appears promising (Freitas-Silva et al., 2023). For example, the market for lauric acid alone, primarily sourced from palm kernel and coconut oils, is estimated to exceed USD 1.4 billion annually, while the total revenue associated with biosurfactants, in general, is estimated at USD 6.588 million (Silva et al., 2014).

2.3. Lubricants

More than forty million tonnes of lubricants are utilized across various industries, with their primary purpose being consistent across applications, including lubrication, heat transfer, power transmission, and corrosion protection (Hamnas and Unnikrishnan, 2023). Presently, lubricants are typically composed of a blend of different base oils (Pinheiro et al., 2021; Yin et al., 2021). Petroleum-based oils, both mineral and synthetic, constitute the majority, ranging from 60% to 99% of lubricant formulations, with diverse additives employed to enhance their properties further (Salih and Salimon, 2021). In addition to viscosity, which is the most critical property of a lubricant, other essential attributes encompass availability and economic factors, chemical and temperature stability, compatibility, corrosiveness, flammability, environmental impact (biodegradability), and toxicity (Shah et al., 2021; Hamnas and Unnikrishnan, 2023). Petroleum-derived lubricants often fall short of meeting some of these criteria, particularly concerning environmental impact and toxicity. Consequently, the lubricant industry is increasingly shifting towards alternative feedstocks, such as plant oils, to develop more environmentally friendly (biodegradable) and less toxic lubricants, commonly referred to as biolubricants (Salih and Salimon, 2021; Sancheti and Yadav, 2022).

Biolubricants derived from plant oils exhibit superior lubricity and anti-corrosion properties compared to their nonpolar petroleum-based counterparts (Singh et al., 2020b). This capability can be attributed to the presence of ester bonds in the structure of plant oils. These bonds enable biolubricants to offer enhanced cohesion to metal surfaces, resulting in more efficient boundary lubricity (Salih and Salimon, 2021). Additionally, plant oil-based lubricants boast high flash points, typically exceeding 300 °C compared to 200 °C for petroleum-based lubricants, and demonstrate a lower rate of evaporation, approximately 20%. Consequently, this leads to significantly reduced losses (Singh et al., 2020a). These advantageous characteristics stem from the high viscosity index (VI) of plant oils, generally exceeding 200, in contrast to 90-100 for petroleum-based lubricants (Singh et al., 2020b; Gemsprim et al., 2021). This higher VI can be attributed to the high molecular weight and low volatility of plant oils (Njuguna et al., 2022).

Another significant characteristic of plant oil-based lubricants is their biodegradability (Shah et al., 2021), which becomes particularly crucial when considering factors such as aquatic toxicity or situations where total loss of lubricant is anticipated, such as in drilling processes and hydraulic equipment (Ellafi et al., 2020; Njuguna et al., 2022). However, there exists a negative correlation between biodegradability and chemical and thermal stability. Consequently, plant oil-based lubricants are highly susceptible to oxidation (Owuna, 2020). This low oxidative stability, coupled with poor cold flow properties, has significantly limited the application of plant oil-based lubricants.

To address the mentioned shortcomings, several approaches can be employed, including the chemical modification of plant oils, the utilization of additives to enhance their performance or properties, and the use of genetically-modified plant oils (Wickramasinghe et al., 2021; Sarwer et al.,

2022). Generally, there is a trade-off between the degrees of saturation and unsaturation in plant oils used in biolubricants. High levels of polyunsaturated FA, such as linoleic and linolenic acids found in typical plant oils like soybean or rapeseed, make them highly susceptible to oxidation. However, these oils offer suitable cold flow properties due to their low degree of saturation (Mujtaba et al., 2020; Sia et al., 2020). Thus, increasing the content of monounsaturated FA, such as oleic acid, is desirable to achieve this trade-off (Wang et al., 2021). This change can be accomplished through genetic modification to develop high oleic plant oils (Porokhovinova et al., 2022). An integrated strategy involving genetically improved high-oleic plant oils combined with chemical additives could be considered the most effective approach to further promote plant oil-based lubricants (Salimon et al., 2012). This strategy will play a crucial role in expanding the global biolubricants market, which is valued at over 2,000 million USD in the present decade (**Fig. 3**).

2.4. Metal working fluid

Metalworking fluids (MWFs), also referred to as cutting fluids, primarily function as lubricants or coolants in wet machining operations at the cutting zone of metal pieces (Patole and Kulkarni, 2018; Muralidhar and Chaganti, 2020). These fluids use extensive use in various processes such as grinding, drilling, milling, and cutting, among others, and are categorized as lubricants that extend the lifespan of machines by reducing friction between metal parts (Khan et al., 2022; Afonso et al., 2023). The impact of utilizing MWFs becomes more noticeable, particularly when working with difficult-to-cut materials (Mahesh et al., 2021). Moreover, these lubricants aid in the removal of chips remaining on the cutting zone, reduce the deformation of cutting tools and enhance the accuracy of the cut as well as the quality of the final product (Muralidhar and Chaganti, 2020; Wickramasinghe et al., 2021). MWFs find widespread applications in machinery, transportation equipment, metal fabrication, and various other industries.

MWFs are typically classified into four main types: straight or neat oils, water-miscible oils, synthetic oils, and semi-synthetic oils (Muralidhar and Chaganti, 2020; Sankaranarayanan and Krolczyk, 2021). Straight or neat oils consist of aliphatic hydrocarbons that are water-immiscible and derived from petroleum. Water-miscible oils can be either naphthenic or paraffinic-based, while semi-synthetic and synthetic oils are mineral oil-based (Ibrahim et al., 2023). The global market for MWFs was estimated to be USD 11.1 billion in 2022 and is projected to reach USD 15.9 billion by 2032, with an annual growth rate of 3.7% from 2023 to 2032 (ACUMEN, 2023).

Despite their widespread applications, MWFs pose various environmental hazards and negative impacts on human health. (David and Niculescu, 2021; Ghatge and Ramanujam, 2023). Environmental pollution, including water and soil contamination, is often observed due to the poor degradability of mineral MWFs, which dominate the market compared to synthetic and bio-based alternatives (Ullah and Dhar, 2018). Studies indicate that petroleum-based mineral MWFs constitute over 85% of the MWFs used worldwide (Muralidhar and Chaganti, 2020). Notably, the evaporation of liquid aerosol and its inhalation can lead to various respiratory diseases such as asthma, hypersensitivity pneumonitis, cancer, chronic bronchitis, throat irritation, and allergies.

To address these challenges, the use of synthetic, solid, or vegetable-based lubricants has been proposed (Uppar et al., 2023). Utilizing vegetable-based lubricants presents an environmentally friendly solution due to their biodegradable nature, stemming from the absence of non-polar functional groups (Chowdary et al., 2021). Oils such as canola, sunflower, coconut, sesame, castor, rapeseed, and others have been suggested for use as lubricants due to their relatively low cost compared to synthetic lubricants and their demonstrated satisfactory performance (Singh et al., 2020b; Kazeem et al., 2022). Given global concerns and new regulations regarding the use of MWFs, which contribute to environmental damage and health hazards, further research into bio-based MWFs is imperative. **Table 7** presents various MWFs utilizing plant-based oils and their characteristics.

2.5. Stabilizers and plasticizers

Stabilizers and plasticizers have played a vital role in enhancing the performance of thermoplastics, particularly polyvinyl chloride (PVC), by improving their thermal stability, flexibility, workability, and durability. PVC stands out as one of the most widely consumed thermoplastics (Arrieta

Table 7.
Various metalworking fluid studies on plant-based oils and their characteristics.

Reference	Base Oil	Material Tested	Additive/ Surfactant/ Modification	Technique	Viscosity	Density (g/cm³)	Conditions Tested	Machining Operation	Main Findings
Singh et al. (2020a)	Canola	Ti–6Al–4V-ELI	Graphene nanoplatelets	MQL*	42.49 (mPa.s) at 35 °C	0.9183	Specific Grinding Energy = 13.079 - 18.040 (J/mm³)	Grinding	Canola oil has the highest tribological potential over sunflower and olive oil. Graphene nano-additives improved the tribological potential of vegetable oils.
Singh et al. (2020a)	Sunflower	Ti–6Al–4V-ELI	None	MQL	41.55 (mPa.s) at 35 °C	0.9167	Specific Grinding Energy = 15.935-19.495 (J/mm³)	Grinding	Observed the lowest tribological performance of sunflower oil compared to olive and canola oils.
Singh et al. (2020a)	Olive	Ti–6Al–4V-ELI	None	MQL	46.29 (mPa.s) at 35 °C	0.9048	-	Grinding	The oxidation stability of olive oil is high due to higher monounsaturated fatty acid molecules. Olive oil has a low performance because of low specific heat capacity and higher dynamic viscosity.
Talib and Rahim, (2015)	Jatropha	-	Chemical modification with acid-based catalyst transesterification	MQL	30.66 (mm²/s)	0.9143	Coefficient of friction = 0.059 Wear scar diameter = 0.641		Oil viscosity influences on coefficient of friction and wear scar diameter.
Fernando et al. (2020)	Coconut	AISI 304 austenitic stainless steel	-	MQL	36.605 (mm²/s)	0.9068	-	Turning	Coconut oil has a better tool flank wear compared to a mineral oil MWF.
D'Amato et al. (2019)	*Jatropha curcas* L. oil	Aluminum alloy AA2030 and Carbon steel	-	-	-	-	-	Milling	-
Krishna et al. (2010)	Coconut	AISI 1040 steel	Boric acid particles	-	27.9	0.9300	-	Turning	Coconut oil-based nanoparticle suspension has a better performance than SAE-40 oil suspensions.
Belluco and De Chiffre, (2004)	A blend of five vegetable oils	AISI 316L	-	-	--	-	Tool life increase = 177%	Drilling	Longer tool life, better chip breaking, lower wear, and cutting forces were observed with vegetable-based oil compared to mineral oil.

*Minimum Quantity Lubrication.

et al., 2017), with a global market of approximately 44.3 million tonnes in 2018 (Statista, 2023a). It finds extensive use in various applications such as food packaging, children's toys, bottles, wallpapers, blood bags, coatings, medical devices, and more (Arrieta et al., 2017; Wang et al., 2020a).

To achieve the desired flexibility in PVC materials, a significant amount of plasticizer is utilized, with projected usage expected to reach 22.5 million tonnes by 2027 (Mohammed and Ikiensikimama, 2023). Petroleum-based phthalates are the most commonly used type of plasticizer for PVC, dominating over 80% of the industrial market (Kumar, 2019; Zhang et al., 2021) due to their cost-effectiveness and high plasticizing effect (Jia et al., 2017). However, concerns have arisen regarding their direct contact with humans through various products like food packaging, toys, and medical applications, potentially impacting human health negatively. Their low molecular weight and degree of branching facilitate migration from their matrix, posing risks to organs such as kidneys, heart, testicles, liver, and others and contributing to diseases like cancer and asthma (Bereketoglu and Pradhan, 2022; Peivasteh-Roudsari et al., 2023). Additionally, challenges associated with phthalates include their petroleum-based origin, which is unsustainable, their flammability, necessitating the use of fire protection materials, and their persistence in the environment (Yang et al., 2017). These concerns have spurred researchers to explore sustainable alternatives that are less toxic and environmentally friendly.

Epoxidized vegetable oils, including epoxidized soybean oil (ESBO), epoxidized palm oil (EPO), epoxidized broccoli oil (EBO), epoxidized sunflower oil, and epoxidized cottonseed oil (ECO), present promising alternatives to conventional plasticizers on the market (Carbonell-Verdu et al., 2017a). ESBO, safflower oil, cottonseed oil, cardanol diethyl phosphate, and sunflower oil, among others, serve as examples of epoxidized oils suitable for use as sustainable plasticizers and heat stabilizers for PVC (Arrieta et al., 2017; Zheng et al., 2018). They offer favorable cost-effectiveness and environmental degradability due to their straight-chain FA and glycerides (Giannakas et al., 2017; Stolp et al., 2019). ESBO stands out as the most commonly used vegetable oil-based plasticizer for PVC (Jia et al., 2018). Designing an efficient plasticizer with optimal compatibility with the polymer matrix necessitates consideration of three crucial parameters: optimized aliphatic chain, presence of an ester group, and availability of aromatic rings, ensuring acceptable solubility, polarity, and compatibility (Hassan et al., 2019). Despite advancements, further efforts are required to achieve these goals cost-effectively. **Table 8** provides an overview of studies on plant oil-based plasticizers and their corresponding characteristics.

2.6. Composites

Petroleum-based composites, which consist of more than one phase synthetically combined, with each phase naturally formed and composed of one or more fillers within a matrix, are currently used due to their light weight, high corrosion resistance, great flexibility, stability, and low cost. These composites have broad applications across various industries,

Table 8.
Various metalworking fluid studies on plant-based oils and their characteristics.

