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Recent advances in research on the molecular markers, genetic map and QTL mapping for fatty acid content in African oil palm (Elaeis guineensis Jacq.)

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ABSTRACT
The oil palm (Elaeis guineensis) is a crucial source of global vegetable oil, and understanding the genetic basis of its fatty acid composition is essential for improving oil quality and yield. Recent advances in molecular marker development, genetic mapping, and quantitative trait loci (QTL) mapping have significantly enhanced our understanding of the genetic architecture underlying fatty acid biosynthesis in oil palm. This review consolidates recent findings in these areas, highlighting the integration of genomic technologies, such as marker-assisted selection and association mapping, which have facilitated the identification of key genes and regulatory networks involved in fatty acid metabolism. Molecular markers, including single-nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs), have been employed to construct high-resolution genetic maps. These maps serve as a foundation for QTL identification, linking phenotypic variations in fatty acid profiles to specific genomic regions. Advances in bioinformatics tools have further refined the analysis of large datasets, enabling the identification of candidate genes associated with desirable traits. Moreover, the review discusses the implications of these advancements for breeding programs aimed at enhancing oil palm varieties with optimized fatty acid compositions. By integrating traditional breeding approaches with modern genomic tools, researchers are poised to accelerate the development of oil palm cultivars that meet the growing demands for high-quality oil while addressing sustainability concerns. In conclusion, the convergence of molecular markers, genetic mapping, and QTL analysis represents a transformative step in oil palm research, paving the way for improved fatty acid profiles and increased oil yield. Future directions emphasize the need for continued exploration of gene functions, interactions, and the environmental influences on fatty acid synthesis, which will be crucial for the sustainable advancement of the oil palm industry.

Keywords: *Oil palm; Fatty acid composition; Genetic mapping; Molecular markers; Quantitative trait loci (QTL); Candidate genes.*

INTRODUCTION
The oil palm belongs to the monocotyledonous species Elaeis and belongs to the family Palmae (Singh et al., 2009). It is the highest oil-producing perennial allogamous tree crop with a diploid genome that

comprises of 16 pair of chromosomes (2n = 32) (Montoya et al., 2013). The Elaeis genus encompasses of two commercial species, including E. guineensis and E. oleifera. E. guineensis is commercial oil producing (high palmitic acid content) planting material instigates from West Africa, also referred as African Oil Palm and the E. oleifera is a stubby plant having high characteristic oleic acid containing material natively originates from central and south America, also termed as American Oil Palm (Jeyakumar et al., 2022; Sambanthamurthi et al., 2000). The uniqueness of palm crop is producing two different types of oils namely palm kernel oil and palm oil. The plumpy mesocarp yields edible palm oil and the soft part of kernel seed (endosperm) produces palm kernel oil which both have extensive applications in the field of food and chemical industries (Mancini et al., 2015). Oil palm is categorized into three parts on the basis of fruit structure, dura, psifera and tenara. Dura and psifera are parental cultivated oil palm lines with thick shell/ less mesocarp in dura and very thin shell / rarely embryo found in psifera. Tenara is commercially cultivated D x P hybrid with more mesocarp and thin shell having prominent oil content (Montoya et al., 2013). Tenara (F1 hybrid) is resulted after the conventional cross breeding

The oil palm (Elaeis guineensis) is a key agricultural cash crop, renowned for its high yield and economic significance in the global vegetable oil market (Alhaji et al., 2014). With a growing demand for palm oil, understanding the genetic basis of its fatty acid composition has become increasingly important for both improving oil quality and meeting sustainability challenges (Afifi et al., 2024; Ong et al., 2025). Fatty acids play a crucial role in determining the physical and chemical properties of palm oil, influencing its stability, nutritional value, and applicability in various industries (Koushki et al., 2015; Günenc et al., 2022). Recent advances in molecular genetics have opened new avenues for enhancing the oil quality of oil palm through the identification and manipulation of specific genetic traits associated with fatty acid biosynthesis (Allemann and Allen, 2021; Mota-Martorell et al., 2025). Molecular markers, particularly single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs), have emerged as vital tools for genetic mapping and marker-assisted selection (MAS) (Katral et al., 2024; Alwan et al., 2024). These markers facilitate the dissection of complex traits by linking phenotypic variations to underlying genetic loci (Jeyakumar et al., 2022).

The knowledge of molecular marker has provided the roadmap of linkage relationship and inheritance of trait of interest to accelerate the efficiency and productivity of crop improvement over marker assisted selection (Tuvesson et al., 2021). Genetic mapping has progressed significantly due to the advent of high-throughput sequencing technologies and improved bioinformatics tools. The integration of these technologies has enabled the construction of detailed genetic maps, which serve as a foundation for quantitative trait loci (QTL) mapping. QTL mapping is essential for identifying genomic regions that control traits of interest, including those related to fatty acid profiles. Such insights are vital for developing oil palm varieties with optimized fatty acid compositions through targeted breeding strategies (Yue et al., 2021). Research has identified key genes involved in fatty acid metabolism, including those encoding enzymes responsible for fatty acid synthesis, elongation, and desaturation (Kim and chen, 2015; Xu et al., 2024). Understanding the genetic architecture of these pathways is crucial for enhancing oil yield and quality. Recent studies utilizing genome-wide association studies (GWAS) have further refined the identification of candidate genes linked to desirable traits (Teh et al., 2016; Deng et al., 2022).

