Oil Palm: Genome Designing for Improved Nutritional Quality

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Abstract

Edible palm oil products are free from trans fats, making them healthier and safe for application in food industry. Palm oil contains valuable vitamins and phytonutrients that exhibit cardioprotective mechanisms, immune system enhancement, neurodegeneration protection, and antioxidative as well as anti-carcinogenic properties. Red palm oil (RPO), a component of crude palm oil, is beneficial as a vitamin A supplement for treating vitamin A deficiency and its related diseases. The nutritional value of palm oil can be further enhanced via conventional breeding, using, for instance, palms exhibiting high carotene and

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vitamin E contents that are available in the oil palm germplasm collection. Genes for key enzymes involved in carotene synthesis in palm oil have been isolated and characterized. These, together with the oil palm genome builds and its associated databases, provide resources for developing marker-assisted selection (MAS) programs and support genetic engineering technologies toward improving the nutritional values of oil palm and palm oil.

Keywords

Palm oil · Phytonutrients · Red palm oil · Vitamin E · Nutritional genomics

1 Agricultural Importance of the Oil Palm Crop

Oil palm is a perennial tree crop that produces two types of oils, namely, palm oil which is extracted from the fleshy mesocarp and palm kernel oil which is obtained from the oil palm kernel. The former has vast applications in the food industry, while the latter is mostly used in the oleochemical industry. Oil palm is a monocotyledon classified under the genus *Elaeis*. This genus consists of two species, *Elaeis guineensis* and *Elaeis oleifera*. *Elaeis guineensis* originates from Central and West Africa and is presently the main oil palm planting material planted commercially. *E. oleifera* has a South and Central America origin and possesses interesting features such as high carotene content (Mohd Din et al. 2002), low height increment rate, high oil unsaturation (Hardon 1969), and tolerance to diseases (Turner 1981), which are pertinent to oil palm improvement.

The oil palm has the highest productivity among oil-producing plants, producing approximately 3.7 tons of oil hectare^{-1} year^{-1}. With 11 and 10 times the yield capacity of soybean and rapeseed, respectively (Khosla and Sundram 2010), oil palm produces 75 million tons of oil from only ~24 million hectares of planted area. This output is obtained from less than 5% of the total area planted with oil crops. For many years, palm oil has contributed approximately 30% of the total oils and fats produced worldwide (Oil World 2022). Palm oil recorded a 53.4% market share of the major global oil and fat exports in 2021 (Oil World 2022). The main producers of palm oil are Indonesia (58.8%), Malaysia (23.8%), and South and Central America (6.9%). Palm oil is a rich source of vitamins and phytonutrients. The abundance of worldwide supplies and vast applications in the food industry make palm oil a prospective source of vitamins and phytonutrients that could meet the micronutrient requirements across the globe.

2 Chemical Composition of Palm Oil and Oil Palm

Palm oil and palm kernel oil differ in terms of their fatty acid compositions, particularly in the proportions of saturated fatty acids (SFA) and unsaturated fatty acids (UFA). Palm kernel oil has properties similar to coconut oil, with 82% SFA and

18% UFA. The 82% SFA is mainly composed of lauric (~50%), myristic (~16%), and palmitic acids (~8%), while the 18% UFA includes oleic acid (15%) and linoleic acid (~3%) (Ibrahim 2013). On the other hand, palm oil contains balanced amounts of SFA and UFA. The main SFAs in palm oil are palmitic acid (45%) and stearic acid (5%). Oleic acid and linoleic acid are the UFA present in palm oil at 40% and 10%, respectively. Besides fatty acids, palm oil also contains a wide range of health-benefiting phytonutrients such as tocopherols, tocotrienols, carotenoids, polyphenols, phytosterols, squalene, phospholipids, and coenzyme Q_{10} or ubiquinone-10 (Choo and Nesaretnam 2014). The detailed fatty acid composition of palm oil and palm kernel oil is listed in Table 1.

There are also active research and development (R&D) programs to improve and innovate the milling and processing of palm oil to preserve the natural phytonutrients. The phytonutrients in red or cold-pressed palm oil, for instance, are extracted for food, cosmetic, and pharmaceutical applications (Hassan et al. 2021; Abd Rashid et al. 2021). Red palm oil (RPO) contains vitamin E (α-, β-, and γ-tocotrienols), carotenoids (xanthophylls, α- and β-carotenes), phytosterols, ubiquinone, and squalene and is a competitive and better alternative to other consumer oils due to its nutritional content (Loganathan et al. 2017). Oil palm-based products and by-products from the fruit bunches, kernel shells, trunk, fronds, and pressed fruits also contain phenolic compounds, terpenes, lignin, lignans, vitamins, sugar, and minerals (Ofori-Boateng and Lee 2013). The aqueous waste from the palm fruit milling and processing has been extensively studied and valued for its high content of phenolic compounds (Syarifah-Noratiqah et al. 2019).

Table 1 Palm oil and palm kernel oil fatty acid composition

Fatty acid	Lipid number, carbon/double bond (C:D)	Saturation	Palm oil (%)	Palm kernel oil (%)
Palmitic acid	16:0	Saturated	39.2–45.8	7.5–9.3
Oleic acid	18:1	Unsaturated	37.4–44.1	13.7–17.0
Linoleic acid	18:2	Unsaturated	8.7–12.5	2.1–2.9
Stearic acid	18:0	Saturated	3.7–5.4	1.8–2.4
Myristic acid	14:0	Saturated	0.9–1.5	15.4–17.2
Arachidic acid	20:0	Saturated	0.0–0.5	0.0–0.1
Linolenic acid	18:3	Unsaturated	0.0–0.6	–
Lauric acid	12:0	Saturated	0.0–0.5	45.4–49.8
Palmitoleic acid	16:1	Unsaturated	0.0–0.4	
Capric acid	10:0	Saturated	–	2.9–3.7
Caprylic acid	8:0	Saturated	–	3.2–4.7
Caproic acid	6:0	Saturated	–	0.2–0.4

Source: Bustamam et al. (2019), Japir et al. (2017), Mancini et al. (2015), Choo and Nesaretnam (2014), Ibrahim (2013)

3 Oil Palm Phytochemicals

The natural chemical components of plants are known as phytochemicals. The term "phyto" comes from a Greek word that means plant (Liu 2004). Phytochemicals are of fundamental biological importance to plants; they provide protection against pathogens, herbivores, and solar radiation and function as signaling molecules and regulators (Csepregi and Hideg 2017; Winkel 2004). Phytochemicals are known to be bioactive and antioxidative against free radicals, cancerous cells, bacteria, and viruses and have various therapeutic functions comprising anti-inflammatory, antimutagenic, and antitumor effects on human health (Ciucure and Geană 2019; Naithani et al. 2008). They are also the source of fine products for dyes, drugs, fragrances, and flavors which are important to the commercial industry (Shilpa et al. 2010).

Apart from the prized palm oil, the palm fruit contains phospholipids which are initially part of the cell membrane. Phospholipids are amphiphilic and are a source of lecithin and an important releasing agent in food products (Choo et al. 2004). Crude palm oil contains very low amounts of phospholipids due to the milling process, and, therefore, phospholipids are better extracted from the palm fruit fiber and calyx (Gold et al. 2016; Choo et al. 2004). The primary phospholipids in palm oil are phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylinositol (PI), and phosphatidylglycerol (PG) with a small amount of phosphatidic acid (PA), diphosphatidylglycerol (DPG), lysophosphatidylethanolamine (LPE), lysophosphatidylcholine (LPC), and phosphatidylserine (PS) (Goh et al. 1982). The fibrous by-products retained after oil extraction from the oil palm fruit, also known as oil palm fruit fiber, predominantly contain PC, PE, PG, and PA (Choo et al. 2004). Galactolipids of monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG), which are also part of palm fruit cell membranes, were profiled from palm oil (Cheong et al. 2014). These glycolipids are reported to show health-promoting effects (Christensen 2009).