Reference	Plant oil	Polymer	Plasticizer's content	Influence on Glass Transition Temperature (°C)	Influence on Modulus (GPa)	Mechanical properties	Other information
Brüster et al. (2019)	Limonene	PLA	20%	-33.7	-1.3	• Limonene enhanced the impact strength and ultimate tensile strain more than myrcene • the influence of limonene was more than myrcene on reduction of tensile strength.	• Limonene/PLA matrix absorbs more water than PLA/myrcene due to the higher influence of limonene on Tg. • PLA/limonene was transparent and is suitable for transparent packaging • PLA/myrcene was opaque and is suitable for opaque packaging
	Myrcene		20%	-10.9	-0.4		
Xuan et al. (2020)	(3:1) eugenol: levulinic acid (TL)	PLA	30%	-22	≈-1.5	• All plasticizers caused enhancements in strain break of the PLA. MV had the highest strain break in comparison with other samples. • After one week of storage, blends with levulinic acid ad eugenol showed phase separation.	• MV had the highest plasticization effect due to its low molecular weight, longer flexible alkane chain and higher concentration of ester group. • MV, ML, and TL made PLA bactericidal against *Staphylococcus aureus* • MV could inhibit *Escherichia coli* as well
	(1:1) eugenol: levulinic acid (ML)		30%	-24	≈-1.8		
	(1:1) valeric acid:eugenol (MV)		30%	-43	≈-2		
Carbonell-Verdu et al. (2017a)	Maleinized linseed oil (MLO)	PLA	5%	-2.1	≈-0.47	• The lower content improved the elongation at break. In higher percentages, phase separation started. • Although the elongation at breaks increased by blending 5%, it was reduced by adding 10% of MCSO due to the phase separation.	• The higher miscibility of MCSO in PLA than MLO made the mechanical properties of the PLA/MCSO matrix better than MLO/PLA. • Tensile strength was reduced more by using MLO. Moreover, the crystallinity improved by adding the plasticizers.
			10%	-2.4	≈-0.74		
	Maleinized cottonseed oil (MCSO)		5%	-1.4	≈-0.47		
			10%	-1.9	≈-0.79		
Orue et al. (2018)	Epoxidized linseed oil	PLA	10%	-2.4	≈-1.9	• With 20%, 100% raise in elongation at break, 50% reduction in tensile strength, and 100% reduction in impact resistance	• The crystallinity is enhanced by adding plasticizers in various percentages. • Among all plasticizers, just epoxidized soybean oil made the matrix in two phases. • Epoxidized oils had higher thermal stability than those for non-oxidized. • None of the mentioned plasticizers improved the thermal strength of the matrix.
			20%	-4.24	≈-2.05		
	Non-epoxidized linseed oil		10%	-6.48	≈-1.55	• With 20%,170% raise in elongation at break, 43% reduction in tensile strength, and 110% reduction in impact resistance	
			20%	-8.98	≈-1.7		
	Soybean oil		10%	-2.48	≈-1.25	• With 20%, 120% raise in elongation at break, 44% reduction in tensile strength, and 115% reduction in impact resistance	
			20%	-4.37	≈-1.55		
	Epoxidized soybean oil		10%	-3.92	≈-1.1	• With 20%,190% raise in elongation at break, 42% reduction in tensile strength, and 83% reduction in impact resistance	
			20%	-4.9	≈-1.45		
Chieng et al. (2014)	Palm oil	PLA	5%	Reduced	≈-0.3	• • Adding just 5% enhanced the elongation at the break of about 2000%	• The influence of palm oil in reducing tensile strength and enhancement of the elongation at break was more than that of mixed palm oil with soybean. • The mixed plasticizer showed higher thermal strength than the palm oil plasticizer.
			10%		≈-0.37		
	Palm oil+soybean oil		5%	Reduced	≈-0.28	• Adding just 5% enhanced the elongation at a break of about 4000%	
			10%		≈-0.43		
Mangeon et al. (2018)	Linalool	PHB	10%	-2	-0.655	• Stress at break reduced, while strain at break increased by plasticizers in all contents.	• Segment bearing an ester Group in geranyl acetate could increase molecular mobility and free volume and it is more effective than others to plasticize PHB and make it flexible.
			20%	-9	-0.715		
	Geraniol		10%	-4	-0.615	• Stress at break reduced, while strain at break increased by plasticizers in all contents.	
			20%	-11	-0.915		
	Geranyl acetate		10%	-8	-0.765	• The influence of this plasticizer on the mentioned properties was greater than other plasticizers.	
			20%	-13	-1.08		
Arrieta et al. (2014)	D-limonene	25 wt% PHB+ 75 wt% PLA	15%	-19.16	-0.76	• Elongation at break enhanced about four times. • The reduction in tensile strength was negligible.	• The melting point was reduced, and it is a good additive in the food packaging industry. • The crystallinity was enhanced by about 90.
Qin et al. (2017)	Bergamot	PLA	9%	-2.7	-0.956	• 62% reduction in tensile strength, while the elongation at break increased from 5 to 155%	• By adding bioplasticizers, the transparency was reduced. • The influence of bergamot in this reduction was the highest among all additives. • The depletion in melting point was negligible. • Crystallinity was improved by plasticizers, especially by clove oil. • The plasticizers could inhibit *E. coli* and *B. Subtilis* due to the inhibition ability of essential oils.
	Lemongrass			-5.4	-1.076	• 63% reduction in tensile strength, while the elongation at break increased from 5 to 57.	
	Rosemary			-4.3	-0.144	• 36% reduction in tensile strength, while the elongation at break increased from 5 to 26.	
	Clove			-5.8	-0.983	• 63% reduction in tensile strength, while the elongation at break increased from 5 to 64%	

including automotive, infrastructure, military, aerospace, and marine sectors. Natural rubber, proteins, cellulose, sugar, and plant oils are types of renewable raw materials that can be used for manufacturing composites (Thangadurai et al., 2020; Chang et al., 2021). Vegetable oils, composed of triglyceride acids, are abundant in nature, low-cost, low-toxicity, and highly biodegradable, making them excellent sources of polymer precursors for producing polymers and composite materials (Díez-Pascual and Rahdar, 2021; Rajput et al., 2023). The global market size for composite materials was valued at approximately USD 113.7 billion in 2022, with a compounded annual growth rate of 8.2% from 2022 to 2027 (Kan et al., 2019; Polaris Market Research, 2024).

The production of polymeric composites using vegetable oils as the base material has been successful for both synthetic and natural fiber-reinforced composites, as well as for nanocomposites reinforced with metal and silica oxides, carbon, nanoclay, cellulose, and lignin (Hasan et al., 2020; Ebrahimnezhad-Khaljiri and Ghadi, 2023). However, despite the extensive use and industrial application of vegetable oils in composite materials, more research is needed to bridge the performance gap between vegetable oil-based and conventional petroleum-based composites (Zhang et al., 2017). **Table 9** shows recent studies on vegetable-based composites.

2.7. Pesticides

Chemical pesticides are traditionally used to control plant pests but come with significant disadvantages, such as resistance to pests, ecosystem disruption, soil and environmental contamination, and hindrance to decomposer microorganisms, affecting soil nutrients (Telaumbanua et al., 2021). Due to the serious negative effects of synthetic pesticides on the environment and human health, there is a growing demand for more environmentally friendly alternatives (Telaumbanua et al., 2021; Ali et al., 2023). Oil-based pesticides offer benefits like low cost, environmental friendliness, excellent wettability, effective pest control, and no resistance induction in target pathogens (Kavetsou et al., 2019). The global pesticides market was valued at nearly USD 78.16 billion in 2019 and is projected to grow to about USD 105.32 billion by 2026 (Vantage Market Research, 2022). Biopesticides comprised 6-7% of the global pesticides market value in 2021 (USD 1.8 billion) and are expected to exceed 10% by 2031 (Statistica, 2023b).

Various vegetable oils, including safflower (*Carthamus tinctorius*), coconut (*Cocos nucifera*), soybean (*Glycine max*), castor bean (*Ricinus communis*), cottonseed (*Gossypium* spp.), peanut (*Arachis hypogea*), mustard, and maize (*Zea mays*), have been successfully used as pesticides (Rathnakumar and Sujatha, 2022; Vaikuntapu and Kumar, 2023). **Table 10** presents research studies focusing on the use of plant-based pesticides on various organisms.

The growth of organic farming and the increasing demand for organic crops have driven the implementation of Integrated Pest Management (IPM) solutions. The global biopesticides market, including bioinsecticides, biofungicides, bionematicides, and bioherbicides, is projected to expand from USD 4.3 billion in 2020 to USD 8.5 billion by 2025, with a compound annual growth rate (CAGR) of 14.7%. This growth is driven by global concerns about hazardous pesticides, a rising interest in organic crops, increasing awareness of biopesticides, and expanding research into new biopesticides. The availability, price, and regulatory approval of vegetable oils play a significant role in determining their suitability for biopesticide production (Isman, 2020).

2.8. Paint, coating and adhesives

Vegetable oils have been used as painting material since prehistoric times, as evidenced by cave paintings. Based on their structure, vegetable oils serve as an attractive source of corrosion inhibitors and coatings (Phulpoto et al., 2021; Harikrishnan et al., 2024). Corrosion inhibitors are materials added to a medium (liquid or gas) to inhibit or reduce the reaction between the media and a surface, typically made from metal or alloy. Given their composition of TAGs of FA, vegetable oils can form dry oils that react with atmospheric oxygen, resulting in component crosslinking (Pizzimenti et al., 2021; Pattnaik and Mishra, 2022; Machado et al., 2023).

This property makes highly unsaturated dry oils suitable for applications such as varnishes or oil paintings through polymerization or oligomerization (Kalita et al., 2022; Rehan and Usman, 2023). Additionally, oil coatings are widely used in wood deck staining or finishing and cedar shingles coating

(Tanasă et al., 2021; Van Acker et al., 2023). **Table 11** provides details on the use of vegetable oils in coating materials and their important properties.

2.9. Inks

A solution, sol, or gel containing at least one colorant, such as a dye or pigment, used to color a surface to form an image, text, or pattern is known as ink (Aydemir et al., 2018). Inks are broadly used in various areas, including textile printing, fabric printing, cartridge inkjet printing, and markers. In 2022, the global ink market reached USD 19.8 billion and was estimated to reach USD 24 billion by 2028, with a CAGR of 3.24% (Haregu et al., 2023).

Traditionally, synthetic resins and oils, which are the main components of ink, have been petroleum-based, and the solvents are volatile organic compounds that can evaporate at room temperature, creating toxicity. However, vegetable oils have been increasingly used as raw ingredients in resin manufacturing in recent years. Several studies have explored the use of different types of essential oils to create eco-friendly printing inks, which are particularly important in the production of ink, varnish, and paint (Chen et al., 2021a; Hayta et al., 2022). The shift towards using vegetable oils in inks not only addresses environmental concerns but also promotes the sustainability of raw materials in the printing industry.

2.10. Emollients

A moisturizer, also known as an emollient, is a cosmetic product that protects, moisturizes, and lubricates the skin, available in various forms such as sprays, creams, and ointments. Humectants, which are water-attracting compounds, include emollients such as glycerin, honey, and seaweed. These are frequently used to hydrate the skin and treat conditions like eczema, psoriasis, ichthyosis, and other dry, inflamed, and scaly skin diseases (Pavlačková et al., 2020).

Moisturizers are widely used worldwide to improve skin health, with North America and Europe dominating this market. However, the fastest growth rate is observed in the Asia-Pacific region. The global emollient market size is estimated to grow from USD 1.5 billion in 2019 to USD 2.6 billion by 2032, with a CAGR of 5.6% (Insight, 2023).

There are various emollients on the market, including silicones, paraffin, and oleochemical-based solutions. Other emollients include glycerides, esters, alcohols, ethers, and carbonates, which can be customized based on the required performance. Due to several adverse effects associated with these traditional emollients, researchers have begun exploring new types with higher performance (Salaheldeen et al., 2021). One of the latest alternatives is plant and vegetable oils, which have been increasingly used as emollients. Although vegetable oils do not supply moisture to the skin directly, they prevent dehydration by allowing moisture to be retained, making them effective emollients rather than moisturizers.

Several factors make natural oils ideal, such as being anti-inflammatory, antimicrobial, barrier-repairing, having a minimal risk of irritation or allergy, and being widely available and cost-effective (Vaughn et al., 2018). Avocado, soursop, olive, coconut oils, and other plant oils provide essential nutrients to the skin and act as moderately occlusive emollients (de Lima Souza et al., 2021). While clinical studies have reported several benefits of olive oil as an emollient, some researchers caution that it can be harmful to human skin. The oleic acid in olive oil can enhance skin penetration by disrupting the structural order of the stratum corneum's lipids, causing lipid phase separation (Poljšak et al., 2020; Elmowafy et al., 2021).

2.11. Wax esters

Wax esters, though produced in small quantities, boast significant profit margins and command high prices in the industrial market. These esters, formed between fatty acids and fatty alcohols, are aptly named wax esters. Various enzymatic and chemical methods can be employed to manufacture wax esters from diverse materials, such as different types of palm oils paired with oleyl alcohol and isobutyl alcohol using a range of catalysts.

The classification of wax esters as liquid or solid depends on the saturation levels of the FA and alcohols, resulting in varying melting characteristics at room temperature. Carnauba wax, candelilla wax, and beeswax esters are three economically significant variants, constituting the primary components widely used in lubricants, cosmetics, linoleum,

Table 9.
Recent studies on the vegetable-based composites.

Reference	Plant oil	Content (%)	Base materials	Purpose	Influence on tensile strength (Mpa)	Influence on elongation at break (%)	Inhibited microorganisms	Other findings
Souza et al. (2013)	Cinnamon	0.4	Cassava starch with different content of glycerol	To improve the mechanical properties and antimicrobial activity of the composite	-1.43	127.32	*Penicillium Commune Eurotium amstelodami*	• Even at a minimum concentration of cinnamon oil, the inhibition rate against the selected microorganisms was high. • Both water vapor permeability and oxygen permeability coefficient were enhanced by cinnamon oil.
		0.8			-2.7	62.46		
Carbonell-Verdu et al. (2017b)	Tea tree	2	hydroxypropyl methylcellulose	Influence of essential oils on mechanical properties of two different composites.	-14	-3.7	Not investigated	• Different oils with various contents caused changes in particle size and size distributions. Particle size with limonene was the highest. • The water vapor permeability of the polymer was reduced by bergamot more than limonene and limonene more than tea tree. • The influence of tea tree oil in film thickness reduction was the highest and lemon was the second highest.
	Bergamot				-16	-5		
	Lemon				-15.6	-4		
	Tea tree		chitosan		-59	-22		
	Bergamot				-63	-16		
	Lemon				-16	-17		
Akhter et al. (2019)	Mint oil+Nisin	0.5+0.5	chitosan pectin starch biocomposite film	Synthesis of active chitosan pectin/starch-based biocomposite with nisin as antimicrobial agents and rosemary and mint oil as antioxidant agents	-9.27	-9.61	*Bacillus subtilis, Escherichia coli,* and *Listeria monocytogenes*	• The antimicrobial activity of biocomposite incorporated with rosemary and nisin was higher than the second one. • The influence of rosemary+nisin in reducing water vapor permeability was more.
	Rosemary+ Nisin	0.5+0.5			-18.23	-12.92		
Amalraj et al. (2020)	Black pepper essential oil	10	polyvinyl alcohol/gum Arabic/chitosan	Due to advancements in antimicrobial activity and healing properties of used oils compared to traditional packing and dressings, they were used to increase their antibacterial activities for pharmaceutical, nutraceutical, and food applications	-4.3	7.56	*B. cereus, Staphylococcus. aureus, E. coli,* and *Salmonella Typhimurium*	• Film thickness increased by adding essential oils, especially black pepper. • The loss of black pepper through storage time was less than ginger oil. • The black pepper inhibition rate for all examined microorganisms was more than the second one.
	Ginger essential oil				-3.11	4.76		
Lee et al. (2019b)	Oregano essential oil nanoemulsion	2.5	hydroxypropyl methylcellulose	To study the mechanical, antioxidant, barrier, optical, and mechanical properties of the composite films incorporated with EO	≈-5	≈2	*S. aureus, B. cereus, L. monocytogenes, E. coli, S. Typhimurium, Microcystis aeruginosa,* and *Vibrio parahaemolyticus*	• Young modulus and water vapor permeability (WVP) are reduced by blending essential oil. • For WVP, by increasing the oil contents, the rate of reduction is reduced.
		7.5			≈-16	≈3		
Liu et al. (2019)	Tannic acid-crosslinked epoxidized soybean oil oligomers	10	bamboo fibers-reinforced poly(lactic acid) biocomposites	to improve the interfacial adhesion of the composite and study the influence of mechanical properties by plant oil	≈-25	≈14	Not investigated	• At low content, the plant oil creates a flexible interfacial layer between Bamboo fiber and PLA and increases the mechanical properties, such as storage modulus, impact strength, and tensile toughness of the composite.
		20			≈-35	≈10		
Montava-Jordà et al. (2019)	walnut shell flour+5 phr maleinized linseed oil	20	polylactide (PLA) 64 wt% /poly(ε-caprolactone) (PCL) 16 wt%	to study the influence of multi-functionalized vegetable oils on thermal, morphological, and mechanical properties of the matrix	-29	5.7	Not investigated	• Water uptake improved sharply by blending plant oils, while the degradation temperature, glass transition temperature, and impact strength of the composite were reduced by adding essential oils. • The tensile modulus decreased by about 35% in most essential oils.
	Walnut shell flour+5 phr maleinized linseed oil	30	PLA 48 wt% / PCL 12 wt%		-40.4	-8.3		
	Walnut shell flour+5 phr maleinized linseed oil	40	PLA 48 wt% / PCL 12 wt%		-41.9	-8.9		
Arfat et al. (2018)	Clove oil	15	PLA/PEG (80:20)	Using clove oil as an antibacterial (gram-positive and gram-negative bacteria) agent for composite	-7.8	39.47	*S. aureus* and *E. coli*	• Clove oil significantly reduced glass transition temperature. • The melting point of the composite is influenced negatively by clove oil. • It could inhibit two types of bacteria that were used in the experiment.