Despite these advancements, challenges remain in translating genetic findings into practical breeding applications. The complexity of fatty acid biosynthesis, influenced by environmental factors and gene interactions, necessitates a comprehensive understanding of both genetic and phenotypic variations (Song et al., 2024). This review aims to consolidate recent research on molecular markers, genetic mapping, and QTL mapping related to fatty acids in oil palm, emphasizing their implications for breeding programs and sustainable agricultural practice.

Importance of Oil Palm in Agriculture

Oil palm is known for its exceptional oil yield compared to other oil-seed crops. The total global vegetable oil producing crop is oil palm takes first place (75.69 million MT), and next is soybean oil (56.73 million MT) and then followed by rapeseed oil (27.04 million MT) (Figure 1) (Herrero et al., 2020).

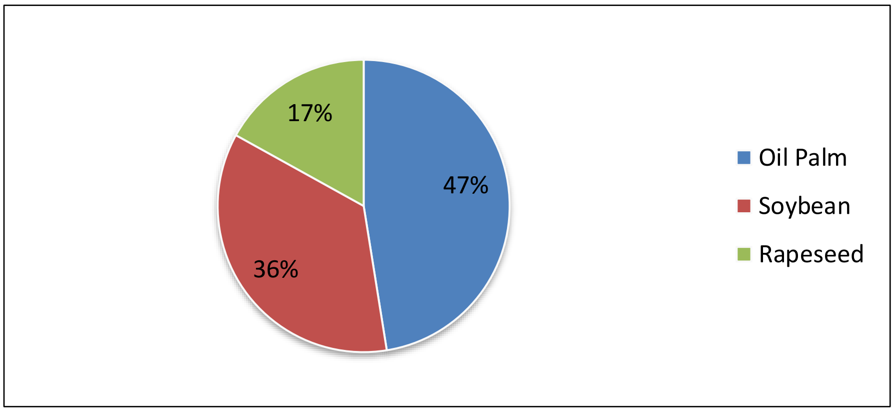

Figure 1. Worldwide ranking of vegetable oil producing crops (USDA)*. *United State Department of Agriculture

This high productivity makes oil palm industry plays a crucial role in the economies of several tropical countries, particularly in Southeast Asia. In nations like Indonesia and Malaysia, palm oil is a major export commodity, contributing to 86% national income and providing livelihoods for millions of smallholder farmers and workers in the supply chain (Mancini et al., 2015). The increasing global demands of palm oil is a phenomenon directed breeders' efforts towards getting GMO free oil and 13% more oil per unit area likely to surpass other oilseeds crops particularly soybean oil as the major vegetable oil (Mancini et al., 2015). Palm oil is widely used in oleochemicals, textiles, cosmetics, and food products like margarine, butter, cooking oils, animal feedstock, pharmaceuticals and industrial applications, including biofuels (Ting et al., 2016). Its unique properties, such as a high melting point and stability at high temperatures, make it an ideal ingredient in various products, thereby increasing its market demand (Koushki et al., 2015). While the cultivation of oil palm has faced criticism for environmental concerns, ongoing efforts in sustainable farming practices and certification schemes, such as the Roundtable on Sustainable Palm Oil (RSPO), aim to promote responsible production. These initiatives focus on reducing deforestation and promoting biodiversity, addressing some of the industry's environmental challenges (Jeyakumar et al., 2022). As the global population continues to rise, the demand for food and edible oils is increasing. Oil palm's high productivity positions it as a key crop for enhancing food security, particularly in developing countries where vegetable oil consumption is rising (Koh & Wilcove, 2008). Advances in agricultural research and technology including genetic improvement and sustainable agricultural practices promote the oil palm productivity and sustainability. Continued research into the genetic basis of traits such as fatty acid composition is vital for developing improved varieties that will be adapted in variable environmental conditions.

Nutritional Enhancement and Significant of Fatty Acid Composition

The fatty acid profile determines the nutritional value of palm oil. It has a balanced mix of saturated, monounsaturated, and polyunsaturated fatty acids, which influence heart health and nutrition (Tan et al., 2021). Crude palm oil, also known as red palm oil (RPO), contains beneficial compounds like tocopherols, tocotrienols, carotenoids, vitamin E, and phytosterols, as well as impurities such as free fatty acids and phospholipids, which can be removed during refining (Madoromae and Lertcanawanichakul, 2025). These nutritional components have antioxidant properties, help combat reactive oxygen species, may aid in cancer treatment, slow aging, and inhibit cholesterol production (Mancini et al., 2015; Tan et al., 2025).. Palm kernel oil (PKO) and palm oil (PO) differ in composition. PKO is about 85% lauric and myristic acids, while PO contains roughly 44% palmitic acid, 40% oleic acid (monounsaturated), 10% linoleic acid (polyunsaturated), and 5% stearic acid. Oleic acid is linked to several health benefits, such as slowing adrenoleukodystrophy progression and improving cardiovascular health by lowering LDL cholesterol and maintaining HDL levels. It may also help regulate insulin production (Wang et al., 2015). Palmitic acid occurs naturally in many vegetable oils, animal fats, and human milk. Table 1 and Figure 2 illustrate the fatty acid composition of palm oil (Mancini et al., 2015; Korbecki and Bajdak-Rusinek, 2019).

Table 1. Fatty acids composition of palm oil

Fatty Acids	Palm Kernel Oil (%)	Palm Oil (%)	Palm Stearin (%)	Palm Olein (%)
12:0	47.8	0.2	0.18	0.27
14:0	16.3	1.1	1.27	1.09
16:0	8.5	44	56.79	40.93
18:0	2.4	4.5	4.93	4.18
18:1	15.4	39.2	29	41.51
18:2	2.4	10.1	7.23	11.64
18:3	-	0.4	0.09	0.4
20:0	0.1	0.1	0.24	0.37

*12:0: Lauric acid, 14:0: Myristic acid, 16:0: Palmitic acid, 18:0: Stearic acid, 18:1: Oleic acid, 18:2: Linoleic acid, 18:3: Linolenic acid, 20:0: Arachidic acid.