Terpenes are natural unsaturated hydrocarbons that form the largest class of plant secondary metabolites. They are made up of five carbon isoprene units assembled into multiple pairs of isoprene pairs and various additions of side chains and functional groups (Perveen 2018). Terpenes can take linear or cyclic forms and are categorized according to their isoprene units and structural variations. Terpenoids are terpenes with additional, removal, or substitution of functional groups, for example, oxygen, methylene groups, or hydrogen atoms (Masyita et al. 2022). Terpenes include squalene, sterol, saponin, and carotenoid, while the terpene isoprene unit is the side chain of tocotrienols (Ahsan et al. 2015). Squalene is found in palm oil and palm oil milling waste. It is a biochemical intermediate in the synthesis of phytosterols in plants and hormones in humans. Squalene acts as an antioxidant and is an important ingredient especially in the cosmetic industry (Gonzalez-Diaz and García-Núñez 2021). Crude palm oil and its by-products contain phytosterols of β-sitosterol, campesterol, and stigmasterol (Jalani et al. 2021; Choo and Nesaretnam 2014). These plant sterols modulate membrane-bound enzyme activities and demonstrate cholesterol-lowering activity (De Smet et al. 2012).

Derived from tetraterpenes, carotenoids can be classified into xanthophylls and carotenes based on their oxygen content (Cazzaniga et al. 2016). Xanthophylls of

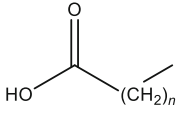
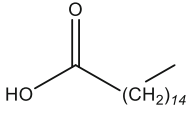
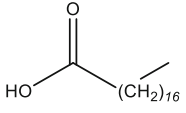
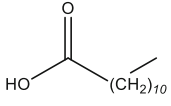
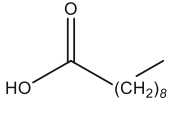
lutein and carotene epoxides and at least 11 other types of carotenes were profiled in palm oil, namely, phytoene, phytofluene, α-carotene, β-carotene, ξ-carotene, γ-carotene, δ-carotene, lycopene, α-zeacarotene, β-zeacarotene, and neurosporene (Ping and Gwendoline 2006; Ng and Choo 2016). Tocopherols and tocotrienols are collectively identified as vitamin E and are important palm oil constituents. Crude palm oil, palm olein, and red palm olein were all reported to retain α-tocopherol (α-T), α-tocotrienol (α-T3), γ-tocotrienol (γ-T3), and δ-tocotrienol (δ-T3).

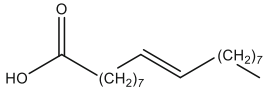
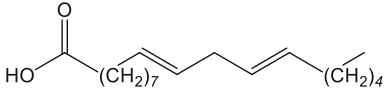
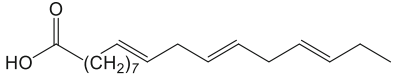
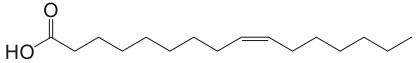
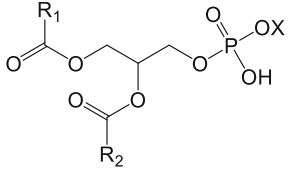
Lignans are water-soluble polyphenols formed from monolignols of coumaryl, coniferyl alcohol, or sinapyl alcohols. On the other hand, lignin is synthesized from similar monolignols but is linked differently by dirigent proteins resulting in hydrophobic natural polymers in the plant cell wall (Davin and Lewis 2000). Isolariciresinol, lariciresinol, and pinoresinol are examples of lignans detected in palm oil (Tardugno et al. 2022). These lignans exert beneficial effects on human health (Rodríguez-García et al. 2019). Other secondary metabolites such as phenolic compounds are detected in the by-products of the milling process due to their low lipophilic nature. The term "phenolic" includes metabolites with hydroxyl-substituted benzene ring synthesized by the phenylpropanoid biosynthetic pathway. Flavonoids, the largest group of phenolics, are composed of a diphenyl-propane (C6-C3-C6) backbone in which two aromatic rings are connected via a three-carbon chain (Alseekh et al. 2020). Flavonoids occur naturally as aglycone or as conjugates with sugars, organic acids, and other molecules and are present in the oil palm fruit and leaf (Hazir et al. 2012; Tahir et al. 2013).

Organic acids in plants typically form alkaline salt, ester, and glycoside that are very important in human nutrition as biochemical pathway intermediaries (Gundogdu et al. 2014), while amino acids are the building blocks for tissue proteins and are substrates for the synthesis of numerous substances of physiological importance in the human body (Wu 2013). Table 2 explains each class of the nutritive phytochemicals characterized in palm oil and oil palm tissues and their biosynthesis pathway references from the Kyoto Encyclopedia of Genes and Genomes (KEGG) (Kanehisa and Goto 2000).

Other oil palm plant parts such as the leaves, fruits, and cabbages (palm heart) are mostly edible by humans and ruminants (Reddy et al. 2019; Ebrahimi et al. 2015). Alkaloids are bitter to the taste and can be found in plants in small quantities (Muñoz et al. 2020). A qualitative investigation revealed that alkaloids are the least phytochemical component found in oil palm leaves (Yin et al. 2013) and were not identified exhaustively except for β-phenylethylamine derivatives of tyramine and catecholamines in environment and disease studies (Tahir et al. 2022; Rodrigues-Neto et al. 2018). Catechins are a well-studied group of flavonoids found at high levels in tea and are also recorded in oil palm leaf and root (Tahir et al. 2013, 2022). Procyanidin B, the oligomer of catechin, is also found in oil palm root (Nurazah et al. 2013). Ferulic, sinapic, coumaric, and caffeic acids are among the hydroxycinnamic phenolic acids found in oil palm fruits (Sambanthamurthi et al. 2011). Dietary fibers and sugars derived from cellulosic and hemicellulosic components from oil palm biomass are also valuable and gaining attention from food and fuel industries (Mazlan et al. 2021; Palamae et al. 2017).

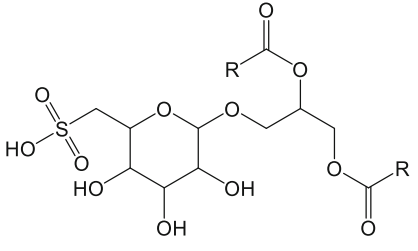
Table 2 Phytochemicals in oil palm products and by-products

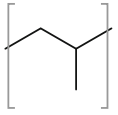
Class	Structure	Biosynthesis/pathway	References for oil palm
Palm oil			
Lipids			
Fatty acids		Fatty acid biosynthesis (KEGG pathway map00061)	Japir et al. (2017); Tahir et al. (2021)
Palmitic acid			
Stearic acid			
Lauric acid			
Capric acid			

Oleic acid			
Linoleic acid			
Linolenic acid			
Palmitoleic acid			
Phospholipids			
Glycerophospholipid (phosphoglyceride)		Glycerophospholipid metabolism (KEGG pathway map00564)	Gold et al. (2016); Choo et al. (2004)
	R = fatty acids		

(continued)

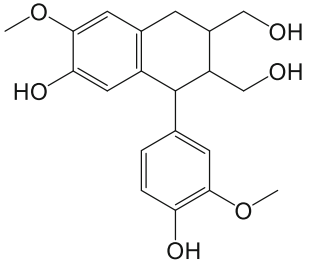
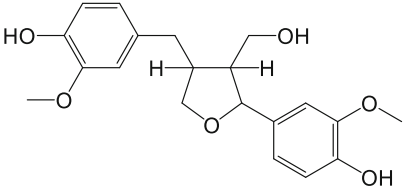
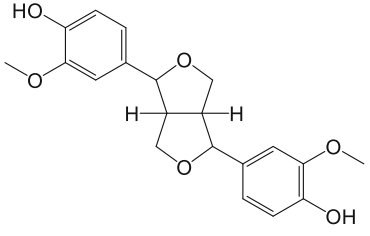
Table 2 (continued)