Table 10.
Research studies on using plant-based pesticides on various organisms.

Reference	Plant Oil	Oil concentration	Application	Targeted Species	Time (h)	Mortality /Inhibitory (%)	Results
Kavetsou et al. (2019)	Encapsulated *Mentha pulegium* EO	0.10%	Used in yeast cell microcarriers	Insect pest *Myzus persicae*	24	5	• Encapsulated-oil showed higher insecticidal activity than non-encapsulated one.
					48	5	
	Non-encapsulated *M. pulegium* EO	0.10%			24	0	
					48	5	
Vasantha-Srinivasan et al. (2018)	Betel leaf oil	500 mg/kg	In soil against earthworm and redworm	*Eudrilus eugeniae* (Kinberg)	168	≈1.5	• Innovative and safe insecticides for soil-dwelling creatures.
					336	≈1.2	• The enzyme level was not affected by the essential oil of *P. betle*. Thus, the plant-derived volatile oil did not affect biochemical reactions
		1000 mg/kg			168	≈3.5	
					336	≈2.5	
		500 mg/kg		*Eisenia fetida* (Savigny)	168	≈1.9	
					336	≈1.5	
		1000 mg/ kg			168	≈3.2	
					336	≈2.5	
Tabari et al. (2017)	α-thujone-rich *Artemisia sieberi* essential oil	2 μg/cm^3	Poultry industry	*Dermanyssus gallinae* (Dermanyssida)	24	3.22	• Prolonged toxicity of the oil.
		5 μg/cm^3				10.88	• On adults of the poultry red mite, D. gallinae, -thujone-rich A. sieberi essential oil showed promising toxicity and repellant action.
		10 μg/cm^3				25.77	
Adak et al. (2020)	Eucalyptus	1 μg/cm^3	Rice	*Sitophilus oryzae*	24	55	• Downsized essential oils have higher insecticide potential than normal size.
		2 μg/cm^3				100	• Nanoemulsion eucalyptol can improve efficiency and reduce the cost of essential oils.
		3 μg/cm^3		*Tribolium castaneum*		17	
		7 μg/cm^3				58	
Klein et al. (2020)	Thyme	0.148% (v/v)	Laboratory and greenhouse bioassays	*Deroceras reticulatum*	24	50	• By 1% (v/v), after 24 hours, the mortality by all types of essential oils reached 100%, showing that these plant extracts might be usable as new rational molluscicides.
		0.26% (v/v)				99	
	Garlic	0.204% (v/v)				50	
		0.329% (v/v)				99	• Thyme showed the highest performance as a pesticide than other oils.
	Rosemary	0.307% (v/v)				50	• Although thyme proved beneficial against the targeted species, the open environment could influence the results.
		0.554% (v/v)				99	
	Lemongrass	0.32% (v/v)				50	
		0.72% (v/v)				99	
	Cinnamon Cassia	0.42% (v/v)				50	
		0.799% (v/v)				99	
Idoko and Ileke (2020)	*Aframomum melegueta*	1 mL/L	Cowpea seeds	*Callosobruchus maculatus*	12	13.33	• Protect stored cowpeas against *C. maculatu*s.
		5 mL/L				26.67	• The influences of essential oils on C. maculatus mortality increased with the exposure time and treatment rates.
	Annona muricata	1 mL/L				13.33	
		5 mL/L				16.67	
	Eucalyptus globules	1 mL/L				13.33	• The significant mortality induced by essential oils may be owing to the essential oils' suffocating odor, which must have disturbed the insects' regular respiratory mechanism.
		5 mL/L				20	
	Ficus exasperate	1 mL/L				16.67	
		5 mL/L				20	
	Tetrapleura tetraptera	1 mL/L				6.67	
		5 mL/L				20	
Papadimitriou et al. (2019)	*Pulegone* extracted from *M. pulegium*	500 μL/L	Cucumber Tomato	*Tetranychus urticae* females	72	47	• Incorporating these two EOs did not influence the mortality rate of helpful insects (*Nesidiocoris tenuis*).
		1000 μL/L				51	
	Piperitone extrcted from *M. pulegium*	500 μL/L				65	• No phytotoxic influences were recorded after using EOs on the plants.
		1000 μL/L				71	
Janaki et al. (2018)	*Cyperus rotundus*	0.4 μl/cm^2	Cowpea Chickpea Dates	*C. maculatus*	24	64	• The used EO exhibited a repellent effect on all three kinds of insects examined in the study.
		1 μl/cm^2				88	
		0.4 μl/cm^2		*Trogoderma granarium*		66	• The repellent effect in *O. surinamensis* and *T. granarium* was more than in *C. maculatus*.
		1 μl/cm^2				77	
		0.4 μl/cm^2		*Oryzaephilus surinamensis*		44	
		1 μl/cm^2				72	

Table 11.
Use of vegetable oils in coating materials and their important properties.

Reference	Plant oil	Oil content (%) or concentration	Purpose	Time (d) (factor)	Important property	Influence on the property	Important information
Dong and Wang (2017)	Garlic essential oil	1	The influence of essential oils coating for improving the quality of strawberries that contain carboxymethyl cellulose	3 (storage time)	Decay percentage (%)	≈-13.5%	• Using carboxymethyl cellulose in conjunction with garlic essential oil improved decay percentage, weight loss, total soluble solids, titratable acidity, and ascorbic acid content, as well as retaining greater total phenol and anthocyanin concentrations in strawberries.
					Total phenol conc.(mg/g)	≈0.3	
				6 (storage time)	Decay percentage (%)	≈-40%	
					Total phenol conc.(mg/g)	≈0.12	
		3		3 (storage time)	Decay percentage (%)	≈-12.5%	
					Total phenol conc.(mg/g)	≈0.37	
				6 (storage time)	Decay percentage (%)	≈-42%	
					Total phenol conc.(mg/g)	≈0.21	
Alotaibi and Tahergorabi (2018)	Thyme essential oil	2	Sweet potato starch based-coating of refrigerated storage with essential oil and studying the influence on the shrimp quality	4	Hardness (N)	5.8	• Significant reduction in the bacterial population by thyme. • A sweet potato starch-based coating incorporated with thyme essential oil might be a feasible option for preserving shrimp meat quality and reducing losses.
					Resilience	-0.03	
		4			Hardness (N)	7.06	
					Resilience	-0.01	
Fernández et al. (2020)	Citronellol	2 (mg/mL)	Develop an antifungal hybrid filler for coatings that is both environmentally friendly and affordable	10	*C. globosum* inhibition (%)	77	• Plant extracts containing EOs can be utilized as antifungal agents. • The main active component was found to be citronellol. • Producing functional bioactive hybrids was the benefit of blending citronellol.
					A. alternata inhibition (%)	78	
		5 (mg/mL)			*C. globosum* inhibition (%)	96	
					A. alternata inhibition (%)	98	
	Citral	2 (mg/mL)			*C. globosum* inhibition (%)	75	
					A. alternata inhibition (%)	75	
		5 (mg/mL			*C. globosum* inhibition (%)	98	
					A. alternata inhibition (%)	98	
Vital et al. (2018)	Ginger	0.10%	Acceptability of fish fillet with an alginate-based coating containing essential oils	7	Shear force (N)	-1.85	• Reduction in color losses and lipid oxidation of fish fillet. • The antioxidant activity increased. • Using these additives is an effective way to eliminate undesirable properties of the food.
					Weight loss (%)	-0.03	
					pH	-0.04	
	Oregano				Shear force (N)	1.58	
					Weight loss (%)	0.18	
					pH	-0.06	
Buendía et al. (2020)	Carvacrol:oregano:cinnamon (70:10:20)	≈1%	Coating of cardboard, including EO entrapped within cyclodextrins nanotube	6	TA (% citric acid)	0.001	• The lowest decay incidences and the highest firmness were for cyclodextrins nanotube blended with EOs. • That blend showed the highest antimicrobial activity compared to samples without plant oil. • The changes in pH were negligible. • The additives did not influence the physicochemical quality of the product (tomatoes).
				6 with a supplementary commercialization period	Firmness (N)	3.2	
					TA (% citric acid)	0.015	
			Coating of cardboard including EO entrapped within cyclodextrins halloysite nanotube	6	Firmness (N)	1.5	
					TA (% citric acid)	-0.01	
					Firmness (N)	-2.7	
				6 with a supplementary commercialization period	TA (% citric acid)	-0.029	
					Firmness (N)	2.7	

Table 11.
continued.

Reference	Plant oil	Oil content (%) or concentration	Purpose	Time (d) (factor)	Important property	Influence on the property	Important information
Klangmuang and Sothornvit (2018)	Plai	15g/L	Incorporating essential oils into hydroxypropyl methylcellulose-based nanocomposite on mango (cv. *Namdokmai Sithong*) against an anthracnose disease	15	Weight loss (%)	From ≈9 to ≈7.4	• Incorporating essential oils into the matrix inhibited *C. gloeosporioides* fungus. • Ginger showed the highest performance. • Essential oils did not influence the taste, flavor, and quality of mango and extend the fruit's shelf life.
					Disease severity (score)	From ≈3 to ≈2.2	
					Firmness (N)	From ≈1.95 to ≈7	
					Color	From ≈4.35 to ≈4	
	Ginger				Weight loss (%)	From ≈9 to ≈7.8	
					Disease severity (score)	From ≈3 to ≈1.9	
					Firmness (N)	From ≈1.95 to ≈6.8	
					Color	From ≈4.35 to ≈3.7	
Majdinasab et al. (2020)	Shirazi thyme	2%	The influence of used EOs on antimicrobial and antioxidant coating and shelf-life extension of chicken fillet	10	Cooking loss (%)	-15.5	• The change in color by thyme was less than summer savory. • The shelf-life of chicken fillets is extended. • The overall acceptability was more than the control (Basil-seed gum) when they used EOs, and thyme influence was higher than summer savory.
					Overall acceptability	From 2.4 to 3.8	
					Texture	From 2.4 to 4.4	
	Summer savory				Cooking loss (%)	-13.5	
					Overall acceptability	From 2.4 to 3.5	
					Texture	From 2.4 to 4.3	

printing inks, candles, and polishes due to their distinctive properties (Zhukov and Popov, 2022). The global wax and wax ester markets, particularly in the UK, the USA, Brazil, Japan, and other countries, are highly appealing and anticipated to grow at a rate of 3.83, reaching USD 15.91 billion by 2030 (**Fig. 3**) (Verified Market Research, 2023). While some plants naturally produce wax esters in their seed oil, like jojoba, they are unsuitable for large-scale cultivation as they yield an undesirable mixture of very long-chained wax esters unfit for technological applications (Langsdorf et al., 2021; Simonsen et al., 2023). However, numerous other plants show promise in producing wax esters, such as sunflower seed, olive, palm, *Camelina sativa*, and *Arabidopsis thaliana*, exhibiting high performance (Qi et al., 2020; Clews et al., 2023).

Olive and palm oil-based wax esters are particularly noteworthy, with those derived from olive oil consisting of long, straight-chain fatty alcohols esterified with FA (Abdelmoez and Mustafa, 2014; Mariani et al., 2018). Several factors influence the rate of esterification in olive oil, including refining process variables, storage conditions, and reagent concentration (Mariani et al., 2018; Diarte et al., 2021).

2.12. Textile finishing

Washing, bleaching, dyeing, and coating constitute the primary stages of the textile finishing process, utilized to enhance the bulk of textiles or garments post-weaving and synthetic material manufacturing (Achaw and Danso-Boateng, 2021; Al-Sayed and Abdelrahman, 2021). Textile finishing plays a crucial role in determining the final appearance and aesthetic qualities of textiles while also imparting desirable properties such as flame retardancy, wrinkle resistance, water-and-oil repellency, and more (Haule and Nambela, 2022; Javaid et al., 2024).

Over the projected period (2017-2024), the global market for textile finishing chemicals is forecasted to grow at a CAGR of 3.8%, rising from USD 8.9 billion in 2022 to USD 12 billion in 2030 (Prescient and Strategic Intelligence, 2023). However, a significant portion of textile finishes currently available in the market pose potential harm to the environment and human health, with compounds like triclosan known for accumulating in aquatic environments and posing toxicity risks to aquatic organisms (Bhat et al., 2022; Periyasamy, 2023).

In light of these concerns, plant oils present a sustainable alternative for use as additives in textile finishing processes (Natarajan et al., 2022). One notable application is their use as insect repellents, leveraging their natural properties to repel insects, along with their utilization in aromatherapy textiles for antibacterial, olfactory, and medicinal purposes (Mittal et al., 2019). It is important to note that antimicrobial textiles, while effective, maintain eco-friendly credentials, making them favorable in contemporary contexts, particularly amidst the COVID-19 crisis, which has underscored the importance of controlling infectious diseases (Bouaziz et al., 2021).

Beyond textile applications, plant oils serve various industries. In medicine, they demonstrate potent antifungal, antimicrobial, anticancer, and wound-healing properties. In the food and food packaging sectors, they function as natural antifungal and antibacterial agents. Additionally, in the cosmetics and perfume industries, their aromatic qualities make them invaluable ingredients. Plant oils also contribute to mining processes through ore froth flotation and serve as surfactants in oil-well drilling muds. Moreover, in rubber production, plant oils serve as vulcanizing agents, softeners, and mold release agents. They also find use as solvents and anti-dust agents, and they aid in paper recycling by efficiently removing printing inks. Subsequent sections will delve into plant oil production pathways and fatty acid synthesis.