Palm oil has two main fractions, palm olein also known as low melting liquid fractions, 65%-75% and second is palm stearin also known as high melting solid fractions, 30%-35% (Figure 3). The extensively grown application of palm oil in food industries is just because of its different characteristic compositions of fractions. Palm olein is used as cooking oil for frying and mayonnaise/margarines preparation because of its high smoke point, i.e., 230 °C and palm stearine has hydrogenated and shortenings properties used as butter replacements in developing and poor countries. Palm oil is usually found in candies, cakes, baked goods, chips, chocolate, cheese analogs, confectionary fats, crackers, cookies, cooking oil, frozen meals doughnuts, (pancakes, pies, pizza, potatoes), ice cream, instant noodles and oatmeals, industrial frying fats, margarines, non-dairy creamers, microwave popcorn, peanut butter, snacks, salad dressings, soups, vegetable ghee and supplements/vitamins and much more (Mancini et al., 2015).

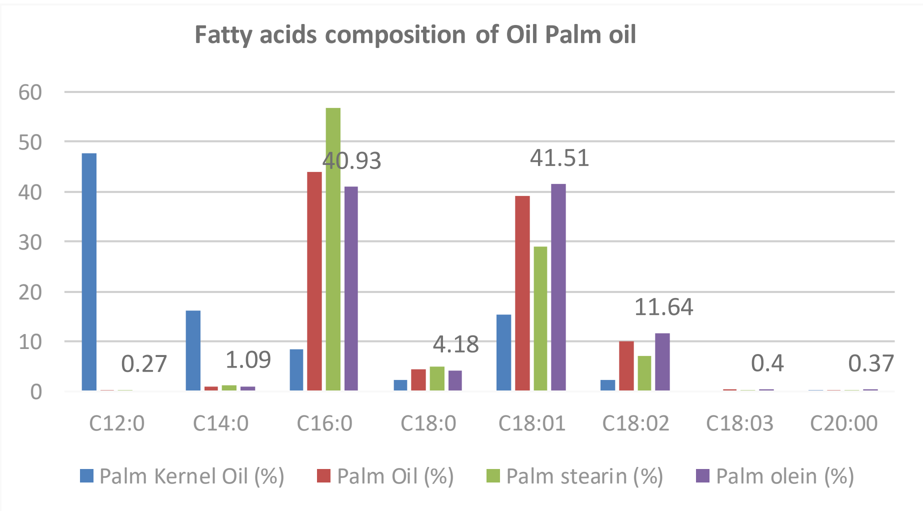

Figure 2. Distribution of fatty acids components among palm oil fractions

A favorable fatty acid composition is essential for meeting dietary guidelines and promoting health. The functional attributes of palm oil, such as stability and texture, are influenced by its fatty acid composition. High levels of saturated fatty acids, particularly palmitic acid, contribute to the oil's solid consistency at room temperature, making it suitable for various culinary applications, including frying and baking (Norhaizan et al., 2013).

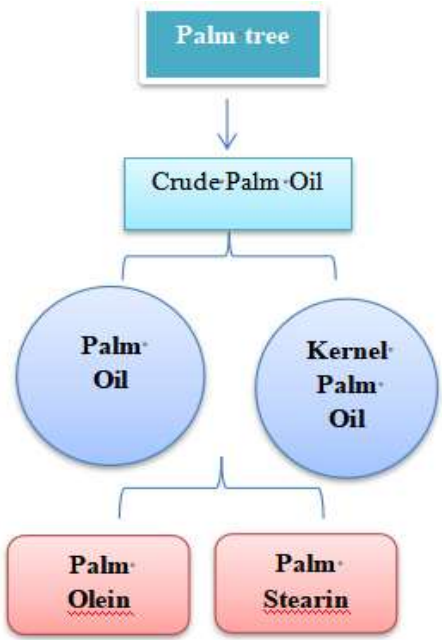

Fig 3. Fractional outlines of Oil Palm oil

Understanding these properties aids in product formulation in the food and cosmetic industries. Consumer preferences are increasingly shifting toward oils with healthier fatty acid profiles. Palm oil's composition affects its marketability, as products with higher monounsaturated and lower saturated fat content are often favored. This shift has implications for breeders and producers aiming to enhance the fatty acid composition of oil palm varieties to meet market demands. As public awareness of health issues grows, the significance of fatty acid profiles in dietary oils becomes increasingly important. The fatty acid composition of palm oil also impacts its suitability for various industrial applications, such as biodiesel production and surfactants. The presence of specific fatty acids can influence the physical and chemical properties of these products, determining their performance and efficiency (Zahan, 2018). Understanding fatty acid profiles is essential for optimizing formulations in these industries. With the rising demand for healthier oils, there is a need for genetic improvement of oil palm varieties to enhance favorable fatty acid compositions while maintaining high yields. Advances in molecular markers and QTL mapping facilitate the identification of genetic traits associated with desirable fatty acid profiles, allowing for targeted breeding strategies (Meena et al., 2023).