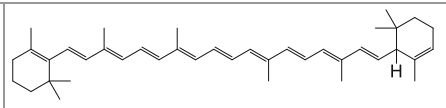
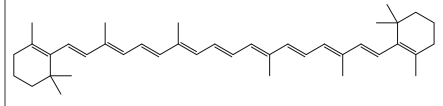
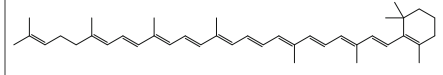
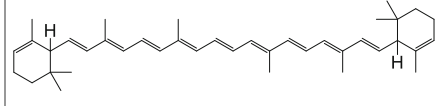
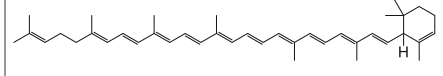
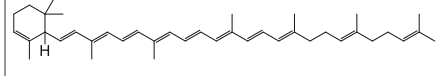
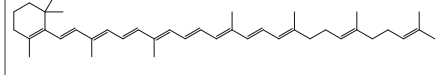
Class	Structure	Biosynthesis/pathway	References for oil palm
Phosphatidic acid (PA)	X = H		
Phosphatidylcholine (PC)	X = choline		
Phosphatidylethanolamine (PE)	X = ethanolamine		
Phosphatidylserine (PS)	X = serine		
Phosphatidylglycerol (PG)	X = glycerol		
Phosphatidylinositol (PI)	X = inositol		
Galactolipids			
Sulfoquinovosyl diacylglycerols (SQDG)		Glycerolipid metabolism (KEGG pathway map00561)	Cheong et al. (2014)
	R = fatty acid		

Terpene			
		Biosynthesis of terpenoids and steroids (KEGG pathway map01062)	Gonzalez-Diaz and García-Núñez (2021); Hoe et al. (2020)
	$(C_5H_8)_n$		
Monoterpene	$n = 2$, $C_{10}H_{16}$		
Sesquiterpene	$n =$, $C_{15}H_{24}$		
Diterpene	$n = 4$, $C_{20}H_{32}$		
Sesterpene	$n = 5$, $C_{25}H_{40}$		
Triterpene, e.g., squalene	$n = 6$, $C_{30}H_{48}$ usually contains 30 carbon atoms consisting of 6 isoprene units		
Sesquarterpene	$n = 7$, $C_{35}H_{56}$		
Tetraterpenes	$n = 8$, $C_{40}H_{64}$		
Meroterpene	Partial terpenoid skeleton		
Polyterpenes	Long chains of many isoprene units		
Terpenoid	Terpenes with additional functional groups, usually containing oxygen		

(continued)

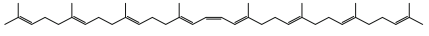
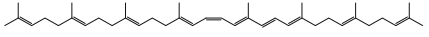
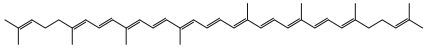
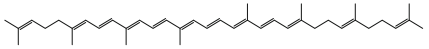
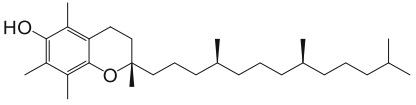
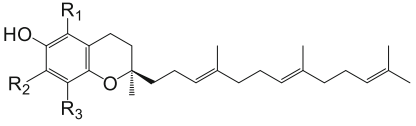
Table 2 (continued)

Class	Structure	Biosynthesis/pathway	References for oil palm
Lignans			
Isolariciresinol		Biosynthesis of various plant secondary metabolites (KEGG pathway map00999)	Tardugno et al. (2022)
Lariciresinol			
Pinoresinol			

Red palm oil			
Carotenoids			
α-Carotene (alpha)		Carotenoid biosynthesis pathway (KEGG pathway map00906)	Ping and Gwendoline (2006); Ng and Choo (2016)
β-Carotene (beta)			
γ-Carotene (gamma)			
ξ-Carotene (epsilon)			
δ-Carotene (delta)			
α-Zeacarotene			
β-Zeacarotene			

(continued)

Table 2 (continued)

Class	Structure	Biosynthesis/pathway	References for oil palm
Phytoene			
Phytofluene			
Lycopene (ψ-carotene, psi)			
Neurosporene			
Tocols			
Tocopherol		Ubiquinone and other terpenoid-quinone biosynthesis (KEGG pathway map00130)	Hoe et al. (2020); Ibrahim (2013)
α-Tocopherol (α-T)			
Tocotrienol			
α-Tocotrienol (α-T3)	$R_1 = CH_3$, $R_2 = CH_3$, $R_3 = CH_3$		
γ-Tocotrienol (γ-T3)	$R_1 = H$, $R_2 = CH_3$, $R_3 = CH_3$		
δ-Tocotrienol (δ-T3)	$R_1 = H$, $R_2 = H$, $R_3 = CH_3$		

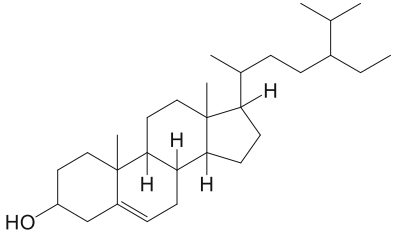
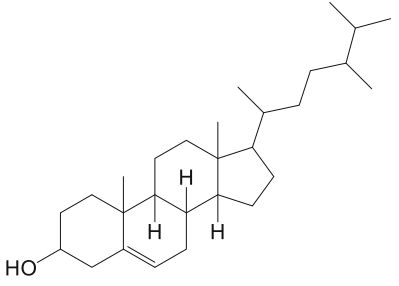
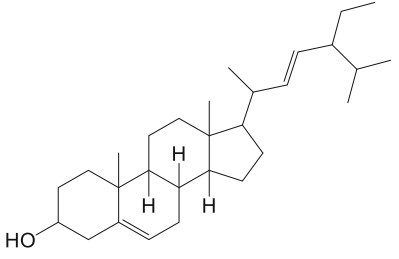
Phytosterols			
β-Sitosterol		Steroid biosynthesis (KEGG pathway map00100)	Jalani et al. (2021); Choo and Nesaretnam (2014)
Campesterol			
Stigmasterol			

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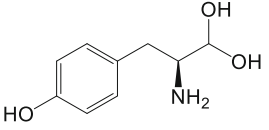
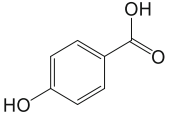
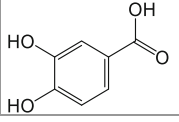
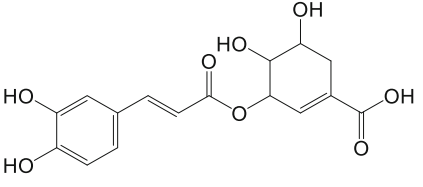
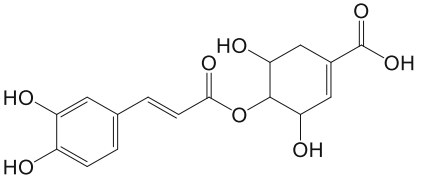
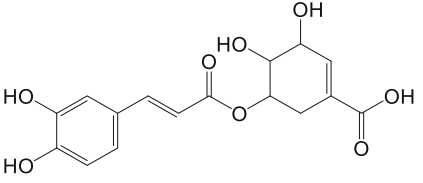
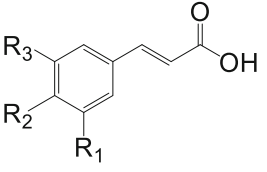
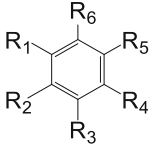
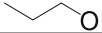
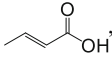
Table 2 (continued)