3. Plant oil production pathways

Plant oils primarily consist of TAGs and are predominantly stored in the seeds or mesocarp of fruits (Ge et al., 2021; Hernández et al., 2021). However, notable exceptions exist, such as *Simmondsia chinensis* (jojoba), where oils accumulate in the form of esters of long-chain alcohols and FA (Guzha et al., 2023). From a chemical standpoint, TAGs result from the esterification of FA (C_8–C_{24}) with glycerol (Wei et al., 2024). It is intriguing to note the close similarity between the generic chemical formulas of these FA and those of fossil-oriented hydrocarbons, i.e., $CH_3(CH_2)_nCOOH$ *vs*. $CH_3(CH_2)_nCH_3$, respectively (Rajaeifar et al., 2019). This similarity has sparked widespread investigations into using plant oils and their derivatives as alternatives to fossil fuels. Overall, the properties of plant oils and their applications are largely attributed to their fatty acid composition (Mannu et al., 2020).

It is important to acknowledge that while palmitic acid (16:0), stearic acid (18:0), oleic acid (18:1), linoleic acid (18:2), and linolenic acid (18:3) are the major FA found in plant oils (Wei et al., 2019; Piovesana et al., 2021), there is remarkable diversity among different plant species in terms of their oil compositions. For instance, there are over 300 variations in fatty acid profiles in higher plants (Liu et al., 2022b). Moreover, some plants produce uncommon FA, further enriching plant oil compositions. Examples of such uncommon FA include short carbon chain FA (C$_8$ to C$_{14}$) in Cuphea, long carbon chain FA (C$_{20}$ to C$_{24}$) in rape, Crambe, *B. napus*, and *A. thaliana*, and hydroxy fatty acid (C18:0-OH) in castor bean (*R. communis*), among others (Roscoe et al., 2015). From an application standpoint, these FA impart specific characteristics that make these oils suitable for use across various industries. Consequently, such plants offer unique gene pools that could be leveraged to modify or manipulate conventional oil crops.

To achieve this objective, it is crucial to gain in-depth insights into the metabolic pathways governing plant oil production, including the involved genes and their regulatory mechanisms. Therefore, fatty acid synthesis and modification (elongation and desaturation), as well as TAG synthesis and accumulation, are presented and discussed in the subsequent sections.

3.1. Fatty acids synthesis

The synthesis of FAs, primarily occurring in plastids, serves as the cornerstone of plant oil production pathways. As illustrated in **Figure 4**, the process commences with the carboxylation of acetyl-CoA, leading to the formation of malonyl-CoA. It is noteworthy that acetyl-CoA is synthesized differently in photosynthetic (e.g., leaves) and non-photosynthetic (e.g., fruits and seeds) plant tissues (Li-Beisson et al., 2016). In photosynthetic tissues, acetyl-CoA is produced in chloroplast stroma through the fixation of CO$_2$ into triose-phosphates (TP) via the Calvin cycle (**Fig. 4a**). These TPs are subsequently converted into pyruvate and eventually acetyl-CoA through the glycolysis pathway (Tang et al., 2022). Alternatively, TPs may be directed into the starch synthesis pathway (Xu et al., 2024) (**Fig. 4a**).

In contrast, sucrose acts as the precursor for acetyl-CoA synthesis in non-photosynthetic tissues. However, as sucrose cannot enter plastids where acetyl-CoA is synthesized, it undergoes cleavage into its constituent components by invertases or sucrose synthases. The resulting hexoses are then converted into hexose phosphates (i.e., glucose 6-phosphate and fructose 6-phosphate) (Xu et al., 2024). These hexose phosphates undergo
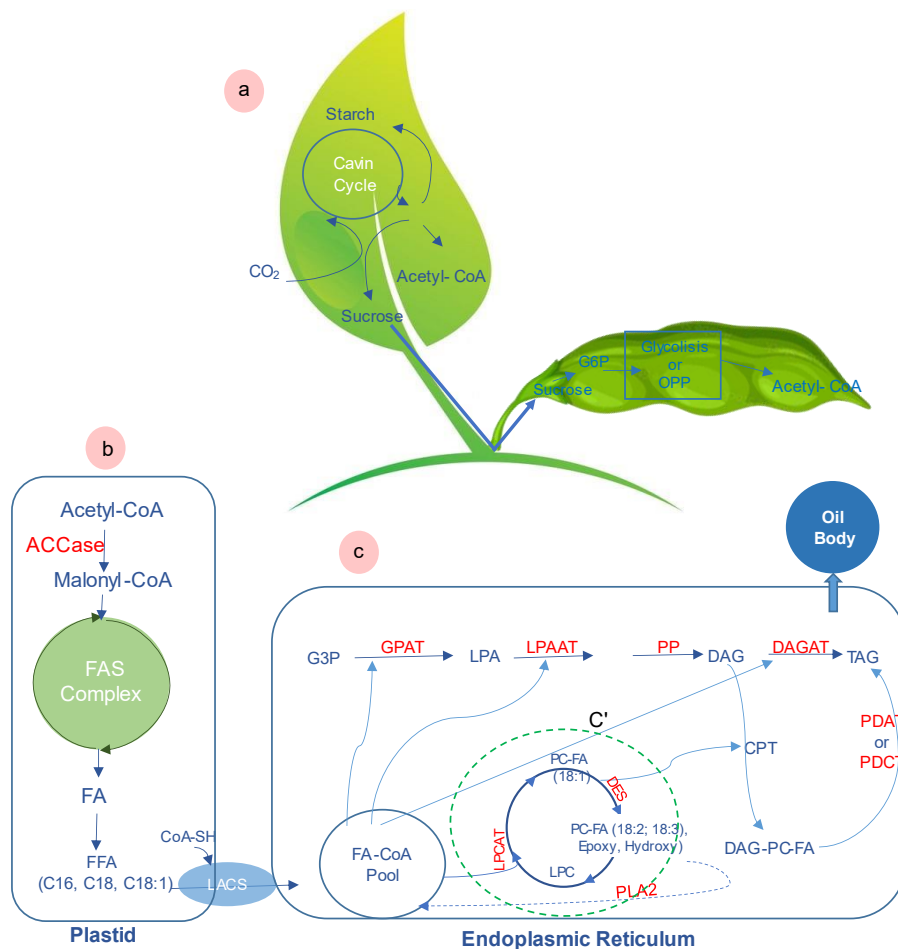
Fig. 4. Overview of major reactions involved in fatty acid and triacylglycerol synthesis. (**a**) Glycolysis is used to make proteins, storage starches, or lipids from absorbed carbohydrates from photosynthesis. Sucrose is transported from photosynthetic tissues into developing seeds, where it is metabolized into precursors such as glucose 6-phosphate and phosphoenolpyruvate in the cytosol of embryo and/or endosperm cells before being transferred to plastids for fatty acid synthesis.; (**b**) De novo fatty acid production and modification: the precursors for the synthesis of C8–C18 saturated fatty acyl-ACPs on a plastidial multienzyme fatty acid synthetase complex include acetyl-CoA and malonyl-CoA. Unsaturated and monounsaturated fatty acids are transported from plastids to the endoplasmic reticulum for further processing by an acyl-CoA transporter (ACT). (**c**) TAG synthesis. A complex process combining successive acylation of a glycerol moiety and substantial acyl editing via phosphatidylcholine-dependent desaturases or desaturase-like enzymes results in triacylglycerols. *Abbreviations:* TP: Triose phosphate; G6P: Glucose 6- phosphate; OPP: Oxidative pentose phosphate; Pyr, pyruvate; ACCase, acetyl-CoA carboxylase; FAS, FA synthase; FA, fatty acid; FFA, Free Fatty Acid; CoA, coenzyme A; LACS, Long Chain acyl-CoA Synthetase; G3P, Glycerol 3-phosphate; GPAT: G3P acyltransferase; LPA: lysophosphatidic acid; LPAAT: lysophosphatidic acid acyltransferase; PA: phosphatidic acid; PP: phosphatase; DAG: diacylglycerol; DAGAT: DAG acyltransferase; TAG: triacylglycerol; DGAT: diacylglycerol acyl trans acylase; PDAT: phosphatidylcholine-dependent acyltransferase; PDCT: phosphatidylcholine: diacylglycerol choline phosphotransferase; PC: phosphatidylcholine; PLA2: phospholipase A2; LPC: Lys phosphatidylcholine; LPCAT: Lys phosphatidylcholine acyltransferase; DES: Desaturase; CPT: CDP-choline: DAG choline phosphotransferase.

further conversion into various intermediates, such as phosphoenolpyruvate and malate, through the glycolysis and/or the oxidative pentose phosphate (OPP) pathway before being transported into plastids for acetyl-CoA production (Seliniski and Scheibe, 2019; Bu et al., 2023).

In the subsequent step, the pivotal reaction catalyzed by acetyl-CoA carboxylase (ACCase) results in the formation of malonyl-CoA, the building block of the FA synthesis pathway, via acetyl-CoA carboxylation (**Fig. 4b**). The fatty acid synthase enzyme complex (including 3-ketoacyl-ACP synthase of type III, type I, and type II, or KASIII, KASI, and KASII, respectively, as well as acyl-ACP thioesterases, FAT A or FAT B) then utilizes malonyl-CoA to synthesize FAs ranging from 4 to 18 carbons in length (Bates et al., 2013). Initially, KASIII catalyzes the condensation, yielding C4:0 FAs. Subsequent condensation reactions are carried out by KASI, producing FAs up to C16:0. Finally, KASII facilitates the final steps of FA elongation from C16:0 to C18:0 (Manan et al., 2017). FAT A or FAT B plays a crucial role in determining the chain length of the synthesized FAs within the enzyme complex (Liu et al., 2022a and b). Notably, the accumulation of medium-chain FAs, such as C10:0 and C12:0, involves the presence of evolved FAT A or FAT B, capable of premature hydrolysis of the growing acyl thioesters. Considering the significant role of acetyl-CoA in the overall FA synthesis pathway, the reaction it is involved in is regarded as a major rate-limiting step (He et al., 2020).

Furthermore, FA ranging from C8:0–C18:0 may undergo unsaturation catalyzed by fatty acid desaturases (FADs), specifically FAD6, 7, and 8 (Manan et al., 2017), while still within plastids (Elahi et al., 2016). The resulting saturated and monounsaturated FAs in the C8–C18 range are transported as acyl-CoAs to the endoplasmic reticulum (ER) for further modification and elongation (Bu et al., 2023; Fell et al., 2023).

Continued FA elongation in the ER involves a series of reactions utilizing cytosolic malonyl-CoA and imported acyl-CoA (Bu et al., 2023; Fell et al., 2023). These reactions are catalyzed by an ER-specific fatty acid elongation complex comprising four enzymes: 3-ketoacyl-CoA synthase, 3-ketoacyl-CoA reductase, 3-hydroxyacyl-CoA dehydrase, and enoyl-CoA reductase (Bu et al., 2023; Fell et al., 2023). This enzymatic complex facilitates the production of FAs up to C24. Additionally, Fatty acid desaturase 2 (FAD2) and Fatty acid desaturase 3 (FAD3) are responsible for sequential desaturation reactions occurring in the ER, leading to the formation of polyunsaturated FA (Manan et al., 2017).

3.2. Triacylglycerol biosynthesis

TAG synthesis generally occurs through a series of reactions known as the Kennedy pathway, located in the endoplasmic reticulum (ER) (Kim, 2020) (**Fig. 4c**). This pathway initiates with the introduction of glycerol-3-phosphate (G3P), which is sequentially acylated by acyl-CoAs of chloroplast origin (Schmid, 2021). G3P is generated from dihydroxyacetone phosphate (DHAP) through a reaction catalyzed by glycerol-3-phosphate dehydrogenase (G3PDH) (Kim, 2020). The enzymes involved in this sequential acylation process include glycerol-3-phosphate acyltransferase (GPAT), lysophosphatidic acid acyltransferase (LPAAT), and diacylglycerol acyltransferase (DGAT) (Li et al., 2015a). Prior to the third acylation by DGAT, a dephosphorylation step is necessary, which is catalyzed by phosphatidic acid phosphatase (PAP) (Kim, 2020; Lutkewitte and Finck, 2020).

It is noteworthy that TAG biosynthesis may involve additional complexities beyond the traditional Kennedy pathway. For instance, acyl-CoAs could also be supplied from membrane lipid phosphatidylcholine (PC) through alternative pathways. Acyl-CoAs may be incorporated or released from PC through a series of reactions known as acyl editing reactions, catalyzed by lyso-PC acyltransferase (LPCAT). Alternatively, a reaction catalyzed by phospholipase A2 (PLA2) may result in the release of free FA, which can then be acylated to form acyl-CoA (Lutkewitte and Finck, 2020; Schmid, 2021) (**Fig. 4c**).

Another alternative pathway complicating TAG biosynthesis is the incorporation of diacylglycerol (DAG) into phosphatidylcholine (PC), catalyzed by choline phosphotransferase (CPT) (Kim, 2020). The existing acyl groups can be desaturated by fatty acid desaturase (FAD). These PC-incorporated DAG molecules can then be acylated into TAG through reactions catalyzed by phospholipid: diacylglycerol acyltransferase (PDAT) or PC:DAG phosphocholine transferase (PDCT) (Kim, 2020). It is important to note that the reaction catalyzed by CPT is reversible, allowing

DAG to be released at later stages and converted into TAG through the catalytic action of DGAT (Eichmann and Lass, 2015).

3.3. Triacylglycerol storage

Upon completion of TAG biosynthesis, TAGs are stored within oil bodies (OBs), also known as oleosomes, ranging from 0.2 to 2.5 µm (Lutkewitte and Finck, 2020). The structure of OBs comprises a stabilizing monolayer of phospholipids containing proteins such as oleosins, caleosins, stereoleosins, and aquaporins (Lutkewitte and Finck, 2020). Among these proteins, oleosins, being the most abundant, play pivotal roles in the TAG storage capacity of various plant tissues and across different plant species. Indeed, the absence of these proteins in vegetative tissues is the reason behind their inability to store lipids (Xu et al., 2024). Mechanistically, these proteins prevent the coalescence of oil bodies during storage through steric hindrance and electronegative repulsion, thus determining the final size of the OBs (De Chiriko et al., 2018; Kanai et al., 2019). For example, Hu et al. (2009) suggested that a low concentration of oleosins is associated with the formation of larger OBs and, consequently, lower oil contents.

4. Genetic engineering for improved oil production

In recent decades, researchers have devoted significant attention to enhancing the quality and quantity of seed oils for both food and non-food purposes, as well as exploring new oil sources (Subedi et al., 2020a and b; Bhati et al., 2021; Chen et al., 2021a; Sheri et al., 2021). The fatty acid composition of plant oils plays a crucial role in determining their quality and suitability for various applications, primarily by distinguishing between saturated and unsaturated FA. Saturated FA lack double bonds in their carbon structure and exhibit a linear configuration, whereas unsaturated FA contain at least one double bond in their carbon chains.