Recent Advances in Oil Palm Genetic Linkage Map Construction

Molecular Markers and Genetic Linkage Maps in the Oil Palm Research

A genetic linkage map is based on DNA markers, which are orderly localized on chromosomes based on linkage analysis of reference population's genotyped DNA makers (Yue et al., 2021). The use of high-throughput and robust genotyping platforms have revolutionized genetic mapping in oil palm (app. 1.8 billion bp) (Ting et al., 2014). Technologies such as SNP arrays and next-generation sequencing (NGS) allow for the rapid assessment of genetic variation across large populations (Salim et al., 2024). This capability has significantly increased the density of genetic maps, enhancing the resolution at which QTLs can be identified. Linkage maps are constructed based on the segregation of molecular markers in a mapping population. In oil palm, linkage maps have been developed using both SNPs and SSRs, enabling researchers to identify genomic regions associated with specific fatty acid traits (wang et al., 2015). Recent studies have focused on constructing high-density genetic maps that provide a detailed overview of the oil palm genome. For instance, a comprehensive SNP-based genetic map has been developed, incorporating thousands of markers and covering a significant portion of the oil palm genome (Ting et al., 2023). Such detailed maps are invaluable for identifying QTLs associated with fatty acid profiles, as they enable precise localization of genetic loci. A major research priority worldwide is to breed interspecific hybrid oil palms that produce higher-quality unsaturated oils without sacrificing yield. Strategies to achieve this include optimizing planting density to cultivate more productive genotypes per unit area.. This is a better approach to target the linking markers associated with favorable allels for desiring traits rather than directly targeting the complex polygenic yield parameters traits. All the observing traits other than palm oil content had a great value between E. guineensis and E. oleifera species adding confidence to observing phenotypes (Zulkifli et al., 2020). E. guineensis and E. oleifera are two important commercial oil producing species of the genus Palm bearing annual oil yield about 4,270 kg/hm2, among them 45% of edible oil and 33% of vegetable oil fulfill the global oil demand (Babu et al., 2021). The genetic difference between these two species is quite large, which can proficiently be used to produce the interspecific genetic linkage map. So far, the advancements in genetic linkage between the above species have been deliberate comprehensively (Table 2). Mayes et al (1997), first constructed the first genetic linkage map of oil palm comprising the 97 RFLP markers on 24 LGs with map length of 870 cM (Mayes et al., 1997). In this, RFLP markers with 84 probes were mapped with self-crossed progeny (tenera x tenera). In his study, a total genetic map distance was 860 cM with 24 linkage groups using recombination fraction of 0.4. In this map, more than 95% markers were linked suggesting that this constructed map will be helpful for mapping the targeting commercial genes controlling traits in oil palm. Similarly, Rance et al (2001) constructed the genetic linkage map using the 153 RFLP markers with 84 F2 oil palm populations (Rance et al., 2001).

The first microsatellite (MS and AFLP) based linkage map was constructed with 16 linkage groups. A total of 800 markers (255 MS and 688 AFLP), with genetic map length was 1743cM (Billotte et al., 2005). In this map, 16 linkage groups with LOD score of 3.0 were obtained. Likewise, the first RAPD based linkage map was constructed in 2000, by using the pseudo test crosses strategy (Moretzsohn et al., 2000). In this map, 48 RAPD markers were mapped with 308 F1 progeny populations. A total of 12 linkage groups and distance ranging from 399.7 - 449.3 cM at 5.0 LOD score were obtained.

Table 2. Summary of molecular markers and genetic linkage maps in the Oil Palm research

Populations	Cross	Type of DNA Markers	No. of DNA Markers	Map length (cM)	References
First generation of tenera and pisifera	Interspecific	RAPD	48	399.7 - 449.3	(Moretzsohn et al., 2000)
Colombian *E. oleifera* and Nigerian *E. guinneensis*.	Interspecific	AFLP, RFLP, SSR	252	1815	(Singh et al., 2009)
First generation *(E. oleifera* × *E. guineensis*) × *E. guineensis*	Interspecific pseudo-backcross	SSR, Intra gene SNPs	3,841+12	1.485	(Montoya et al., 2013)
F1 population of *E. guineensis*,	Intraspecific	InDels, SNP	5,278	2,737.6	(Shaha et al., 2024)
E. guineensis genotypes	Intraspecific	SNP	2,388	1,370	(Herrero et al., 2020)
E. guineensis (EG5), *E. oleifera* (O7)	Interspecific backcross BC2	SSR, SNP	1,252	1,618.4	(Kamaruddin et al., 2021)

E. guineensis, *E. oleifera*	interspecific backcross (BC2)	SSR, SNP	1,963	1,793	(Zulkifli et al., 2020)
E. guineensis, *E. oleifera* genotypes	Inter/ Intraspecific	SNP, SSR	4.5 K + 252	1,867	(Ting et al., 2014)
E. guineensis and *E. oleifera*	Interspecific	RFLP	97	870	(Mayes et al., 1997)
E. guineensis genotypes (LM2T x DA10D)	Intraspecific	MS, AFLP	800	1,743	(Billotte et al. 2005)
E. guineensis genotypes (Deli and La Mé)	Intraspecific	SNP	7,324	1,778.52	(Luo et al. 2020)
E. guineensis (Deli dura x AVROS pisifera)	Intraspecific	SNP	27,890	1,151.7	(Ong et al., 2019).

*Some of the information is not mentioned in this table as already describe in this and as well as following section.

Likewise, Seng et al (2011) used AFLP markers, using 120 hybrid crosses of dura (ARK86D) x pisifera (ML161P). For constructing the genetic linkage map, a total of 479 marker loci with a map distance and density of 2,247.5 cM and 4.7 cM respectively with 3.0. LOD score. According to this report, constructed high density genomic map provides the valuable information of closely related breeding population and targeted traits related QTLs (Seng et al., 2011). Later on, another linkage map was constructed using a 281 SSRs marker with 271 oil palm genotyped populations. Generally, a total of 16 linkage groups with the total length of 1935 cM of 281 markers (Cochard et al., 2015).