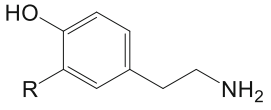
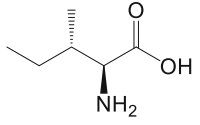
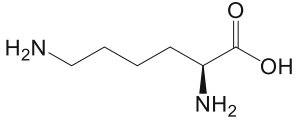
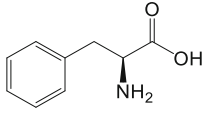
Class	Structure	Biosynthesis/pathway	References for oil palm
Palm oil mill effluent (POME)			
Phenolic acids			
Hydroxytyrosol		Tyrosine metabolism (KEGG pathway map00350)	Syarifah-Noratiqah et al. (2019) Sambanthamurthi et al. (2011)
p-Hydroxybenzoic acid		Biosynthesis of phenylpropanoids (KEGG pathway map01061)	
Protocatechuic acid		Benzoate degradation (KEGG pathway map00362)	
Isomers of caffeoylshikimic acid (CSA)			
3-*O*-caffeoylshikimic acid		Phenylpropanoid biosynthesis (KEGG pathway map00940)	

4-*O*-caffeoylshikimic acid			
5-*O*-caffeoylshikimic acid			
Hydroxycinnamic acids			
Ferulic acid	$R_1 = OCH_3$, $R_2 = OH$, $R_3 = H$		
Sinapic acid	$R_1 = OCH_3$, $R_2 = OH$, $R_3 = OCH_3$		
p-Coumaric acid	$R_1 = H$, $R_2 = OH$, $R_3 = H$		
Caffeic acid	$R_1 = OH$, $R_2 = OH$, $R_3 = H$		

(continued)

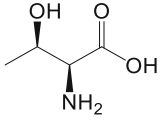
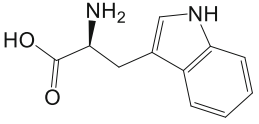
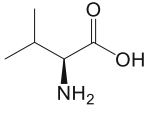
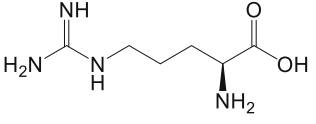
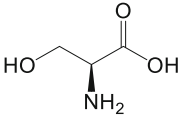
Table 2 (continued)

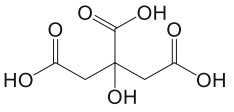
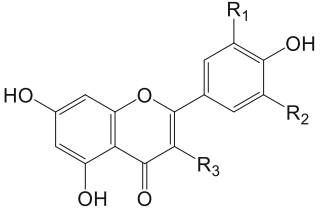
Class	Structure	Biosynthesis/pathway	References for oil palm
Phenolics (in dry matter)			
		Aminobenzoate degradation (KEGG pathway map00627)	Tsouko et al. (2019)
Gallic acid	$R_1 = OH$, $R_2 = OH$, $R_3 = OH$, $R_4 = H$, $R_5 = COOH$, $R_6 = H$		
Homovanillic alcohol	$R_1 = OH$, $R_2 = OCH_3$, $R_3 = H$, $R_4 =$  , $R_5 = H$, $R_6 = H$		
Vanillin	$R_1 = OH$, $R_2 = OCH_3$, $R_3 = H$, $R_4 = C = O$, $R_5 = H$, $R_6 = H$		
Pyrogallol	$R_1 = H$, $R_2 = H$, $R_3 = H$, $R_4 = OH$, $R_5 = OH$, $R_6 = OH$		
Catechol	$R_1 = H$, $R_2 = H$, $R_3 = H$, $R_4 = OH$, $R_5 = OH$, $R_6 = H$		
Guaiacol	$R_1 = H$, $R_2 = H$, $R_3 = H$, $R_4 = OCH_3$, $R_5 = OH$, $R_6 = H$		
Syringaldehyde	$R_1 = OH$, $R_2 = OCH_3$, $R_3 = H$, $R_4 = C = O$, $R_5 = H$, $R_6 = OCH_3$	Phenylpropanoid biosynthesis (KEGG pathway map00940)	
Sinapinic acid	$R_1 = OCH_3$, $R_2 = OH$, $R_3 = OCH_3$, $R_4 = H$, $R_5 =$  , $R_6 = H$		

Other oil palm tissues			
Amines			
β-Phenylethylamine derivatives		Biosynthesis of alkaloids derived from shikimate pathway (KEGG map01063)	Tahir et al. (2022)
Tyramine	R = H	Tyrosine metabolism (KEGG pathway map00350)	
Dopamine	R = OH		
Essential amino acid			
Isoleucine		Biosynthesis of amino acids (KEGG pathway map01230)	Rozali et al. (2021)
Lysine			
Phenylalanine			

(continued)

Table 2 (continued)

Class	Structure	Biosynthesis/pathway	References for oil palm
Threonine			
Tryptophan			
Valine			
Arginine			
Serine			

Organic acid			
Citric acid		Alanine, aspartate, and glutamate metabolism (KEGG pathway map00250)	
Flavonoids			
Flavone		Flavonoid biosynthesis (KEGG pathway map00941)	
Apigenin derivatives	$R_1 = H, R_2 = H, R_3 = H$		Tahir et al. (2012)
Luteolin derivatives	$R_1 = OH, R_2 = H, R_3 = H$		
Myricetin	$R_1 = OH, R_2 = OH, R_3 = OH$		Tsouko et al. (2019)
Flavanol			Che Zain et al. (2020)
Catechin	$R_1 = H, R_2 = OH, R_3 = OH$ (in *trans* configuration)		
Epicatechin	$R_1 = H, R_2 = OH, R_3 = OH$ (in *cis* configuration)		

4 Significance of Palm Oil and Its Phytonutrients in Human Diseases and Health

Palm oil is semisolid in a tropical environment and can be fractionated to separate the liquid component, known as palm olein, from its solid component called palm stearin. Palm olein can be used directly as cooking oil, whereas palm stearin is employed to produce fats such as margarine, shortening, and ghee. Unlike other vegetable oils that require the hydrogenation step to make them solid, more stable, and less reactive for food manufacturing, palm olein can be made more solid by adding the natural palm stearin, resulting in oils that are trans fat-free. The hydrogenation process converts the geometrically cis ("same side") structure of fatty acid molecules into the trans ("opposite side") which causes changes in physical and biological properties (Goh 2006). Consuming food that contains trans fats results in increased low-density lipoprotein (LDL), or "bad" cholesterol, and decreased "good" cholesterol (high-density lipoprotein – HDL) in blood serum and interference of many cellular signaling pathways in humans (Mensink and Katan 1990; Judd et al. 1994). Elevated levels of LDL contribute to accumulation of plaque along artery walls, also known as atherosclerosis. This subsequently causes inflammation and increases the risk of heart disease. Long-term consumption of foods blended with hydrogenated vegetable oils has also been reported to cause other major diseases such as diabetes, cancer, cystic fibrosis, diabetes, inflammatory diseases, macular degeneration, and Parkinson's and Alzheimer's diseases (Goh 2006). Studies have shown that replacing hydrogenated oils with palm olein could decrease heart disease risk by 30% (Mozaffarian and Clarke 2009). Palm olein also demonstrates anticarcinogenic and antioxidant attributes and a wide range of protective properties against diseases (Abdullah et al. 2018). Palm olein appears to be a healthier and better alternative for hydrogenated oils in the food industry as far as health effects are concerned.