Vegetable oils with a higher monounsaturated-to-saturated fatty acid ratio demonstrate improved stability under high-temperature conditions, such as during frying, and exhibit prolonged shelf life when stored. In oils intended for human consumption, cooking oils typically contain higher proportions of monounsaturated FA, such as oleic acid, while salad oils predominantly comprise polyunsaturated FA like linoleic and α-linolenic acids (Kapoor et al., 2021; Saini et al., 2021). To meet the increasing demand for oils, whether for human consumption or other applications like biofuels, metabolic and genetic engineering techniques, including the utilization of recombinant DNA technology, have been employed to manipulate oil content in plants and broaden the range of oil varieties (**Fig. 5**). **Table 12** provides an overview of the fatty acid composition in various plants and vegetable oils.

4.1. Metabolic engineering to enhance oil production

Augmenting oil production in seeds has long been a primary objective for both plant breeders and genetic engineers (Subedi et al., 2020a and b; Bhat et al., 2022; Rauf et al., 2023). Oilseed crops inherently possess higher seed oil content compared to other agriculturally significant crops. However, there exists considerable variation among oilseed crops themselves, with oil content ranging from 20% in soybeans to 60% in sesame, despite similarities in their lipid biosynthesis pathways (Zafar et al., 2019). Remarkably, a mere 1% improvement in soybean oil production per hectare could contribute over USD 1 billion annually to the crop's global value (Bates et al., 2014), emphasizing the profound impact of metabolic engineering in oilseed crops, with the potential to significantly enhance seed oil contents.

Metabolic engineering broadly aims to regulate flux into metabolic pathways by either increasing the availability of upstream substrates or strengthening the sink in the final stages of the pathway. Both strategies have been harnessed to increase seed oil accumulation. In the case of oilseeds, yield improvements can be achieved by increasing the amount of oil per seed, enlarging the size of the seed, or boosting the number of seeds per plant. Strategies to enhance oil production in plants include enhancing the availability of fatty acid (FA) precursors, elevating the rate of FA synthesis, improving TAG assembly processes, and restricting TAG degradation pathways (He et al., 2020; Subedi et al., 2020a and b; Kapoor et al., 2021). In the following section, we review the application of metabolic engineering for the improvement of oil content and its quality.
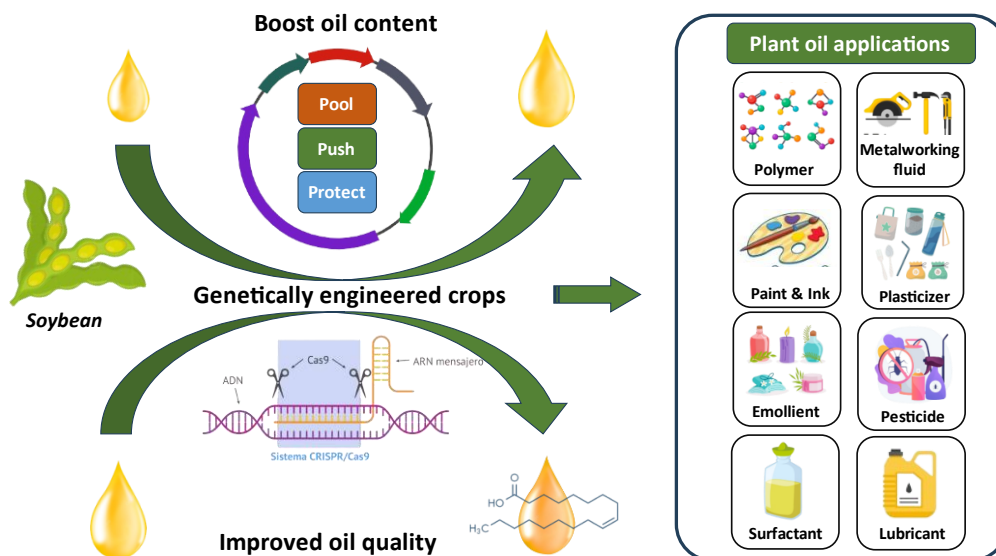
Fig. 5. Genetic engineering of plant oils for different applications.

Table 12.
Fatty acid composition of plants and vegetables.

Plant	Fatty acid composition (%)																			Reference
	Saturated fatty acids										Unsaturated fatty acids										
	Caprylic 8:0	capric 10:00	Lauric 12:00	Myristic 14:0	Palmitic 16:0	Stearic 18:0	Arachidic 20:0	Behenic 22:0	Lignoceric 24:0	Cerotic 26:0	myristoleic 14:1	Palmitoleic 16:1	Sapienic 16:1	Oleic 18:1	Linoleic 18:2	α-linolenic 18:3	Eicosenoic 20:1	Erucic 22:1	Others	
Avocado	-	-	-	0.33	23.6	1	-	-	-	-	-	3.58	-	47.2	13.4	0	-	-	11.7	Moreno-Camacho et al. (2019)
Castor bean	-	-	-	-	1	1	-	-	-	-	-	-	-	3	4	trace	-	-	91	Aid (2020)
Cocoa butter	-	-	0-1	0-4	24.5-33.7	33.7-40.2	1	-	-	-	-	0-4	-	26.3-35	1.7-3	trace	-	-	-	Naik and Kumar (2014)
Coconut	8	7	49	8	8	2	-	-	-	-	-	-	-	6	2	0	-	-	-	Boateng et al. (2016)
Corn	-	-	-	-	6.7-16.5	0.7-6.6	0-1	-	-	-	-	-	-	16.2-43.8	39.5-69.5	0-3.1	-	-	-	White (2007)
Linseed	-	-	-	-	5--6	4--5	-	-	-	-	-	-	-	15-20	14	50-55	-	-	-	Aid (2020); Bayrak et al. (2010)
Olive	-	-	-	-	7.5-20	0.5-5	0-0.8	0-0.2	0-1	-	-	0.3-3.5	-	55-83	3.5-21	0-1.5	-	-	-	Tsimidou et al. (2003)
Palm	-	-	0.2	1.1	44	4.5	0.1	-	-	-	-	-	-	39.2	10.1	0.4	-	-	-	Mancini et al. (2015)
Palm kernel	3.3	3.5	47.8	16.3	8.5	2.4	0.1	-	-	-	-	-	-	15.4	2.4	-	-	-	-	Mancini et al. (2015)
Rapeseed	-	-	-	-	3.63	2.32	-	-	-	-	-	-	-	85.31	3.41	4.4	0.94	-	-	Guan et al. (2016)
Soybean	-	-	-	-	10	4	-	-	-	-	-	-	-	18	55	13	-	-	-	Clemente and Cahoon (2009)
Sunflower	-	-	-	-	6	5	-	-	-	-	-	-	-	19	68	trace	-	-	-	Aid (2020)
Cottonseed	-	-	-	-	25.39	2.33	-	-	-	-	1	0.6	-	16.35	52.89	-	-	-	-	Yang et al. (2019)

Table 12.
continued.

Plant	Saturated fatty acids										Unsaturated fatty acids									Reference
	Caprylic 8:0	capric 10:00	Lauric 12:00	Myristic 14:0	Palmitic 16:0	Stearic 18:0	Arachidic 20:0	Behenic 22:0	Lignoceric 24:0	Cerotic 26:0	myristoleic 14:1	Palmitoleic 16:1	Sapienic 16:1	Oleic 18:1	Linoleic 18:2	α-linolenic 18:3	Eicosenoic 20:1	Erucic 22:1	Others	
Almond	-	-	-	-	5.07-6.78	-	-	-	-	-	-	-	-	57.54-73.94	19.32-35.18	0.04-0.1	-	-	-	Sathe et al. (2008)
Flaxseed	-	-	-	-	4.9-8	2.44-4.59	-	-	-	-	-	-	-	13.44-19.39	12.25-17.44	39.9-60.42	-	-	-	Goyal et al. (2014)
Hempseed	-	-	-	-	6	3	1	0.44	0.197	-	-	0.098	-	16	55	15	-	-	3.265	Sova et al. (2018)
Walnut	-	-	-	-	5.61-5.82	-	-	-	-	-	-	-	-	22.62-27.27	49.93-54.41	14.32-17.82	-	-	-	Dogan and Akgul (2005)
Rice bran	-	-	-	0.3	22.7	1.8	0.9	-	-	-	-	-	-	43.9	29.2	1.25	-	-	-	Latha and Nasirullah (2014)
Pumpkin seed	-	-	-	0.233	14.82	6.67	0.433	0.058	-	-	-	-	-	25.81	-	50.88	-	0.055	1.041	Bardaa et al. (2016)
Sesame	-	-	-	-	7.9-12	4.8-6.1	-	-	-	-	-	-	-	35.9-42.3	41.5-47.9	-	-	-	-	Wacal et al. (2019)
Peanut	-	-	-	-	8.2-15.1	1.1-7.2	0.8-3.2	1.8-5.4	0.5-2.5	-	-	-	-	31.5-60.2	19.9-45.4	-	0.6-2.6	-	-	Hammond et al. (1997)
Grapeseed	-	-	-	-	8.4-6.51	3.86-3.07	-	-	-	-	-	-	-	16.1-11.62	77.59-72.5	-	-	-	-	Al Juhaimi et al. (2017)
Beech nut	-	-	-	0.18	10.2	5.81	0.47	0.61	-	-	-	0.25	-	37.2	34.1	4.1	5.63	0.83	0.27	Ayaz et al. (2011)
Macadamia	-	-	-	-	9	2	-	-	-	-	-	22	-	60	2	-	-	-	-	Tan et al. (2020)
Hazelnut	-	-	-	-	4.39-8.85	1.67-3.18	-	-	-	-	-	-	-	73.48-81.57	10.46-14.95	0.02-0.34	-	-	-	Balta et al. (2006)
Cashew	-	-	-	0.01	10.3	8.8	0.14	0.13	0.14	0.01	-	0.37	-	61.8	17.3	0.14	-	0.01	0.43	Griffin and Dean (2017)
Pecan	-	-	-	0.4	6.012	-	-	-	-	-	-	-	-	23.91	66.81	1.83	-	-	-	Rivera-Rangel et al. (2018)
Orange seed	-	-	2.96	0.89	12.6	8.9	0.54	-	-	-	-	-	-	43.03	25.11	4.3	0.67	-	-	Iwuagwu et al. (2018)
Citrus seed	-	-	-	-	25.8-32.2	2.8-4.4	-	-	-	-	-	-	-	21.9-24.1	36.1-39.8	3.4-4.4	-	-	-	Reazai et al. (2014)
Watermelon	-	-	-	-	9.88	6.96	0.26	-	-	-	-	-	-	14.25	68.07	-	-	-	-	Rezig et al. (2019)
Argan	-	-	-	-	11--14	4--7	-	-	-	-	-	-	-	46-48	31-35	-	-	-	-	Charrouf and Guillaume (2008)
Mustard	-	-	-	-	1.87	1.52	1.13	1.4	0.41	-	-	-	0.1	15.7	12.99	6.18	-	48.8	9.83	El-Shenawy et al (2014)
Ben	0.03	-	-	0.12	6.25	4.97	3.23	6.02	0.36	0.92	-	-	-	73.57	0.46	-	-	0.11	1.88	Leone et al. (2016)
Eucalyptol	-	-	-	-	36	3	-	-	-	-	-	7.3	-	27.2	19.3	-	-	-	3.6	Rekkab et al. (2012)
Thyme	0.52	0.15	0.18	1.07	12.07	6.15	-	-	-	-	-	2.3	-	33.04	41.73	0.61	-	-	2.18	Attia et al. (2017)

4.1.1. Increasing the content of oil per seed

As mentioned previously, TAG biosynthesis involves three primary metabolic steps: glycolysis, FA synthesis, and TAG production (Yang et al., 2022b). Glycolysis, as the initial step in TAG synthesis, provides the carbon resources necessary for TAG production. Metabolic engineering strategies aimed at increasing oil accumulation in plants may involve promoting the production of precursors for lipid synthesis (e.g., G3P and acetyl-CoA), enhancing the rate of FA synthesis, increasing TAG assembly, and inhibiting TAG degradation pathways (Xu et al., 2024).

Augmenting FA accumulation is achievable through various approaches, including increasing the carbon flux towards FA synthesis, overexpressing transcriptional regulators in FA synthesis, promoting the expression of ACCase, the pivotal enzyme in plastid FA synthesis, suppressing competing pathways for FA utilization (e.g., membrane lipid synthesis), and enhancing the allocation of carbon for FA synthesis by limiting starch synthesis (Mulgund, 2022; Ranjbar and Malcata, 2022).

The lipid metabolic pathways in plants are highly intricate, involving at least 120 enzymatic reactions and over 600 genes (Lee et al., 2017; Vanhercke et al., 2019). However, physiological and developmental factors can influence oil biosynthesis in plants (Li et al., 2020a; Yang et al., 2022b).

Additionally, regulatory pathways governing carbon flux to storage and membrane lipid biosynthesis remain incompletely understood (Li et al., 2020b; Yang et al., 2022b). Therefore, a comprehensive understanding of the complex networks of oil biosynthesis and its regulatory framework in plants can aid in identifying and engineering key genes involved in increasing oil content (Savadi et al., 2017).

4.1.1.1. FA synthesis (Carbon flux redirection)

Increasing seed oil content necessitates redirecting carbon flux towards fatty acid biosynthesis, as it can significantly impact TAG production (Muñoz et al., 2021; Song et al., 2023). Genes encoding enzymes associated with the FA biosynthetic pathway are key targets for genetic modification (Savadi et al., 2017). However, it is important to note that attempts to enhance the availability of precursors for FA synthesis by altering central carbon metabolism have not always been successful, as flux control in a pathway typically involves multiple components rather than individual enzymes (Song et al., 2023).

ACCase, the rate-determining enzyme governing FA biosynthesis, has been extensively studied in various model plants (Wan et al., 2017a). ACCase catalyzes the production of malonyl-CoA, providing two carbon units to the FA synthase complex. Overexpression of the cytosolic multifunctional form of ACCase in the plastids of rapeseed led to a modest increase in seed lipid content (Zhukov and Popov, 2022). Conversely, overexpression of the gene encoding the biotin carboxyl carrier protein 2 (BCCP2), a component of plastidial ACCase, resulted in decreased seed oil content and increased levels of sugar and protein (Zhukov and Popov, 2022), indicating that ACCase activity is not the sole limiting factor in FA synthesis (Savadi et al., 2017).

Mitochondrial pyruvate dehydrogenase (PDH), responsible for converting pyruvate and coenzyme A (CoA) into acetyl-CoA, is regulated negatively by pyruvate dehydrogenase kinase (PDHK). Repression of PDHK activity through antisense RNA technology during seed maturation has been shown to enhance seed oil content and seed weight in *A. thaliana* (Subedi et al., 2020a and b). Silencing the Pyruvate dehydrogenase kinase cDNA (AtPDHK) gene using RNAi technology increased seed oil in transgenic plants by up to 50%, altering fatty acid composition (Schewender and Hey, 2012). Additionally, pyruvate, a key product of glycolysis, serves as a major carbon source for fatty acid production in plastids (Schewender and Hey, 2012). Seed-specific overexpression of a pyruvate transporter, BASS2, increased oil production by 24-43% in transgenic Arabidopsis compared to wild-type plants (Lee et al., 2017), highlighting the potential of promoting oil biosynthesis by enhancing pyruvate flux into plastids.