The first SNP based genome mapping was done by Jeennor and Volkaert using 89 SSRs, 11 non-gene and 90 genes based SNP marker were mapped with LOD of 3 and fraction of 0.45. The total map length of 1,233 cM, having 2 to 20 markers containing an average distance of 6.5 cM between markers. These finding helped to identify the candidate genes QTLs involved in lipid synthesis and other economic yield related traits. This also indicates the using of markers for MAS strategy to improve the targeted trait selection for the oil palm (Jeennor & Volkaert, 2014). Furthermore, Pootakham et al (2015) constructed a linkage map of GBS method based 1085 SNP markers in the African oil palm genotypes. The produced map length was 1,429.6 cM with an average distance of 1.26 cM. They reported that GBS approach was helpful in producing the high density genetic map and also enhance our knowledge for genomic structure of economically important traits related genes (Pootakham et al., 2015).

Similar studies was appeared in 2018, GBS technique based 2,413 SNP markers were used for Deli Dura and Avros Pisifera population for constructing the map. A total map length of 1,161.89 cM, and 0.48 cM was marker spacing (Bai et al., 2018). Furthermore, the first DArT-based linkage map was constructed by Gan e al., in 2018 (Gan et al., 2018). A total of 1,399 DArT and 1,466 SNP markers were used for mapping the two related populations. They produced 16 major linkage groups with lengths of 1,873.7 and 1,720.6 cM and marker density of 1.34 and 1.17 cM, respectively. The integrated genetic map length was 1,803.1 cM with 0.87 cM marker density (Gan et al., 2018). Ong et al (2019) also constructed the linkage map in oil palm. They used 27,890 SNP markers and produced 16 linkage groups with a total length of 1,151.7 cM and an average interval of 0.04 cM (Ong et al., 2019). Recently, SPET (Single Primer Enrichment Technology) markers were used to construct a genetic linkage map from cross of two oil genotypes. A total of 3,501 SPET markers with a total length of 1,370 cM and 1.74 markers per cM were used for constructing the map. This produced 16 linkage groups with a total of 1,054 loci (Herrero et al., 2020). Ting et al (2014) reported the first comparative genome mapping study of two oil palm hybrids. They constructed the high density SNP and SSR based genetic map, which include 4.5 K SNPs and 252 SSRs (Ting et al., 2014). The map resolution was further increased by combining the interspecific (108 palms) integrated map with intraspecific (108 palms) maps, with recombinant length was 1,867 cM. This comparative study is useful to identify the closely linked markers of targeted traits. An integrated genetic map was constructed from two interspecific backcross (BC2) populations consisted of 1,814 SNPs and 149 SSRs markers with a total integrated map length of 1,793 cM (Zulkifli et al., 2020). A high density integrated genetic map was constructed by using the interspecific backcross (E. guineensis (EG5), E. oleifera (O7)) BC2 population. A total of 1,252 markers (100 SSR, 1,152 SNPs) were used to build the linkage maps with spanning 1,618.4 cM (Kamaruddin et al., 2021). Herrero et al (2020) constructed the very first time Single Primer Enrichment Technology (SPET) markers technology based high density saturated linage map from controlled intraspecific cross between two E. guineensis genotypes. In this novel technique, mainly 2,388 SNP markers were utilized for constructing the saturated map with a total length of 1,370 cM, leading 1.74 of marker density. The saturated genetic maps were constructed from intraspecific cross of 112 F1 population of E. guineensis and parents. A total of 5,278 markers consisted of 440 insertion and deletion markers (InDels) and 4,838 SNPs with recombinenet lengths of maternal map was 2,737.6 cM and for paternal map was 4,571.6 cM, with marker densities 2.9 cM and 2.0 cM correspondingly (Shaha et al., 2024). Singh et al (2009) was constructed a linkage map by using the AFLP, RFLP and SSR markers from an interspecific cross between Colombian Elaeis oleifera and Nigerian E. guinneensis (Singh et al., 2009). A total of 252 markers including 38 RFLP, 199 AFLP, and 15 SSR) were used to produce 21 linkage groups with spanning 1,815 cM. An ultra-high density genetic map was constructed from two complex oil palm populations, Deli and La Mé (943 individuals), with 7,324 SNP markers. The total recombinant length of map was 1,778.52 cM in 16 linkage groups (Luo et al. 2022). A high density genetic map was constructed by using the intraspecific cross between Deli dura x AVROS pisifera anchoring 27,890 SNP markers. A total genetic map length was 1,151.7 cM with mapping interval was 0.04 cM (Ong et al., 2019). Based on these outcomes of all findings, mapping of oil palm using variable high-density makers carries comprehensive information for QTL mapping and other MAS based research in the oil palm.

Role of Molecular Markers in Oil Palm Research and Marker Assisted Selection (MAS)

In the maker assisted selection, molecular markers are served as a tool for indirect selection of phenotypically not visible challenging traits at the seedling stage. Molecular markers are the region of DNA that are spread crosswise the plant genome and traced by segregation through generations. Presence of molecular markers can facilitate the breeders to track the gene of interest at seedling stage. Moreover, MAS enable the breeders to recognize the interested traits that cannot be simply indomitable using conventional breeding methods (Varshney et al., 2005). Marker-assisted selection approaches can support the phenotypic screening while increasing the efficiency and accuracy of selection thus overwhelming the traditional breeding short comes (Lee et al., 2015; Xu and Crouch, 2008). This technique is especially valuable for traits with low to moderate heritability, which are difficult to be improved by traditional selection. MAS have proven to be useful in speeding up genetic improvement in agronomic plant species6. In MAS, DNA markers, genetic linkage maps, and QTL mapping on the whole agronomic plant genome are valuable steps for improving the genetic makeup for the traits of low to moderate heritability which cannot be enhanced by traditional selection (Morrell et al., 2012). Both dominant (RAPDs, AFLPs) and co-dominant (SNP, SSR) molecular markers are widely developed and play as a pivotal tools in the genetic improvement of oil palm (Elaeis guineensis), especially for traits related to fatty acid composition (Jeennor and Volkaert, 2013).