RPO is trans- and cholesterol-free and has pro-vitamin A activity. Children fed with red palm oil and confectionaries containing red palm oil recorded increased blood retinol levels (Manorama et al. 1996; van Stuijvenberg et al. 2000), which significantly reduced night blindness and Bitot's spots occurrences due to vitamin A deficiency (Sivan et al. 2002). Several other studies also supported the safety and efficacy of using RPO for fighting vitamin A deficiency (Hedrén et al. 2002, Zagré et al. 2003, Canfield et al. 2001, Radhika et al. 2003,Lietz et al. 2001). RPO also potentially confers anticancer properties (Boateng et al. 2006; Yamanushi et al. 2001) and plays an important role in tumor suppression by increasing natural killer cells and B-lymphocyte populations which enhances the immune system (Nesaretnam et al. 2002).

In general, phytonutrients exhibit bioactive properties, i.e., inhibition or initiation of gene expression and enzyme activity and suppression of receptors. Phytonutrients are directly beneficial to humans as a nutraceutical or supplemental product or indirectly through use as a livestock feed (Tahir et al. 2013). Tocotrienol is the major vitamin E component extracted from palm oil. In fact, palm oil is one of the plant species offering the highest source of tocotrienols, apart from rice bran. Several

in vitro and animal studies showed that palm oil tocotrienols have anticarcinogenic potential (Komiyama et al. 1989; Sundram et al. 1989; Wada 2009; Samant et al. 2010; Shah et al. 2003; Sylvester and Shah 2005; Nesaretnam et al. 2004) and neurodegeneration protection (Nesaretnam et al. 2004; Shah et al. 2003; Sen et al. 2007; Khanna et al. 2005; Park et al. 2011). Tocotrienols could also prevent heart disease through their ability to reverse arterial blockage (Nafeeza et al. 2001; Black et al. 2000) and are involved in other cardioprotective mechanisms (Li et al. 2010; Budin et al. 2009; Das et al. 2005).

Phenolics are another phytonutrient extracted from the vegetative liquor of palm oil mill (Sambanthamurthi et al. 2011). Based on animal studies, oil palm phenolics (OPP) are beneficial for heart health and neurons (brain) and are bioactive against free radical damage and atherosclerosis (Leow et al. 2013; Sambanthamurthi et al. 2011). Palm oil and palm products with phenolics and phytosterols are strong inhibitors of peroxidation, and the dietary intake of lignan-rich foods such as oil palm products is known to prevent certain types of cancers and cardiovascular diseases. Figure 1 illustrates the human health-promoting properties of palm oil and oil palm products. Other phytonutrients such as phytosterols, squalene,

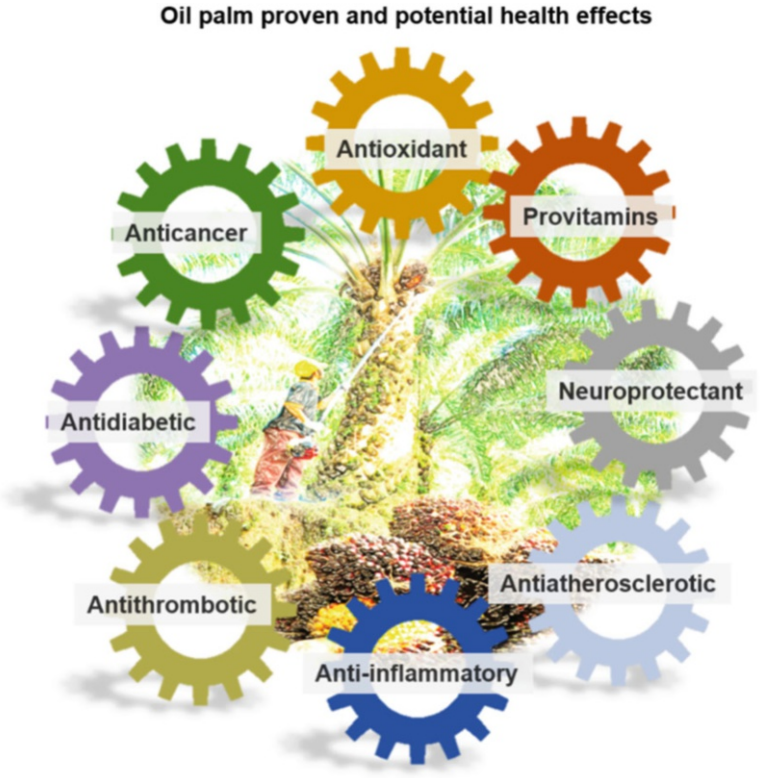


Fig. 1 Oil palm and its health-promoting properties

coenzyme Q10, phospholipids, and polyphenols play a crucial role in the stability and quality of the oil. In addition, these phytonutrients have antioxidant properties, and some exhibit nutritional and health benefits beyond their antioxidant functions (Choo and Nesaretnam 2014).

Oil palm leaves contain bioactive agents such as antioxidants and are anti-hyperglycemic with organ-protective effects against hypertension (Tahir et al. 2022). The leaf extracts also possess pharmacological activities of wound healing, hypoglycemic, vascular relaxation, hypocholesterolemic, neurogenesis, phytoestrogenic, osteogenic, fungicidal, and antimicrobial properties (Tow et al. 2021).

5 Oil Palm Genetic Diversity

The assessment of genetic diversity in any crop species helps to identify genotypes for crossing, generating hybrids with increased heterosis and variability (Adon et al. 1998). In oil palm, the diversity of germplasm populations is determined to evaluate their value for increasing diversity of the present genetically narrow breeding populations as well as identifying accessions carrying economically important genes or traits. Such efforts would benefit the oil palm industry by developing new planting materials that produce diversified products and are more sustainable against extreme climate changes as well as fatal diseases.

The genetic diversity among oil palm populations and genotypes has been evaluated by means of phenotypes and molecular markers. Phenotypic characteristics have conventionally been used to select individual plants for genetic improvement programs. Phenotypic evaluation of oil palm populations for improvement programs in Malaysia started in the 1920s. For selection and incorporation into breeding programs, oil palm breeders initially focused on evaluating oil yield and bunch quality components contributing to yield. Thus, parameters such as fresh fruit bunch (FFB), oil-to-bunch (OTB), mesocarp-to-fruit (MTF), and kernel-to-fruit (KTF) ratios are emphasized in selecting oil palms to be included in crossing programs. However, despite good progress in improving oil yield via conventional breeding, the average yield in commercial fields is 3.7 tons per hectare per year which is far below the potential yield of about 8 tons per hectare per year (Woittiez et al. 2017).

The Malaysian Palm Oil Board houses the largest oil palm genetic resource, covering both *Elaeis guineensis* and *E. oleifera*. These resources, which were collected from the species' center of distribution, are maintained as *ex situ* living collections. Field evaluation of the oil palm germplasm identified oil palms exhibiting other traits contributing to oil yield, namely, large fruit and thin-shelled (Kushairi et al. 2003) and high bunch index (Junaidah et al. 2004). Selected oil palms originating from Nigeria exhibited high oil yield (Rajanaidu et al. 2006). Incorporating these palms into breeding schemes resulted in offsprings with higher FFB, OTB, and oil yield than commercial planting materials (Marhalil et al. 2013). Besides yield, further evaluation of the oil palm germplasm populations revealed other secondary traits such as slow height increment (Rajanaidu et al. 2006), high carotene content (Mohd Din et al. 2002; Mohd Din et al. 2006), high iodine value (IV), high kernel content (Rajanaidu et al. 2006), longer stalk

(Noh et al. 2005), and high vitamin E (Kushairi et al. 2011) which gained interest among breeders. Several *Elaeis guineensis* palms, which originated from Nigeria, Cameroon, Zaire, Angola, and Tanzania, recorded high vitamin E content of between 1300 and 2496 ppm as compared to commercial varieties (800 ppm) (Kushairi et al. 2011). Carotene content ranging from 2000 to 3000 ppm, higher than the 500–700 ppm from commercial planting materials, was recorded in *E. guineensis* from Tanzania and *E. oleifera* palms from Panama and Costa Rica (Mohd Din et al. 2002, 2006). The selected palms are presently being selfed and intercrossed for introgression into oil palm genetic improvement programs to develop planting materials that produce palm oil with increased nutritional value. Apart from the simple and straightforward method of introgressing new traits from *E. guineensis*, oil palm breeders also adopted the inter-specific hybrid breeding program to integrate the fascinating traits observed in the pure *E. oleifera* into the commercial oil palm variety. This is due to the extremely low yield attained in *E. oleifera*; thus, direct commercialization of this species is not possible.