4.1.1.2. Glycerol backbone

G3P plays a critical role in regulating the production and retention of TAGs in plant tissues. However, G3P supply has been shown to be insufficient to maintain high G3P levels during the peak oil accumulation period in oilseed crops (Pollard and Hill, 2021).

G3P is generated in plants through two distinct enzymes: cytosolic glyceraldehyde 3-phosphate dehydrogenase (GAPDH) and glycerol kinase (GK) (Jeelani et al., 2023). Glycerol kinase converts glycerol into G3P, primarily in germinating seeds, while cytosolic GAPDH catalyzes the conversion of dihydroxyacetone phosphate (DHAP) into G3P in various plant tissues, including seeds. Genetic modification to enhance G3P levels has been successful in boosting seed oil content. For instance, the seed-specific expression of yeast cytosolic GAPDH in *B. napus* resulted in a 3-4-fold increase in G3P levels and a 40% increase in seed oil content. Similarly, engineering *C. sativa* by co-expressing *A. thaliana* diacylglycerol acyltransferase1 (DGAT1) and yeast cytosolic GAPDH led to a 13% increase in seed oil content and up to a 52% increase in seed mass compared to wild-type plants (Chhikara et al., 2018). Moreover, overexpression of DGAT1 in transgenic tobacco plants resulted in a 2.19-fold increase in oil content compared to non-transgenic control lines (Chenarani et al., 2022).

4.1.1.3. TAG biosynthesis

TAGs in plants are synthesized through the Kennedy pathway in the ER via a sequential acylation of G3P by membrane-bound glycolipid acyltransferases. These enzymes include GPAT, LPAAT, and diacylglycerol acyltransferase (DGAT) (Chenarani et al., 2022).

The first acylation of G3P is carried out by GPAT, which produces lysophosphatidic acid in the ER, chloroplast (CHP), or mitochondria (MIT). LPAAT, located in the ER, CHP, MIT, plasma membrane (PM), and cytoplasm (CP), performs the second acylation of lysophosphatidic acid to generate phosphatidic acid. DGAT completes the final step in the Kennedy pathway by converting diacylglycerol (DAG) into TAG (Wan et al., 2017a). Since these enzymes are rate-limiting in TAG synthesis, researchers have explored genetic modifications to enhance LPAAT, GPAT, and DGAT activity in plants. Among these, DGAT is considered a critical rate-limiting step due to its comparatively lower enzyme activity compared to the other enzymes in the pathway (Wan et al., 2017a).

Enhancing GPAT and LPAAT activity has proven effective in increasing seed oil content. Arabidopsis genetically engineered to express plastidial safflower GPAT and E. coli GPAT exhibited increased seed oil content during seed maturation (Wan et al., 2017b). Similarly, the expression of genes from *B. napus* encoding microsomal LPAAT isoforms in *Arabidopsis* seeds unexpectedly increased seed total FA content and seed weight (Zhang et al., 2022). Furthermore, the expression of a mutant yeast LPAAT gene (SLC1-1) under the control of the CaMV35S promoter in Arabidopsis and high-erucic acid *B. napus* resulted in a 48% increase in seed oil content (Wan et al., 2017b).

4.1.1.4. Lipid transfer proteins

Lipid transfer proteins (LTPs), also known as plant lipid transfer proteins (PLTPs), are small, compact proteins with a hydrophobic cavity that facilitates the transfer of phospholipids and FA between cell membranes (Getz, 2018). Known for nearly half a century, LTPs are divided into two structurally related subfamilies based on their molecular weights: LTP1s (9 kDa) and LTP2s (7 kDa) (Fan et al., 2013).

Puroindoline A and B (PINA and PINB) proteins exhibit a structure similar to that of non-specific lipid-transfer proteins found in plants (Zhang et al., 2019b). Heterologous expression of wheat (*Triticum aestivum* L.) puroindoline genes (PINA and PINB) in corn plants (*Zea mays* L.) increased the germ size without affecting the seed size. As a result, the overall seed oil content increased by 25%, and the germ yield rose by approximately 34% (Zhang et al., 2019b).

4.1.1.5. Transcription factors (TFs)

In general, the accumulation of seed oil requires coordinated transcriptional control of numerous biosynthetic pathways (Kong et al., 2019; Niu et al., 2020; Yang et al., 2022b). Multiple transcription factors (TFs) play a pivotal role in synchronizing the regulatory networks of genes involved in fatty acid and TAG biosynthesis. These TFs control gene expression by recognizing and binding to specific sequences in gene promoters (Kong et al., 2019; Papadimitriou et al., 2019; Tian et al., 2019; Kumar et al., 2020).

Manipulating TFs represents an alternative strategy for enhancing seed oil yield alongside single-enzyme approaches (Santin et al., 2021; Yang et al., 2022a). Positive TFs, such as LEAFY COTYLEDON genes (LEC1 and LEC2), FUSCA3 (FUS3), ABSCISIC ACID INSENSITIVE3 (ABI3), and WRINKLED1 (WRI1), are known for their pivotal roles in regulating the activities of other TFs involved in seed maturation and oil accumulation (Fatihi et al., 2013; Kumar et al., 2020). However, to regulate the expression of these positive TFs, plants have evolved mechanisms to suppress their expression during the vegetative phase of development. Negative regulators, including TFs, microRNAs (miRNAs), and proteins, act by modulating the chromatin conformation of their target genes (Kumar et al., 2020).

A common strategy for manipulating seed oil content in plants is overexpression of positive regulators such as WRI1, LEC1/2, and MYB96 or suppression of negative regulators like MYB89 and WRKY6. Ideally, genetic engineering should focus on TFs that activate FA and TAG biosynthesis genes. Overexpressing TFs involved in FA synthesis can lead to increased TAG content. For example, overexpressing MYB96, a TF that activates TAG biosynthesis genes DGAT1 and PDAT1, can significantly boost TAG storage in seeds. However, overexpressing certain TFs, chromatin remodeling agents, and miRNAs can have unintended consequences on plant growth, development, and yield. Therefore, tissue-

specific overexpression or silencing of desired genes in transgenic seed oil plants is recommended.

WRINKLED1 (WRI1), belonging to the APETALA 2/ethylene-responsive element binding protein (AP2/EREBP) subfamily of TFs, plays a crucial role in regulating plant oil accumulation by promoting carbon partitioning into FA synthesis within the glycolysis pathway. WRI1 regulates the expression of at least 15 enzymes involved in FA synthesis and the glycolytic pathway, making it an ideal target for genetic manipulation to enhance oil accumulation in plants. Overexpressing transcription factors that regulate WRI1 expression have been shown to increase seed oil content in transgenic plants. For example, overexpressing soybean ZF351 and GmDREBL increased oil content in transgenic Arabidopsis by binding to the WRI1 promoter. Similarly, overexpressing maize ZmLEC1, an activator of WRI1, led to elevated oil content in Arabidopsis, Camelina, and maize, though it had unintended effects on seed germination and leaf growth. Conversely, overexpressing maize ZmWRI1 increased oil content without these side effects. Numerous studies have shown that overexpressing WRI1 or its orthologs significantly boosts seed oil content in transgenic plants. For instance, constitutive expression of WRI1 in Arabidopsis leads to a 10% to 40% increase in seed oil content and an increase in seed size.

Selecting an appropriate promoter to drive WRI1 expression is critical for genetically engineering oil accumulation in the seeds of transgenic plants. For instance, using the FUS3 or Oleosin promoter to drive WRI1 can increase seed oil content, while using the ZEIN promoter does not result in distinguishable changes in oil content. Table 13 shows the transcription factors and their overexpression on oil content.

4.2. Increasing seed oil content by enhancing seed size

Both genetic and environmental factors shape the final weight and dimensions of plant organs during growth and development. In oilseed crops, seed size significantly impacts crop productivity and yield. Thus, increasing seed size and biomass emerges as a strategy to enhance oilseed crop yield. However, it is crucial to consider that augmenting seed weight might necessitate a reduction in seed numbers due to limited assimilation, potentially affecting seed filling. Furthermore, altering seed oil levels can have repercussions on total seed protein and *vice versa* when working with fixed assimilates. Hence, the key aspect in boosting oilseed plant yield is ensuring genetic manipulation does not adversely affect seed numbers. Redirecting carbon flux toward oil production rather than protein becomes imperative in this regard.

Research on seed size regulation has identified around 88 key regulators responsible for organ size, associated with pathways like KLUH, ubiquitin-proteasome, G-protein signaling, Mitogen-Activated Protein Kinase (MAPK), and plant hormone pathways. Enhancing seed oil content involves expressing genes related to seed development, embryo size, and oil storage tissues in crops such as Arabidopsis, maize, and rice. One approach is to increase oil-carrying tissues while minimally altering non-oil-carrying seed tissues. For instance, enhancing seed oil content in the endosperm, a novel storage tissue in plants, is a viable strategy. These insights into seed size regulation and oil content enhancement pave the way for improving oilseed crop productivity and yield.

Seed size regulation involves a complex interplay of factors, such as plant hormones, ubiquitin, microRNAs, and cytochrome P450s (CYPs). The CYP78A subfamily, a plant-specific gene family, plays a crucial role in controlling plant growth and organ size. Various subfamilies of CYP78A identified in Arabidopsis, rice, wheat, tomato, and soybean regulate organ size and development. Overexpressing CYP78A genes in different plant species has demonstrated significant effects on seed size and organ development.

Additionally, genes and regulatory elements like SWEET, BS1, LEC1, ARF2, DA1, DA2, Abscisic acid biosynthesis-related genes (ABA2 and ABI5), TTG2, AP2, RING-type E3 ubiquitin ligases, Enhancer of DA1 (EOD1), and miRNA172 impact seed size through diverse mechanisms. Enhancing the sink strength of seed oil can increase the number of oil-storing bodies in seeds. Elevating the oleosin protein content in developing seeds enhances oil storage capacity and promotes oil biosynthesis and storage in oil bodies, consequently increasing seed oil content.

Overexpressing oleosin genes has proven effective in increasing seed oil content in plants like Arabidopsis and rice. Achieving embryo-specific overexpression of the appropriate oleosin gene is crucial to augmenting seed oil content without unintended effects. Moreover, transcription factor

ARF2, responsive to auxin, acts as a repressor of cell division, elongation, and organ growth. Mutations in ARF2 can lead to enlarged seed size and weight. Tissue-specific expression of wild-type ARF2 restores normal flower morphology and fertility, underscoring its role in seed setting. Similarly, overexpression of WRI1, a member of the AP2/EREBP family, has been shown to increase seed size in transgenic plants. These findings shed light on the intricate regulatory mechanisms governing seed size and oil content in plants, offering avenues for enhancing crop productivity and yield.

4.3. Genetic Engineering for new oil resources: biomass-derived oil

In addition to traditional plant seeds and fruits, various plant tissues can synthesize TAG or plant oils. This capability has spurred research into genetic engineering strategies to increase oil content in leaves and other vegetative tissues of high biomass crops in an environmentally sustainable manner. Such modified plant biomass can serve as an energy-dense, nutritionally valuable resource suitable for electricity production, biodiesel, renewable fuel production, and nutritionally enhanced animal feed.

Vegetative plant organs typically contain around 1.5% TAG and 5-10% FAs on a dry weight basis, making TAG an essential buffer and intermediate storage pool for toxic and excess FAs released during membrane fatty acid turnover. Despite this, accumulating high levels of TAG in vegetative tissues similar to oilseeds is challenging due to the complex nature of its biosynthetic pathways.

Metabolic engineering studies in model plants have suggested that crops with a 15% improvement in biomass oil content could produce up to ten times more oil per unit area compared to canola oilseed crops. Early efforts focused on the overexpression or downregulation of individual genes involved in FA or TAG biosynthesis, resulting in only modest increases in TAG content in vegetative tissues. Recent approaches have combined multiple metabolic engineering strategies to achieve higher TAG levels in plant biomass.

1. **Triacylglycerol assembly (Pull) approach:** This strategy involves targeting the TAG assembly process to increase the demand for precursors that influence the flux toward TAG accumulation in plant tissues (Vanhercke et al., 2017; Wan et al., 2017b; Park et al., 2021). Overexpressing TAG assembly enzymes has been suggested as an effective means to boost TAG levels in vegetative tissues (Xu and Shanklin, 2016). For instance, overexpressing Arabidopsis DGAT1 in *N. benthamiana* led to a 20-fold increase in leaf TAG content, while targeted expression of the same gene in xylem tissues resulted in a 63% increase in FAs production (Nookaraju et al., 2014). Additionally, overexpression of Chlamydomonas DGAT2 in Arabidopsis resulted in a 25-fold increase in TAG content and changes in TAG composition (Park et al., 2021; Sagun et al., 2023). Notably, overexpressing PDAT1 in transgenic Arabidopsis plants resulted in a remarkable 28-fold increase in TAG content in the leaves (Fan et al., 2013). Additionally, overexpressing mouse monoacylglycerol acyltransferase 1 (MGAT1) and MGAT2 led to diacylglycerol (DAG) accumulation, which subsequently resulted in approximately 7-9-fold increases in TAG content in transgenic tobacco leaves (Petrie et al., 2012; Sagun et al., 2023).

2. **de novo FAs biosynthesis (Push) approach:** This approach involves manipulating key factors like ACCase, WRI, and transcription factors such as LEC1, LEC2, FUS3, and ABI3 to boost the de novo synthesis of FAs (Weselake, 2016; Xu and Shanklin, 2016; Vanhercke et al., 2017). For example, the heterologous expression of Arabidopsis acetyl-CoA carboxylase (ACC1) in potato plants resulted in a five-fold increase in TAG content in transgenic tubers (Vanhercke et al., 2019; Luo et al., 2022). Overexpression of transcription factors (TFs) such as LEC2 and WRI1 has also been shown to enhance lipid content in leaves (Park et al., 2021; Luo et al., 2022). Constitutive expression of Arabidopsis WRI1 resulted in a 22-fold increase in TAG content in the transgenic vegetative tissues of *Nicotiana benthamiana* (Vanhercke et al., 2019). Interestingly, unlike LEC1 and LEC2, overexpression of WRI1 does not appear to have unintended effects on plant growth and development. Therefore, combining WRI1 overexpression with the regulation of other genes may be an effective approach to achieve a significant increase in oil content in the vegetative tissues of plants (Weselake, 2016; Wan et al., 2017b).

Table 13.
Transcription factors and their overexpression on oil content.