These markers serve as identifiable DNA sequences that can be used to track inheritance and identify individuals with desirable traits in breeding programs. The two most widely used types of molecular markers in oil palm research are single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs). Other DNA based tagged molecular makers includes, randomly amplified microsatellite markers (RAM), restriction fragment length polymorphisms (RFLPs), Insertion/Deletions (InDels) (Somyong et al., 2022), PCR based randomly amplified polymorphisms (RAPDs), PCR and RFLP based Amplified fragment length polymorphism (AFLP), DNA amplification fingerprinting (DAF), sequence-tagged sites (STS), sequenced characterized amplified regions (SCARs), variable number of tandem repeats (VNTRs), and Intron polymorphism (IP) markers (Li et al., 2022; Xu et al., 2024). Research studied detected two types of IP markers include, Intron Single Nucleotide Polymorphism (ISNP) and Intron Length Polymorphism (ILP) (Xu et al., 2024). CAPS (Cleaved amplified polymorphism sequence) are another pivotal molecular markers widely utilized for the identification of SNPs (Ong et al., 2015).

The combine use of two CAPS markers and novel SNPs, have been revealed the targeted fruit traits QTL (Li et al., 2023). Moreover, EST (expressed sequence tags) also providing the deep comparative genomic information between E. guineensis and mono/dicotyledonous species. Besides, ESTs are being used to develop the markers for producing the reference genetic linkage maps, which are additionally linked with QTLs mapping and characterizing genes with targeted traits (Ho et al., 2007). Genetic diversity of 51 oil palm genotypes was assessed by RAM markers, generated the total 241 allels with a substantial proportion of polymorphic loci (89%) and heterozygosity (0.64). SSR markers were used to characterize the two oil palm species, E. oleifera and E. guineensis, yielded the 107 alleles, with 0.09% coefficient of similarity (Xu et al., 2024). Moreover, SSRs, known as microsatellites, are short, repetitive sequences of DNA that are highly polymorphic and widely used in genetic mapping. They are favored for their co-dominant inheritance, high levels of variability, and ease of detection. SSR markers have been extensively utilized in oil palm genetic studies to evaluate genetic diversity, population structure, and linkage analysis (Okoye, 2020). In the context of fatty acid composition, SSR markers have been instrumental in QTL mapping efforts. For example, researchers have identified QTLs associated with fatty acid traits by analyzing SSR polymorphisms linked to specific genomic regions. This approach has led to the discovery of key genetic loci that influence fatty acid biosynthesis (Zahan, 2018). SNPs are the most common type of genetic variation found in the genome and represent single base pair changes. They are particularly valuable in oil palm research due to their abundance and the ability to develop high-throughput genotyping methods. Current studies revealed the 62 SNP markers were considerably associated with fatty acid content, including 32 SNPs of palmitic acid content, 4 SNPs of oleic acid content, 1 SNP of linoleic acid content and 25 SNPs of total oil content in oil palm (Xia et al., 2019).These robust and consistent strategies provide pivotal information about population diversity, development of genome and comparative analysis between conserved and divergent genome sequences of oil palms with other plant species and moreover improve the conventional scientific breeding techniques.

Research Progress in QTL Mapping for Oil Palm

Biological agronomic traits are frequently governed by either single gene with significant monogenic inheritance effects, mentioned as qualitative traits or by large number of genes with minimal polygenic inheritance effects, referred as quantitative traits. Quantitative traits associated with genomic loci in agronomic plant species, have been marked by crop breeders for improving the quality, yield, biochemical contents and pest/insect resistance (Singh et al., 2009; Jeyakumar et al., 2022).

In the E. guineensis, oil palm, many significant traits are quantitative and complex in nature, controlled by more than one gene with small effects of environmental factors (biotic and abiotic) and their interactions QTL indicates the gene clusters or DNA chromosomal regions effecting the expression of interested quantitative traits. QTL mapping is the robust technique to discover the relations between traits of interest and DNA markers covering the whole genome of studied species using genetic approaches (Yue et al., 2021). Recent studies have leveraged SNP markers to investigate the genetic basis of traits related to fatty acid profiles. For instance, SNP-based genotyping has facilitated the identification of associations between specific alleles and desirable fatty acid traits, providing insights that can enhance breeding strategies (Salim et al., 2024). The integration of molecular markers into oil palm breeding programs has significantly enhanced the efficiency and precision of trait selection. By utilizing SNPs and SSRs, breeders can implement marker-assisted selection (MAS) to expedite the development of oil palm varieties with optimized fatty acid compositions. This is particularly important in response to market demands for healthier oils and the need for sustainable production practices (Woods et al., 2021). Furthermore, the identification of molecular markers linked to specific fatty acid traits allows breeders to track the inheritance of these traits in progeny, enabling more informed breeding decisions. This genetic information can lead to the development of superior oil palm varieties that meet both economic and environmental goals. Several studies have been published of QTL mapping for oil content and related fatty acids traits of oil palm (Shaha et al., 2024; Kamaruddin et al., 2021; Montoya et al., 2014;; Yaakub et al., 2019), represented in Table 3. These studies exposed that oil and fatty acid contents were resolute by many QTLs located in different chromosomal regions and value of phenotypic variation (PV) were also found from 5 to 45%. However, it is noteworthy that the use of more numbers of DNA markers for anchoring the QTLs higher the chance to find out the candidate genes of desiring traits. Generally two flanking markers were used for each characteristic QTL. For instance, if two flanking markers are closer to significant QTL at the distance of 5cM, it might be a higher probability (99.95% to 95%) to identify the trait related QTL controlled by candidate gene.