Besides phenotypic measurements, oil palm populations have been characterized using molecular marker tools. The randomly amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) markers were initially used to study genetic diversity among Nigeria, Tanzania, Cameroon, and Zaire oil palm accessions (Shah et al. 1994; Mayes et al. 2000). Furthermore, 48 parental populations were analyzed for genetic diversity using amplified fragment length polymorphism (AFLP) markers (Purba et al. 2000). Several genetic diversity studies of *E. guineensis* and *E. oleifera* accessions originating from different collection sites were reported for pre-breeding programs using RAPD, RFLP, and AFLP markers (Moretzsohn et al. 2002; Ithnin et al. 2006). Bakoumé et al. (2015) analyzed 494 accessions representing 49 oil palm populations using simple sequence repeat (SSR) markers. This study revealed an average genetic distance value of 0.796 among accessions, indicating variability for future exploitation. The presence of rare alleles in populations from countries located within low rainfall and dry weather regions revealed their possible association with adaptive traits. The development of next-generation sequencing (NGS) techniques and expressed sequence tag-based SSRs (EST-SSRs or eSSRs) allow for assessment of the diversity of candidate genes of interest. A total of 19,243 EST sequences were mined from an oil palm EST database (http://palmoilis.mpob.gov.my/palmgenes.html) (Ting et al. 2010). Of these, 722 SSRs were designed, and polymorphisms were observed in MADS-box transcription factors, bZIP zinc finger proteins, and NAC-like transcription factors. Many more reports on applying molecular markers to analyze the genetic diversity of oil palm were recently published (Babu et al. 2019a, b, c, 2020; Bhagya et al. 2020; Sowmya et al. 2017; Venu et al. 2018; Ithnin et al. 2017; Ithnin et al. 2021).

6 Linkage and GWAS Mapping of Oil Palm

In oil palm, the relatively long generation times have promoted interest in MAS to accelerate conventional breeding through early selection. Marker trait association for oil palm was initially conducted by exploiting the genetic mapping approach

whereby a RFLP marker associated with shell thickness was identified (Mayes et al. 1997). Rance et al. (2001) and later Billotte et al. (2005) reported evidence on the linkage between SSR markers and quantitative trait loci (QTLs) for FFB yield, OTB, bunch number, oil-to-mesocarp (OTM), and vegetative components. *E. oleifera* exhibited high polyunsaturated fatty acids (PUFAs) and iodine value (IV) but low SFA compared to *E. guineensis*. Using interspecific OxG mapping populations genotyped with SSR, AFLP, and RFLP markers, Singh et al. (2009) identified QTLs influencing oleic acid, linoleic acid, palmitic acid, and iodine value. Montoya et al. (2013) studied the candidate gene mechanism involved in fatty acyl thioesterase A (FATA) and stearoyl-ACP desaturase (SAD) genes of the oleic acid pathway. Fatty acid candidate genes such as β-ketoacyl-ACP synthases (KAS) I and II were discovered within their associated QTL region on linkage group 15. It was anticipated that other candidate genes influencing other related fatty acids could also be found in the same genomic region. Pootakham et al. (2015) constructed a genetic map from 1086 single-nucleotide polymorphism (SNP) markers (Fig. 2) and identified several QTLs associated with height and fruit bunch weight in linkage groups 3, 14, and 15. Another group reported a separate QTL on a different linkage group linked to oil palm stem height (Lee et al. 2015). Palm oil quality is determined by its free fatty acid (FFA) content which is used as its quality index (Tan et al. 2009). High FFA indicates poor palm oil quality. The levels of FFAs are influenced by endogenous lipase activity which is initiated after the oil palm bunches are harvested. High lipase activity results in accumulation of FFAs and causes rancidity of palm oil. Domonhédo et al. (2018) identified the genetic loci influencing lipase activity in oil palm. This major genetic loci for lipase explained 84–92% of the variation for endogenous lipase content in oil palm. They also validated its acidification by the most common gene, viz., FLL1 (fruit lipase-like 1) and two lipase genes.

Other than genetic mapping, researchers also applied the association mapping (AM) procedure to identify loci influencing oil palm economic traits. Teh et al. (2016) employed a 200,000 SNP array to genotype over 2,000 palms and identified significant QTLs on chromosome 5 that are linked to oil-to-dry-mesocarp (OTDM) ratio, one of the key components of yield trait. It was shown that the progeny exhibiting the homozygous favorable allele for the significant SNP marker had an elevated amount of OTDM. Using the same SNP array across 312 palms, Kwong et al. (2016) detected several SNP markers on linkage groups 4, 12, and 15 influencing the shell-to-fruit (STF) ratio, also an important component influencing mesocarp content and subsequently oil content. Using over a million SNPs, Xia et al. (2019) discovered 26 significant SNPs associated with high palmitic acid and major candidate genes (acyl-ACP thioesterase B genes) within the QTL region in oil palm. Likewise, several SNP- and SSR-based molecular markers were associated with oil yield, vegetative traits, height increment, and bunch quality parameters in oil palm (Ithnin et al. 2017; Babu et al. 2019b, c, 2020; Bhagya et al. 2020; Bai et al. 2017). Bai et al. (2017) performed genotyping by sequencing across 153 oil palm DxP population and identified significant QTLs for OTB and OTDM ratios on linkage groups 1, 8, and 10. These associations were detected based on *E. guineensis*