Gene	Function	Host Plant	Reference
WRI1	Increased seed oil and TAG content	*Arabidopsis thaliana*	Sun et al. (2017) Lim et al. (2022), Chen et al. (2020)
		Camelina sativa	An and Suh, (2015)
		Glycine max	Chen et al. (2018), Wang et al. (2022c)
		Zea mays	Pouvreau et al. (2011)
		Oryza sativa	Sun et al. (2017)
		Jatropha curcas	Ye et al. (2018)
LEC1	Increased seed oil content	*Brassica napus*	Elahi et al. (2016)
		A. thaliana	Zhu et al. (2018)
		C. sativa	Zhu et al. (2018)
		Z. mays	Shen et al. (2010)
LEC2	Increased seed oil content	*A. thaliana*	Manan et al. (2017)
	TAG accumulation in leaves		Kim et al. (2015)
FUS3	TAG accumulation in vegetative tissues	*A. thaliana*	Zhang et al. (2016)
ABI3	Increased oil accumulation in leaves	*A. thaliana*	Yang et al. (2021)
DOF-type factors		*Gossypium hirsutum*	Su et al. (2017)
GLABRA2	Increased seed oil content	*A. thaliana*	Chai et al. (2010)
Basic leucine zipper (bZIPs)	Elevated seed oil content	*A. thaliana*	Song et al. (2013)
MYB TFs	Increased seed oil content	Arabidopsis and Lotus	Li et al. (2017), Khan et al. (2019)
	Improved seed oil	*C. sativa*	Kim et al. (2019)
SPT	Correlation with seed oil content	*A. thaliana*	Liu et al. (2017)
G-protein γ subunit 3 (AGG3)	Increased seed size	*C. sativa*	Roy Choudhury et al. (2014)
Purple acid phosphatase 2 (PAP2)	Increased seed size	*C. sativa*	Zhang et al. (2012)
RNAi suppression of AGPase	Increased seed size	*C. sativa*	Na et al. (2018)
CYP78A	Increased seed size	*A. thaliana*	Fang et al. (2012)
	Increased seed size	*O. sativa*	Xu et al. (2015)
	Increased seed size	*C. sativa*	Holz and Dormann (2021)
	Increased seed size	*Nicotiana tabaccum*	Tian et al. (2016)
GmSWEET10a	Correlation with seed size	*B. napus, G. hirsutum*	Shi et al. (2019) Sun et al. (2017)
	Simultaneous increases in seed size and oil content	*G. max*	Wang et al. (2020b)
BIG SEEDS1 (BS1)	Increased seed size and weight	*G. max*	Ge et al. (2016)
BIG SEEDS1 (SHB1)	Increased seed size	*Brassica juncea* *A. thaliana, G. max*	Savadi et al. (2015) Ge et al (2016)
KLUH	Increased seed size	*A. thaliana, G. max*	Adamski et al. (2009) Zhao et al. (2016)
IKU2	Increased seed size	*A. thaliana*	Fatihi et al. (2013)
AUXIN RESPONSE FACTOR 2 (ARF2)	Increased seed size	*A. thaliana*	Schruff et al. (2006)
DA1	Increased seed size	*A. thaliana*	Li et al. (2008)

3. **Triacylglycerol protection (Protect) approach:** TAG from mobilization and β-oxidation of FAs in peroxisomes, or by efficient packaging, can help increase TAG content in plant tissues (Vanhercke et al., 2019). This approach can be achieved through various means, such as overexpressing oleosin proteins or disrupting specific factors like SUGAR-DEPENDENT1 (SDP1) or CGI58 and CGI58-like proteins (Sagun et al., 2023). For instance, RNA interference (RNAi) knockdown of PfeSDP1 resulted in a 12%–16% increase in seed weight and a 14%–19% increase in total seed oil content in *Physaria fendleri* (Azeez et al., 2022). Suppression of the peroxisomal ABC transporter 1 (PXA1), which plays a role in fatty acid uptake into peroxisomes, increased TAG levels by about 1.8% in the dry weight of leaves (Vanhercke et al., 2017). Furthermore, a T-DNA insertional mutation in CGI58 resulted in a ten-fold higher TAG content compared to wild-type Arabidopsis plants (Yurchenko et al., 2017). An alternative approach to safeguarding TAG molecules involves overexpressing oleosin proteins to protect oil bodies containing TAG (Zhai et al., 2021). Simultaneous overexpression of OLE1 and PDAT1 resulted in a remarkable 74-fold increase in TAG content while overexpressing PDAT1 alone led to a 28-fold increase in TAG content in the leaves of transgenic Arabidopsis (Fan et al., 2013). Furthermore, ectopically coexpressing oleosin and DGAT1 in Arabidopsis resulted in 2, 3, and 5-fold increases in FAs in mature leaves, senescing leaves, and roots, respectively (Weselake, 2016; Shao et al., 2019). **Figure 6** shows the integrated metabolic engineering strategies to enhance TAG levels in plant biomass. This includes boosting *de novo* fatty acid synthesis in chloroplasts by increasing carbon flux, known as the 'Push' strategy. Additionally, the assembly of FA into TAGs in the endoplasmic reticulum, referred to as the 'Pull' strategy, and TAGs accumulation in oleosomes (oleosin-coated oil bodies) to protect them from degradation, termed the 'Protect' strategy, are used to enhancing oil content in plant biomass. Candidate genes associated with each approach are outlined.
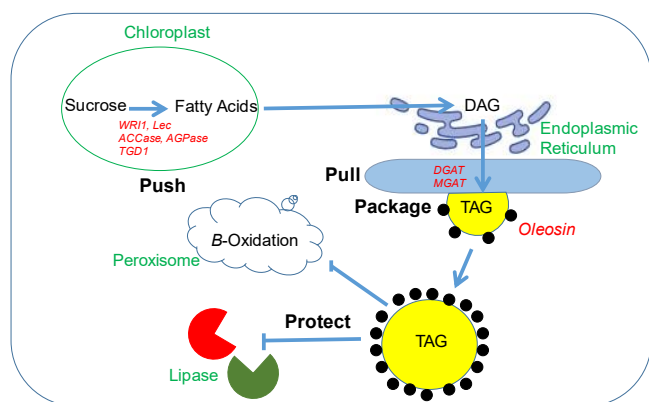

Fig. 6. Integrated metabolic engineering strategies to enhance TAG levels in plant biomass.

4. **Push-pull-protect:** A combination of strategies to increase FAs biosynthesis (Push), TAG assembly (Pull), and prevent lipid degradation (Protect) has been proposed as a comprehensive approach (Wan et al., 2017b; Park et al., 2021). While manipulating individual genes can enhance TAG accumulation in vegetative tissues, many successful approaches involve modulating two or more genes simultaneously (Weselake, 2016; Wan et al., 2017b; Vanhercke et al., 2019). For example, the co-expression of WRI1 and DGAT1 (Push and Pull genes) in *N. benthamiana* has synergistically increased TAG content by 100-fold, accounting for 2.4% of leaf dry weight (Vanhercke et al., 2013). Permanent expression of WRI1 and DGAT1 in Arabidopsis led to a TAG accumulation of about 5% of dry weight, albeit with a reduction in total biomass (Vanhercke et al., 2013). The simultaneous expression of PDAT1 and OLEOSIN1 in Arabidopsis increased TAG content to 6.4% of dry weight without adverse effects on plant growth or oil composition (Fan et al., 2013). By disrupting SDP1 and PXA1 in a tag-1 Arabidopsis mutant, TAG content increased

by 9% of leaf dry weight (Fan et al., 2013). Furthermore, co-expressing WRI1, DGAT1, and OLEOSIN1 in *N. tabacum* led to the accumulation of about 15% of oil in vegetative tissues by dry weight, with no significant impact on plant development (Vanhercke et al., 2019). A study in sugarcane involved constitutive co-expression of WRI1, DGAT1-2, OLE1, and co-suppression of ADP-glucose pyrophosphorylase and PXA1, which led to a significant increase in TAG content in leaves and stems, up to 95- or 43-fold, respectively (Zale et al., 2016). Combining various gene manipulations led to a 1.5- to 9.5-fold increase in TAG content in sugarcane (Zale et al., 2016). TAG levels above 10% on a dry weight basis in high biomass crops are speculated to surpass the oil yield per hectare of oilseed rape by at least two-fold (Vanhercke et al., 2019; Luo et al., 2022). **Table 14** lists different studies that have used various mechanisms of Push, Pull, and Protect to enhance plant seed oil content.

4.4. Modifying the composition of vegetable oils for industrial applications

As previously discussed, common FAs found in vegetable oils include palmitic acid (16:0), stearic acid (18:0), oleic acid (18:1), linoleic acid (18:2), and linolenic acid (18:3), commonly referred to as "usual" FAs. The high levels of these FAs in vegetable oils make them suitable for use in the food industry (Wallis et al., 2022). However, certain plants produce FAs with unique physicochemical properties, differing in carbon chain length, the number and position of double bonds, and the presence of functional groups (e.g., hydroxy, epoxy, conjugated, and acetylenic bonds). This group of less common FAs, often referred to as "unusual FAs", accumulates as TAGs in plant seeds (Lee et al., 2014; Kumar et al., 2020). These variations in the physicochemical properties of FAs make them suitable for biofuels and various industrial applications, including the production of soaps, plastics, nylon, lubricants, paints, coatings, and adhesives (Kumar et al., 2016; Park et al., 2021).

For industrial and other applications of vegetable oils, a high concentration of the desired FAs is preferred to reduce downstream processing costs and achieve high yield efficiency (Vanhercke et al., 2013). Therefore, introducing a novel synthetic pathway or targeted metabolic engineering to accumulate a desired FA can be an approach to developing "designer oilseeds" through genetic engineering (Napier, 2007; Vanhercke et al., 2013). However, achieving a high level of desired FA accumulation presents a major challenge in the development of "designer oilseed" crops (Vanhercke et al., 2013; Msanne et al., 2020; Chellamuthu et al., 2022).

Monounsaturated FAs, such as oleic acid, with fewer double bonds, can enhance the shelf life and oxidative stability of vegetable oil compared to highly or polyunsaturated FAs. Additionally, because of these properties, monounsaturated FAs can be used in industrial products like biolubricants and biodiesel. Moreover, oleic acid can be processed by cleaving at its double bond sites to produce azelaic acid monomers for the production of bio-nylon (Vanhercke et al., 2013; Li et al., 2023).

Various high-oleic oilseed crops have been developed using both conventional plant breeding and genetic engineering methods. For instance, rapeseed historically contained high levels of unhealthy erucic acid. By utilizing a naturally occurring mutant FA elongase to convert oleic acid into erucic acid, Canadian breeders created new rapeseed varieties (referred to as "Canola") with 60-65% oleic acid and very low levels of erucic acid within a decade (Sabbahi et al., 2023). The same approach has been applied to develop high-oleic (60-75%) sunflower plants. Induced mutagenesis has also been used to develop high-oleic linseed crops (Adeleke and Babalola, 2020). These conventional breeding methods have led to the development of high-oleic varieties in rapeseed/canola (75%), soybean (83%), sunflower (90%), safflower (80%), and olive (75%) plants (Wallis et al., 2022).

As a new strategy, genetic engineering technologies have been employed to create high-oleic acid oilseed crops. The FAD2 enzyme, responsible for catalyzing the conversion of oleic acid to linoleic acid, has been targeted for seed-specific inactivation using technologies such as Antisense or RNAi. Researchers have successfully increased the level of oleic acid in various crops, including Arabidopsis, Rapeseed, Indian mustard, Safflower, Soybean, Cottonseed, Flax, and Maize (Okuzaki et al., 2018; Wood et al., 2018).

Furthermore, genome editing technologies like CRISPR (clustered regularly interspaced short palindromic repeats)/Cas9 and TALEN (Transcription Activator-Like Effector Nucleases) have been widely utilized as powerful tools to modify the FA profiles in oilseed crops. For

Table 14.
Push, Pull, Package, and Protect genetic engineering to increase plant seed oil content

Mechanism	Gene	Target species	Increased seed oil content	Reference
Push	α-Carboxyltransferase	*A. thaliana*	14%	Wang et al. (2022a)
		C. sativa	14 %	Wang et al. (2022a)
	ACCase	*G. hirsutum*	22%	Cui et al. (2017)
		Z. mays	54-65%	Dong et al. (2002)
	BASS2	*A. thaliana*	10-37%	Lee et al. (2017)
		B. napus	12%	Tang et al. (2022)
	FATA	*A. thaliana*	9%	Liu et al. (2022b)
	FATB	*A. thaliana*	No significant difference	Liu et al. (2022b)
		B. juncea	5%	Sinha et al. (2007)
	FAX1	*A. thaliana*	17- 34%	Tian et al. (2018); Xiao et al. (2021)
		C. sativa	4%	Cai et al. (2021)
	FAX2	*A. thaliana*	21- 30%	Tian et al. (2019); Li et al. (2020)
	FAX4	*A. thaliana*	30%	Li et al. (2020a)
	GPDH	*G. max*	24%	Zhao et al. (2021)
	LACS2	*B. napus*	8%	Ding et al. (2020)
	MCAMT	*A. thaliana*	15-20%	Jung et al. (2019)
Pull	ABCA9	*C. sativa*	22%	Cai et al. (2021)
	ACBP	*O. sativa*	10%	Guo et al. (2019)
	DGAT + WRI1 + down-regulated SDP1	*A. thaliana*	16%	van Erp et al. (2014)
	DGAT + WRI1	*G. max*	No significant difference	Arias et al. (2022)
	FAE (Downregulation)	*B. juncea*	11%	Sinha et al. (2007)
	FAH	*A. thaliana*	50% decreased	Bates et al. (2014)
Package	FIT2	*A. thaliana*	13%	Cai et al. (2017)
	FSP27	*A. thaliana*	9%	Price et al. (2020)
	Oleosin	*A. thaliana*	30%	Lu et al. (2018)
		O. sativa	46%	Liu et al. (2013)
		G. max	10.6%	Zhang et al. (2019a)
	Seipin	*A. thaliana*	10-62%	Lunn et al. (2018)
Protect	SFAR (Downregulation)	*B. napus*	14-28%	Karunarathna et al. (2020)
	GDSL1 (Downregulation)	*B. napus*	12%	Ding et al. (2019)
	NCP6	*A. thaliana, C. sativa*	6-8%	Cai et al. (2020)
	pPLAIIId	*C. sativa*	14%	Li et al. (2015b)
	PLIP1 (Downregulation)	*A. thaliana*	45%	Wang et al. (2017)
	SDP1 (Downregulation)	*A. thaliana, G. max, B. napus*	8-30%	Kanai et al. (2019)

example, using TALEN to target and cleave conserved DNA sequences in oleate desaturase resulted in higher levels of oleic acid (up to 80%) in soybean crops (Haun et al., 2014). Moreover, CRISPR/Cas9 has been used for targeted mutagenesis of the FAD2 gene in *B. napus*, *O. sativa*, *C. sativa*, and soybean crops (Jiang and Guan, 2017; Okuzaki et al., 2018; Abe et al., 2018; Do et al., 2019; Maraschin et al., 2019; Lee et al., 2019a). **Table 15** presents modifications in industrial FAs in transgenic crops using genetic engineering technologies.