Yaakub et al (2019) identified the 13 QTLs for iodine value and fatty acids (C16:0, C18:0, C18:1 and C18:2) in seven linkage groups using the two inter-specific BC2 mapping populations. For this QTL mapping, they were using 1,814 SNPs and 149 SSRs markers and generated consensus linkage map length was 1793 cM (Yaakub et al., 2019) . Zulkifli et al (2020) did QTL mapping using two inter-specific BC2 mapping populations. Both SNP and SSR markers were used in this purpose. They identified a total of 20 QTLs for vegetative and fatty acids parameters on molecular linage groups. Among them 9 for fatty acids (C16:0, C18:0, C18:1, C18:2) and iodine value was detected on LG-1, LG-4, LG-8, LG-12 and LG-15. Other QTLs were associated for height increment, petiole cross section, rachis length, and carotene contents (Zulkifli et al., 2020). The phenotypic variances of major QTLs linked with fatty acids were 29-89%. Kamaruddin et al (2021) using the two BC2 mapping population of oil palm, for the mapping of QTL for segregating the fatty acids contents. They isolated the three major QTLs for iodine value, palmitic acid content, confined on chromosome 3 and linoleic acid content confined on chromosome 2 with phenotypic variance 56.8%, 62.7% and 38.9% (Kamaruddin et al., 2021) . QTL mapping for hybrid interspecific population was done to isolated the QTL for six fatty acids (C14:0, C16:0, C16:1, C18:0, C18:1, C18:2) contents and iodine value. They isolated the ten major and two conservative QTLs harboring on six LGs (OT1, T2, T3, OT4, OT6, T9). The major QTL for iodine value and palmitic acid on LGOT1 explained the phenotypic variation of 60.0- 69.0 % (Ting et al., 2016). A total of 16 QTLs isolated for fatty acids and iodine value contents. Among them, one QTL for C16:0, two QTLs for C18:0, three QTLs for C18:1, one QTL for C18:2 and two QTLs for iodine value. The phenotypic variation for the identified QTLs was small to average between 10 to 36% (Montoya et al., 2014). A QTL mapping was performed using F1 population of 112 individuals on nine traits including oil and vegetative contents using Indel and SNP markers. Only kernel to fruit ratio (K/F), mesocarp to fruit ratio (M/F), and fruit to bunch ratio (F/B) associated QTLS were significantly identified and explain the phenotypic variation was 18.1-25.6% (Shaha et al., 2024). A total of seven significant QTLs were isolated for iodine value and C14:0, C16:0, C16:1, C18:0, C18:1, C18:2 traits across 1, 2, 3, and 15 linkage groups explained % variance range from 13.1 to 55.8. For this QTL mapping, a set of molecular markers (AFLP, RFLP, SSR) were used for an interspecific cross between Colombian E. oleifera (UP1026) and a Nigerian E. guinneensis (T128) (Singh et al., 2009). Montoya et al (2013) did QTL mapping from interspecific pseudo-backcross (E. oleifera × E. guineensis) × E. guineensis, using microsatellite based linkage map of 362 loci with map length was 1.485 cM. They identified 19 QTLs for fatty acids composition and iodine value traits, explained the % variation range from 5.4 to 61.7 (Montoya et al., 2013). Bai et al (2017) isolated 1 major and 3 putative QTLs for two oil contents O/B (oil to bunch) and O/DM (oil to dry mesocarp) using cross between Dura and Pisifera. A total of 1,480 markers were used for constructing the genetic map with marker spanned was 1,527 cM and marker spacing was 1.03 cM (Bai et al., 2017) .

Table 3. Summary of QTL mapping of Oil Palm for fatty acid composition traits

No. of QTLs	PV (%)	Major Traits	Mapping Population	Type of Markers	References
7	13.1-55.8	C14:0, C16:0, C16:1, C18:0, C18:1, C18:2, IV	Colombian *E. oleifera* and Nigerian *E. guinneensis*.	AFLP, RFLP, SSR	(Singh et al., 2009)
8	18.1-25.6	K/F, M/F, F/B,O/Y	F1 population of *E. guineensis*,	InDels, SNP	(Shaha et al., 2024)
3	56.8, 38.9, 62.7	Fatty acids content (C16:0, C18:2, IV)	*E. guineensis* (EG5), *E. oleifera* (O7)	SSR, SNP	(Kamaruddin et al., 2021)
9	29-89	C16:0, C18:0, C18:1, C18:2, IV	*E. guineensis*, *E. oleifera*	SSR, SNP	(Zulkifli et al., 2020)
12	0.14- 69.0	C14:0, C16:0, C16:1, C18:0, C18:1, C18:2, IV	*E. guineensis*, *E. oleifera* genotypes	SNP, SSR	(Ting et al., 2014)
16	10-36	Fatty acids content (C16:0, C18:2, IV)	Intraspecific cross of *E. guineensis*,	SNP, SSR	(Montoya et al., 2014)
13	-	C16:0, C18:0, C18:1, C18:2, IV	BC2 mapping populations	SNPs, SSRs	(Yaakub et al., 2019)
4	7.6-13.3	Oil content traits (O/B, O/DM)	Intraspecific cross of *E. guineensis*, (Dura × Pisifera)	SNPs, SSRs	(Bai et al., 2017)