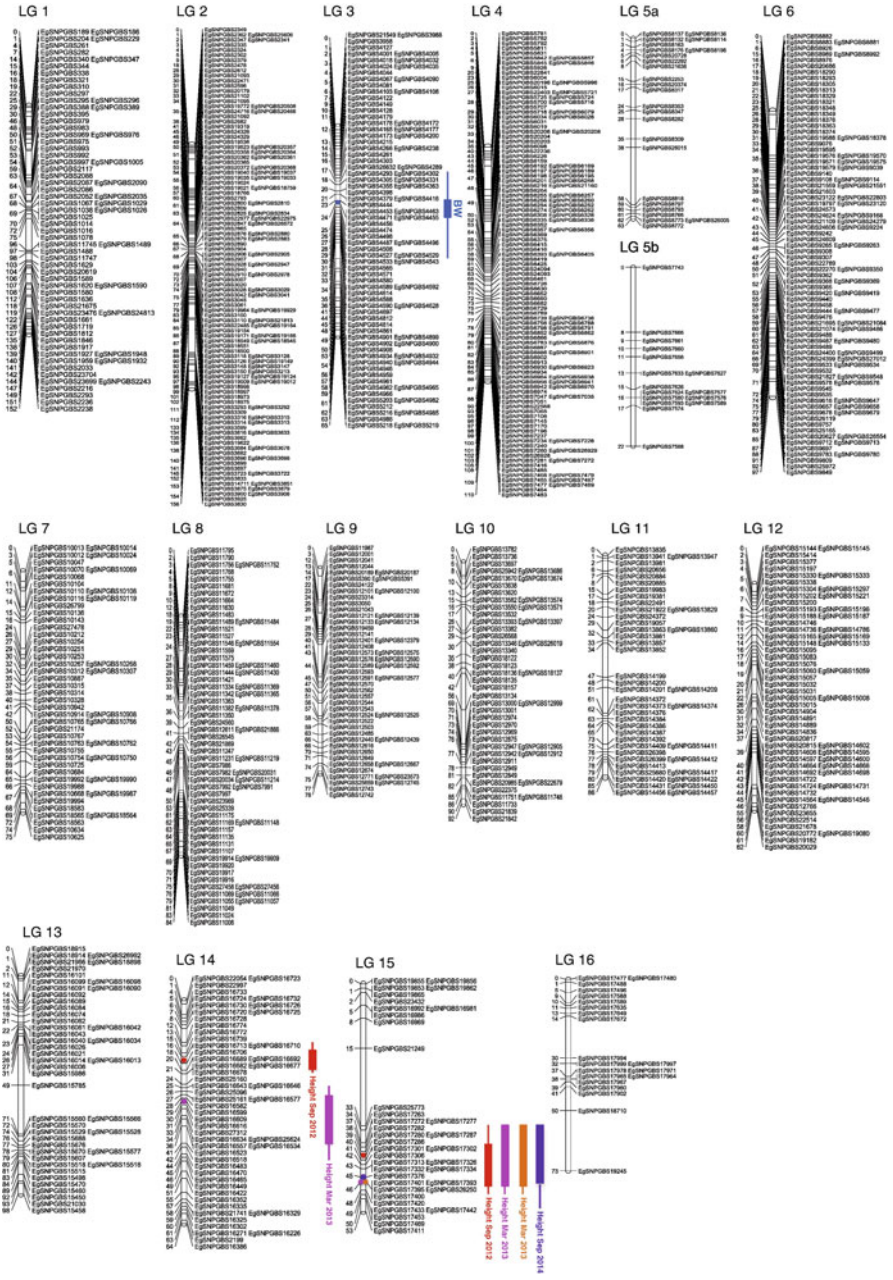


Fig. 2 Oil palm linkage map constructed using SNP markers published by Pootakham et al. (2015). QTLs associated with height and bunch weight (BW) are detected on linkage groups 3, 14, and 15

populations. Ithnin et al. (2021) described QTLs associated with fatty acid composition together with vegetative and yield-related traits from an analysis involving *E. oleifera* natural populations. The group also identified several pleiotropic SNPs linked to multiple correlated traits suggesting that the traits concerned are influenced by common genes and/or involved in the same biological pathways. Similarly, QTLs influencing fatty acid composition were detected in an interspecific (OxG) hybrid population (Shin et al. 2021). In this research, machine learning algorithms were applied to predict the values of the associated traits when different combinations of significant QTLs are used in breeding and selection programs. These outcomes provided the basis for developing MAS tools applicable for breeding programs to improve oil palm productivity and quality.

7 Oil Palm Gene and Genome Databases

Improvements in sequencing technologies and bioinformatic analyses, together with the reduced costs, have contributed to the increased number of crop genomes being sequenced each year. Although many published genomes are incomplete with variable quality, the sequences are a remarkable resource that can be exploited in various ways. The genome sequences have been used to generate high-density molecular markers to map agronomically important traits and subsequently identify candidate genes within a genomic region of interest. These traits can be characterized and bred into commercial varieties. A high-density genetic map also helps in the identification of molecular markers tightly linked to the traits of interest for MAS development. Genome sequences can be annotated with gene models to depict exons, introns, gene names, gene functions, gene regulatory sequences, and protein products, among others, allowing further research toward understanding the genetic control of gene or traits of interest. These inspired oil palm researchers to sequence the oil palm genome (Singh et al. 2013a). The oil palm genome sequence was assembled, published, and stored in Genomsawit (http://genomsawit.mpob.gov.my) (Singh et al. 2013a; Rosli et al. 2014). The database also houses the transcriptome and hypomethylated sequences useful for gene prediction and curation (Amiruddin et al. 2022; Masura et al. 2022; Amiruddin et al. 2020; Rosli et al. 2018a; Rosli et al. 2018b; Chan et al. 2017; Singh et al. 2014; Jayanthi et al. 2013; Singh et al. 2013b) and development of molecular markers (Ting et al. 2014, 2016, 2021; Yaakub et al. 2020). The transcriptome sequences are useful for the identification and analysis of expressed genes (mRNAs). Transcriptome sequencing has enabled researchers to identify differentially expressed genes between tissues, time points, and individuals with contrasting phenotypes. Transcriptomic analyses also play a part in discovering the interactions between biochemical pathways.

The Genomsawit database was integrated into a web-based interface known as MYPalmViewer (http://gbrowse.mpob.gov.my) (Low et al. 2015) for comprehensive search and interactive browsing of the data, to enable direct visualization and exploration of the oil palm genome. A total of 15 tracks were mapped to the EG5.1 genome build including oil palm genomic sequences, GenBank sequences, predicted

genes, genomic markers, other plant genomes, GC content, scaffold gaps, and enzyme restriction sites. Several biological databases were further established to store the results from advanced analysis of oil palm genomic sequences. One of them is PalmXplore-DB which consists of 26,059 EG5.1 predicted genes and their annotation (Sanusi et al. 2018). PalmXplore-DB (http://palmxplore.mpob.gov.my) is useful for the identification of new genes and gene families for biological research in oil palm. Coupled with the transcriptome sequences, research can then be initiated to further understand the biological and molecular role of individual genes and their involvement in regulatory networks. The association of gene expression data from a variety of tissues and developmental stages with gene models creates a new layer of information that contributes to the understanding of gene interactions and regulation. These are essential particularly in developing strategies using genetic engineering technology for oil palm improvement.

From the EG5.1 build, a total of 1714 SSR markers were mined and stored in the Oil Palm SSR Resource Interface (OPSRI-DB), where the primer sequences and their genome locations are available that would help link to phenotypes of interest. The OPSRI (http://opsri.mpob.gov.my) enables browsing of SSR markers together with bioinformatic tools such as Open Reading Frame Search, SSR Search, and BLAST (Rosli et al. 2022). The number of databases from the EG5.1 genome build advance analysis will be expanded in the nearest future.

The information available in Genomsawit could also facilitate researchers in their efforts to improve palm oil nutrition through marker-assisted conventional breeding techniques. Karim et al. (2021) observed an SNP conversion from TAAT to form the CAAT box which could be a promoter activity-enhancing factor leading to an increase in tocotrienol content in palm oil. Using the genomic information in Genomsawit, candidate genes associated with tocotrienol can be identified within the genomic region of the significant SNPs, for instance. New markers can be developed using the candidate gene sequences and then applied to further saturate the associated QTL regions. This will result in the identification of molecular markers tightly linked with tocotrienol in oil palm. The tightly linked QTLs can be applied in MAS to increase selection efficiency and reduce the time needed to produce oil palm with improved tocotrienol content.

8 Biofortification of Oil Palm and Palm Oil

Biofortification is the process of enhancing the nutritional quality of food crops through transgenic, conventional, and agronomic approaches, which involve modern biotechnology techniques, crop breeding, and fertilization, respectively (Garg et al. 2018). In view of the dependency of human nutritional health on plant food and agricultural products, developing different crop varieties with improved nutritional quality is of great importance. Most of the staple crops and some legumes, oilseed crops, vegetables, and fruits, such as rice, wheat, maize, barley, sorghum, soybean, pea, chickpea, canola, mustard, carrot, sweet potato, potato, lettuce, and tomato, have been nutritionally enhanced using micronutrient biofortification through

agronomic practices. Biofortification of crops by foliar spray of iron, zinc, and selenium and fortifying germinating rice plantlets with ferrous sulfate were among the effective ways to promote micronutrient concentrations in plant grains (He et al. 2013; Yuan et al. 2013; Zhang et al. 2013; Poblaciones et al. 2013). A foliar spray of selenium and iodine was favored as the most dynamic and economical method in cereals compared to soil application of the microminerals (Lyons 2018). Other than chemical and organic fertilizers, biofertilizers containing plant growth-promoting soil microorganisms, such as *Bacillus*, *Pseudomonas*, *Rhizobium*, and *Azotobacter* species, have also been applied for crop biofortification (Nooria et al. 2014; Ramzani et al. 2016; Dhawi et al. 2015; Sathya et al. 2013; Nosheen et al. 2011; Hameed et al. 2018). However, these methods are less cost-effective, labor-intensive, and non-sustainable in some cases and therefore cannot be generally applied as a strategy to improve the nutritional quality of most crops. In addition, it is not always feasible to target biofortification of micronutrient into edible plant parts. Thus, the desired nutrients may accumulate in leaves or other non-edible portions of the plants.