4.4.1. Monounsaturated fatty acids

According to existing reports, metabolic engineering can also be employed to produce and accumulate various other FAs in plant organs. In naturally high erucic acid rapeseed (HEAR), the level of erucic acid (22:1) can reach 45–55% of the total FAs (Napier et al., 2014; Kumar, 2019). The limitation in erucic acid content can be overcome by simultaneously overexpressing LPAAT and FAE in transgenic plants. This approach resulted in transgenic *B. napus* plants with 77% erucic acid content in their seed oil (Wang et al., 2022b). Although crambe plants naturally contain a high level of erucic acid (up to 60%) in seed oil, the extremely low activity of endogenous LPAAT enzyme restricts the maximum accumulation of

erucic acid in the plants. The application of combined approaches, including *Limnanthes douglasii* LPAAT (LdLPAAT) to enhance erucic acid incorporation in the sn-2 position of TAG, BnFAE1 for increasing the elongation of oleic acid to erucic acid, and CaFAD2-RNAi for boosting oleic acid content in *Crambe abyssinica*, has resulted in transgenic lines with 73% erucic acid (Li et al., 2012b).

Vegetable oils enriched in palmitoleic acid, a monounsaturated ω-7 FA (C16:1Δ9), and its elongation product, vaccenic acid (C18:1Δ11), have potential applications in nutraceuticals and the development of olefin metathesis to provide a competitive source of 1-octane for the production of low-density polyethylene (Ettaki et al., 2018). However, these FA are typically present at low levels (<2%) in most oilseed crops (Nguyen et al., 2015). Simultaneous overexpression of a designer Δ9-acyl-ACP and an acyl-CoA desaturase, along with seed-specific suppression of 3-keto-acyl-ACP synthase II and the FatB 16:0-ACP thioesterase genes, has led to transgenic *C. sativa* seeds with 60% omega-7 monounsaturated FA. Previously, the same approach applied to Arabidopsis plants resulted in 71% monounsaturated ω-7 FA in transgenic plants (Nguyen et al., 2015). Recently, the co-expression of palmitoyl-ACP desaturases (PADs), which catalyze ω-7 FA biosynthesis, and MYB115, a transcription factor controlling the expression of the related PAD genes, under the control of a

Table 15.
Modified FA compositions in transgenic crops using genetic engineering methods.

Fatty Acid	Gene	Host Plant	Method	FA Level	Reference
Oleic acid	FAD2	*Brassica napus, B. juncea*	Co-Suppression	89% in *B. napus* and 73% in *B. juncea*	Stoutjesdijk et al. (2000)
		Arabidopsis thaliana	MicroRNA-mediated gene silencing	63%	Belide et al. (2012)
		B. napus	RNAi	32%	Baoming et al. (2011)
		G. max	Antisense RNA	51.7%	Zhang et al. (2014)
		Linum usitatissimum	RNAi	80%	Chen et al. (2015)
		Cartamus tinctorius	RNAi	90%	Wood et al. (2018)
		G. max	TALEN	80%	Haun et al. (2014)
		G. max	TALEN	83%	Domorest et al. (2016)
		B. napus	CRISPR/Cas9	80%	Okuzaki et al. (2018)
		Oryza sativa	CRISPR/Cas9	80%	Abe et al. (2018)
		Camelina sativa	CRISPR/Cas9	50%	Jiang and Guan (2017)
		G. max	CRISPR/Cas9	80%	Do et al. (2019)
		C. sativa	CRISPR/Cas9	80%	Lee et al. (2021)
	DGAT2	*A. thaliana*	Overexpression	50%	Zhang et al. (2013)
Erucic acid	*LdLPAAT, BnFAE1, CaFAD2-RNAi*	*Crambe abyssinica*	Overexpression and silencing	73%	Li et al. (2012b)
Palmitoleic acid	Δ9-acyl-ACP, acyl-CoA desaturase, 3-keto-acyl-ACP synthase II, FatB 16:0-ACP thioesterase	*C. sativa*	Overexpression, suppression	60%	Nguyen et al. (2015)
	Palmitoyl-ACP desaturases (PADs), and MYB115	*A. thaliana*	Overexpression	50%	Ettaki et al. (2018)
Lauric acid	Lauroyl-ACP thioesterase	*B. napus*	Overexpression	60%	Wiberg et al. (2000)
Ricinoleic acid	Fatty acid D12-hydroxylase (FAH12)	*A. thaliana, G. max* mutants	Overexpression	20%	Lu et al. (2006)
	Diacylglycerol acyltransferase (RcDGAT2), or phosphatidylcholine diacylglycerol acyltransferase RcPDAT, FAH12	*A. thaliana*	Co-expression	30%	Kim et al. (2011)
Vernolic acid	DGAT1, DGAT2 and D12-epoxygenase	*G. max*	Co-expression	4-fold	Li et al. (2012a)
Wax ester	Fatty Acid Reductases (FAR) and Wax Synthases (WS)	*A. thaliana*	Co-expression	59%	Iven et al. (2016)
		C. sativa	Co-expression	21%	Iven et al. (2016)
	acyl-ACP thioesterases, *Marinobacter hydrocarbonoclasticus* WS, and *Marinobacter aquaeolei* FAR	*C. sativa*	Co-expression	75%	Ruiz-Lopez et al. (2017)
	M. aquaeolei (MaFAR), *Acinetobactor baylyi* (AbWSD1) and MaWSD2	*A. thaliana*	Co-expression	34 mol%	Yu et al. (2018)
	ScFAR and ScWS	*C. abyssinica*	Co-expression	25%	Li et al. (2019)

seed-specific promoter (AT2S2) in Arabidopsis plants, yielded 10 to >50% ω-7 FA in transgenic seeds without any adverse effects on seed germination (Ettaki et al., 2018). However, efforts to increase the production of other monounsaturated FA, such as C16:1Δ6 and C18:1Δ6 (petroselenic acid), have not been successful in plants (Vanhercke et al., 2013). These FA can be converted to adipic acid (C6:0), a building block of 6,6-nylon, with an annual production of about 2.5 million metric tonnes in the petrochemical industry. Overexpression of related acyl-ACP desaturase has resulted in very low levels of these monounsaturated FA (Gan et al., 2022).

4.4.2. Medium-chain saturates

Medium-chain saturated fatty acids (MCFAs) within the range of C8 to C14, such as caprylic (C8:0), capric, and lauric acid, serve as significant resources for the cosmetics, soaps, and detergents industries (Dyer et al., 2008). These specific FA are typically sourced from coconut and palm kernel oils or synthesized from petroleum-derived compounds (Vanhercke et al., 2013; Roscoe et al., 2015). Therefore, the development of an oil crop with a high content of these MCFAs could offer an alternative to traditional

petrochemical production methods. For instance, transgenic plants engineered to express lauroyl-ACP thioesterase were able to produce over 60% lauric acid (C12:0) in their seeds (Liu et al., 2022b).

Metabolic engineering aimed at accumulating various unusual FAs in plants presents more significant challenges. Fatty acids with reactive functional groups, such as hydroxy FAs (HFAs) and epoxy fatty acids s (EFAs), are particularly valuable and find wide-ranging applications as starting materials in the chemical industry (Lee et al., 2014). Castor oil, containing up to 90% ricinoleic acid (18:1-OH), and Bernardia pulchella oil, rich in 92% vernolic acid (an epoxy FA), serve as crucial commercial sources of these unusual FAs (Vanhercke et al., 2013). While efforts to enhance the levels of these FAs in oilseed crops through metabolic engineering have shown promise, the increased levels in transgenic crops have generally fallen short of those found in the organisms serving as the source of the transgenes (Dyer et al., 2008). For example, the overexpression of a castor bean fatty acid D12-hydroxylase (FAH12) in Arabidopsis and soybean mutants resulted in approximately 20% of ricinoleic acid (Δ12-OH oleic acid) in transgenic oilseed plants (Lu et al., 2006). In another attempt, it was found that simultaneous expression of R. communis DGAT2, or phosphatidylcholine diacylglycerol acyltransferase RcPDAT and FAH12 could increase ricinoleic acid levels up to approximately 30% in transgenic Arabidopsis (Park et al., 2022). Similarly, the simultaneous expression of *Vernonia galamensis* DGAT1, DGAT2, and D12-epoxygenase in soybean plants significantly increased the level of vernolic acid in transgenic plants by approximately fourfold (Hatanaka et al., 2022). An increased level of calendulic acid (C18:3), used as a drying agent in painting, ink, and other applications, has been achieved by transferring related genes into Arabidopsis plants (Kumar et al., 2016).

4.4.3. Engineering wax ester synthesis

Wax esters (WEs) are a unique class of lipids that accumulate at high levels (up to 60% of the seed weight) in the seeds of *Simmondsia chinensis*, also known as Jojoba, a perennial desert shrub native to North America (Miklaszewska et al., 2021). WEs are esters composed of long-chain (C20, C22, and C24) monounsaturated FA and fatty alcohols, and they find important applications in medicine, cosmetics, food industries, and lubricants (Beaudoin and Facchini, 2014). While Jojoba is the primary natural source of WEs for commercial use, its production is limited, yields are low, and the process is labor-intensive, making it economically challenging to compete with cheaper petroleum-based products (Vanhercke et al., 2013). Developing a more productive and cost-effective natural source could address these economic constraints.

The synthesis of WEs in any organism relies on the key enzymes, Fatty Acid Reductases (FAR) and Wax Synthases (WS) (Beaudoin and Facchini, 2014). Successful metabolic engineering to induce WEs biosynthesis has been accomplished in bacteria (Kalscheuer et al., 2006), yeast (Wenning et al., 2017), and plants (Iven et al., 2016; Li et al., 2020a). Coexpressing various sources of FAR and Wax Synthase (WS) genes in *A. thaliana* and *C. sativa* led to 59% and 21% WEs in transgenic plants (Iven et al., 2016). Overexpression of FAR and WS genes along with Acyl-ACP thioesterase in *C. sativa* resulted in 75% WEs in transgenic seeds (Ruiz-Lopez et al., 2017). Furthermore, simultaneous expression of genes from Marinobacter aquaeolei (MaFAR), *Acinetobacter baylyi* (AbWSD1), and MaWSD2 significantly boosted WEs in Arabidopsis (62 mol%) and *C. sativa* (by 34 mol%) plants (Ruiz-Lopez et al., 2017; Yu et al., 2018). Simultaneous expression of Jojoba ScFAR and ScWS genes in Camelina abyssinica increased WEs levels up to 25% in transgenic lines (Li et al., 2019). Similarly, the genetic transformation of Lepidium campester using Jojoba ScFAR and ScWS genes substantially increased WEs content in transgenic plants (Ivarson et al., 2017). These findings suggest that these transgenic oilseed crops hold promise as a platform for renewable and sustainable approaches to commercial WE production (Miklaszewska et al., 2021).

5. Policy and practical implications

As mentioned earlier, the global vegetable oil demand for food, industrial, and energy use has increased since the 1980s. To meet this demand, as well as intensifying production practices, the land used for oil crop production increased from 114 million hectares (Mha) in 1961 to 332 Mha in 2020 (FAO, 2023). Although vegetable oil production can result in higher incomes, increased employment, reduced poverty among farmers,

and reduced CO_2 emissions, it can also lead to environmental concerns (e.g., deforestation or loss of other natural ecosystems) as well as disruption of biodiversity (Santika et al., 2019). Moreover, considering the principles of sustainable agriculture, the production of vegetable oil for industrial applications can endanger food security. In order to develop industrial uses of vegetable oils in a sustainable agricultural system, the following are suggested:

1. Using non-edible vegetable oils (e.g., Jatropha, Castor bean, Mustard, Camelina, Algae) as an approach to reduce dependence on edible oil for industrial applications.
2. Cultivating industrial oilseed crops on marginal land unsuitable for food production as an alternative approach to minimize land-use competition for food production and its adverse effects (direct or indirect) on food security, land-based greenhouse gas emissions, and biodiversity loss.
3. Enhancing oil content and composition in edible and non-edible oilseed crops by genetic engineering to meet the need for renewable and clean sources of industrial products.
4. Development of new resources for oil production in non-seed biomass (e.g., leafy plants and algae) using genetic engineering technologies.
5. Strengthening government policies on the development of the use of renewable and environmentally friendly resources, including blending mandates, excise tax reductions or exemptions, renewable or low carbon fuel standards, as well as a variety of fiscal incentives and public financing mechanisms.

6. Challenges and prospects

Recent advancements in the field of metabolic engineering of plant lipids have been significant and sustained. Notably, the engineering of plants to produce long-chain polyunsaturated fatty acids (PUFAs), which involves introducing an entirely new pathway comprising five additional enzymatic steps while enhancing endogenous precursor pathways, is arguably one of the most complex metabolic engineering achievements in plants to date. Importantly, the metabolic engineering of industrial oils, waxes, and other plant lipids is poised for substantial acceleration due to recent major technological breakthroughs.

To begin, our understanding of the biochemical pathways governing FAs, oils, and waxes has progressed at an accelerated rate. This is attributed to the integration of genomic, transcriptomic, transgenic, and biochemical research approaches. Underpinning this advancement is a significant improvement in gene sequencing efficiency, making it feasible and cost-effective to generate full-sequence information for any species within a relatively short timeframe. Whole genome sequencing can now be conducted at the genotype level, and comparative transcriptomics is routinely used to uncover genetic associations with lipid biosynthetic traits.

Furthermore, a variety of extremely efficient transient assay techniques are now available that allow for quick time cycles and high-throughput metabolic engineering in plants. Alongside traditional somatic embryo assay systems have emerged as a sophisticated platform for high-throughput experimental metabolic engineering. Additionally, advances in lipidomic analysis have enhanced sensitivity and reliability, allowing for the simultaneous tracking of numerous intermediates involved in oil and wax biosynthetic pathways. The application of mass spectroscopic imaging to reveal comprehensive lipid species composition across tissue slices, or even specific cellular organelles or oil drops extracted from oil-bearing tissues, promises increased precision for unraveling pathway interactions within developmental biology.

7. Conclusions

These advances will help researchers better understand how pathways interact with developmental biology. Importantly, these breakthroughs now enable the use of combinatorial metabolic engineering in oil plants to optimize component biosynthesis enzyme pathways for the first time. This technical leap will allow researchers to transition from the tedious step-by-step testing and construction of relatively basic transgenic pathways to a rigorous, high-throughput, multistep combinatorial technique. This shift towards synthetic biology promises additional major advancements in plant-based oil engineering for future commercial usage.

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