Crop biofortification through conventional breeding is the most preferred method on account of its success rate, sustainability, and cost-effectiveness. This approach is useful to enhance and improve the levels of micronutrient content in crops when sufficient diversity of the trait of interest is available in the gene pool of the targeted crop (Garcia-Oliveira et al. 2018). In the scenario where genetic diversity is limited or unavailable for the targeted component, genetic engineering or transformation provides another alternative for developing biofortified crops with the desired nutritional composition (Bouis and Saltzman 2017).

The improvement of oilseed nutritional quality has been targeted in some oilseed crops including oil palm, rapeseed, soybean, and sunflower (Kishore and Shewmaker 1999). Apart from increased oil palm productivity and palm oil yield, efforts are also being made to develop a nutritionally enhanced high-yielding biofortified oil palm. The improvement of fat quality traits in palm oil can be executed through biofortification of fatty acids in palm oil, where the SFA level can be controlled to an optimum level while increasing the level of bioactive components such as carotenoids and tocotrienols. Hence, more value-added palm oil can be generated in new emerging markets. This can be feasibly accomplished by identifying candidate genes and transcription factors affecting iodine value and fatty acid composition in palm oil (Singh et al. 2009). This type of oils can lead to wider dietary acceptance and weaken the link between cardiovascular disease risk and palm oil.

9 Oil Palm Genetic Engineering

Genetic engineering involves modifying and manipulating the genome to change the characteristics of an organism. It is believed to be more specific and could accelerate conventional breeding methods. Genetic engineering technique was applied to achieve sustainability in oil palm growth and development particularly improving palm oil quality, productivity, and tolerance to pests and diseases. Successful transformation strategies and regeneration methods play significant roles in the success of genetic

engineering in any crop including oil palm. The oil palm genetic engineering program started more than two decades ago, much later than other oil-bearing plants, mainly targeting to modify the fatty acid composition in the oil, specifically to increase oleic content for industrial purposes. The objectives were expanded to achieve transgenic palms that can produce palm oil with high stearate, palmitoleic, and ricinoleic acids and high lycopene as well as other products including biodegradable plastics (Parveez et al. 2015; Sambanthamurthi et al. 2002). Three methods to deliver genes into oil palm tissues have been reported, namely, particle bombardment (Parveez and Christou 1998), *Agrobacterium*-mediated transformation (Masli et al. 2009), and novel DNA microinjection (Masani et al. 2014).

Modifying the fatty acid composition in palm oil requires a change in the regulation of the genes involved in oil palm fatty acid synthesis. Some of the key genes concerned have been isolated and characterized, including acetyl-CoA carboxylase (Omar et al. 2008), 3-keto-acyl-ACP synthase II (KAS-II) (Ramli and Sambanthamurthi 1996), palmitoyl-acyl carrier protein thioesterase (Abrizah et al. 1999; Parveez et al. 2010), stearoyl-ACP desaturase (Shah et al. 2000), oleoyl-ACP thioesterase (Asemota et al. 2004), oleoyl-ACP desaturase (Syahanim et al. 2007), and lysophosphatidic acid acyltransferase (Manaf et al. 2005). In addition, a handful of genes involved in the carotenoid synthesis including phytoene synthase (Rasid et al. 2008), phytoene desaturase (Rasid et al. 2014), lycopene cyclases (Rasid et al. 2009), and 1-deoxy-D-xylulose-5-phosphate synthase (Khemvong and Suvachittanont 2005) have also been isolated. Analysis of gene expression using RT-PCR revealed that phytoene desaturase and lycopene cyclase convert lycopene to β-carotene (Römer et al. 2000). Thus, genes for both enzymes are important for the genetic engineering of oil palm targeting palm oil with higher β-carotene content.

Regulatory sequences, also known as promoters, which are capable of increasing or decreasing the expression of specific genes in various oil palm tissues, are available. Oil palm promoters that have been identified include the mesocarp-specific (MT3-A) (Zubaidah et al. 2017) and FLL1 (Nurniwalis et al. 2015), kernel-specific (pOP-KT21) (Siti Nor Akmar et al. 2014), root-specific (MT3-B) (Zubaidah and Abdullah 2010), and leaf-specific (LS01) (Chan et al. 2008; Hanin et al. 2016) promoters. With the availability of these genetic materials and establishment of the transformation technique, positive transformants carrying the respective genes have been produced. Palmitoyl acyl carrier protein thioesterase (PATE) that regulates the accumulation of palmitic acid in palm oil was successfully transformed into *E. oleifera* immature zygotic embryos using the bombardment transformation method (Bhore and Shah 2012). Downregulation of this gene will result in improved palm oil quality with reduced palmitic acid content.

The *Cry* genes isolated from *Bacillus thuringiensis*, which are effective in conferring insect resistance in other crops, were introduced into oil palm immature embryos via the biolistic method (Lee et al. 2006). Further analysis revealed successful expression of the transgene in the transformed tissues. In addition, the transformation method to deliver glufosinate-ammonium resistant genes into oil palm tissues using the alternative *Agrobacterium* system was reported by Masli et al. (2009). Although the transformation rate attained was lower than that achieved

using the biolistic method in oil palm, the *Agrobacterium*-mediated technique offers a stable integration of the transgene at a low copy number.

Yeap et al. (2021) recently reported their success in establishing a gene editing method, namely, clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) mutagenesis system for the oil palm. A mutation frequency between 62.5% and 83.33% was recorded when CRISPR was applied to phytoene desaturase (EgPDS), a gene involved in carotenoid biosynthesis. Mutation of this gene resulted in albino phenotypes among the transgenic oil palm shoots. Furthermore, application of CRISPR/Cas9 on EgBRI1 gene, coding for a major receptor of the plant hormone brassinosteroid, resulted in a stunted phenotype of oil palm transgenic shoots due to nucleotide substitutions. The CRISPR/Cas9 method was also employed to knock out the OsFAD2-1 gene in rice as a model system (Bahariah et al. 2021). The goal is to subsequently repeat this highly effective approach in knocking out fatty acid desaturase genes in oil palm, to produce higher oleic acid in palm oil. These achievements lay the foundation for adopting gene editing techniques for nutrition-enhancement programs in oil palm.

10 Conclusion

The enormous amounts of vitamins and phytonutrients present in palm oil have opened up substantial opportunities in research leading to significant discoveries of their health and nutritional benefits. The available germplasm collection and genomic sequences of oil palm provide great opportunities in developing new planting materials to produce palm oil with enhanced nutritional values. Using novel genomic, genetic, and molecular techniques, relevant biochemical pathways can be investigated which leads to an understanding of the genetic control mechanisms underlying the synthesis and accumulation of essential vitamins and phytonutrients. Such knowledge is useful in formulating a more efficient and rapid improvement process through MAS for conventional breeding and/or development of transgenic lines aimed at increasing vitamins and phytonutrient levels in palm oil. While improvement efforts via conventional breeding are rather straightforward, implementing genetic engineering approaches faces a complex legal framework. Nevertheless, such efforts are worthy, particularly when implemented in a highly productive crop like the oil palm. Moreover, palm oil has a wide range of applications in the food industry. Thus, improving palm oil's nutritional value could intensify efforts toward delivering more nutritious food in addressing the malnutrition issues faced globally.

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