Genes/ Enzymes Regulating the Palm Oil Biosynthesis

Fatty acid biosynthesis is a complex and critical procedure in oil palm, as a lot of studies have been made on the identification of enzymes encoded by genes that are involved in biosynthesis of fatty acids, phospholipids, triacylglycerol of oil palm. It is a main roadmap for the synthesis of primary components i.e., unsaturated fatty acids of palm oil (Sambanthamurthi et al., 2000; Li et al., 2020; Jin et al., 2017; Yaakub et al., 2019). Recently 42 candidate genes have been identified which are integrated in the fatty acid synthesis with the help of expression analysis, genomic analysis and characterization of active sites and conserved domains (Xu et al., 2024). Ying et al (2018) isolated a GDSL gene encodes esterase or lipase enzyme, plays a vital role in the accumulation of oil in oil palm palm oil content, named as EgGDSL (Jin et al., 2017). Remarkably, in their study, EgGDSL directly proportional to the oil accumulation in the mesocarp of oil palm (Zhang et al., 2018). Diacylglycerol acyltransferase type 2 (DGAT2), an essential enzyme, significantly associated with the synthesis of TAG (triacylglycerol) by esterification of di-acylglycerol with acyl-CoA (Jin et al., 2017). Their four taxa of DGAT gene (WS/DGAT, DGAT1, DGAT2, DGAT3) have been distinct in their physiological roles, mainly in vegetative processes associated to the formation of fruits, seeds, and reproduction in endosperm and mesocarp tissues (Rosli et al., 2018). Li et al (2020) isolated the EgMADS21 gene regulating the expression of EgDGAT2, thus affecting the accumulation of fatty acids in oil palm (Li et al (2020). Beta-ketoacyl ACP synthase II (KAS II) is a rate regulating enzyme encoding by gene, controlling the high ratio of palmitate content as compared to stearate in oil palm mesocarp. KAS II enzyme activity was screened over various fruits form of oil palm by the researchers, and find out the positive correlation between KAS II and C18:1/C18:2 and iodine value. In addition, increasing the KAS II activity is also increasing the concentration of oleic acid and linolinic acid (Sambanthamurthi et al., 2000). Another important enzyme encoded by gene is acyl ACP thioesterases, play a vital role in termination of fatty acids chain. Thus free fatty acids can be released into cytoplasm from plastids where they are converted into TAG triacylglycerols. Studies have been made on thioesterase activity revealed the palmitoyl ACP and oleoyl ACP act as substrates, suggesting the high content of palmitic acids and oleic acids. In this mechanism, thiesterase cleaved the palmitic acid from palmitoyl-ACP, and thus free palmitic acids exported out from plastid in to cytoplasm where they converted into TAGs via esterification process catalyzing by acyltransferases in the endoplasmic reticulum. Stearoyl ACP desaturase is another important enzyme encoding by gene, specifically binds with stearoyl-ACP, as a substrate and desaturate into oleic aicds under aerobic conditions but do not bind with palmitoyl-ACP to generate palmitoleic acid. That's why palmitic acids and oleic acids are major contents in oil palm oil (Sambanthamurthi et al., 2000). Moreover, another imortant gene KCS11, actively involved in both saturated and unsaturated acyl chains fatty acid biosynthesis. The magnesium dependent phosphatidate phosphatase gene (PAH2), related to C18:1, play a role in catalyzing the de-phosphorylation of phosphatidate to produce di-acylglycerol and might be involved as multiple enzymes repressor in biosynthesis of phospholipid (Yaakub et al., 2019).

Concluding remarks and the way ahead

In this review our major focus to understand the significant integration of molecular markers and mapping technologies towards the genetic mechanism of fatty acid composition in oil palm (Elaeis guineensis), developing the high yield, disease resistant and nutritionally superior oil palm varieties. These strategies have been transformed oil palm breeding efficiency by aiding the characterization of key genes and loci that control the biosynthesis of fatty acids, ultimately improving the palm oil quality and its yield (Gan et al., 2018; Mohd Shaha et al., 2024). High-throughput genotyping approaches, such as genome wide association studies (GWAS) (Osorio-Guarín et al., 2019), next-generation genotyping (Montoya et al., 2024), and high density linkage maps (Ting et al., 2023), have eased the integration of SSR (simple sequence repeat) (Suraninpon et al., 2022) and SNP (single nucleotide polymorphism) markers (Ngoot-Chin et al., 2021) and marker assisted selection associated which generate the elite varieties of oil palm and vital fatty acid profiles via reducing the breeding cycle time laps. The identification of QTLs associated with the major fatty acids such as palmitic acid, oleic acid, and linoleic acid is the major breakthrough in recent researches (Ting., 2016). The genetic regulation of these fatty acids is complex, involving multiple transcription factors, genes, enzymes, and metabolic pathways that interrelate with variable environmental conditions (Luo et al., 2024; Wei et al., 2024). Regardless of these remarkable advancements, challenges must be persisting, comprising the complicated polygenic nature of oil content traits, genotype environment interaction ratio (G*E), and the validation of identified QTLs across diverse genetic backgrounds (Land et al., 2023). Addressing these issues needs an integrative method that combines all omics techniques involves genomic, proteomic, transcriptomic, and metabolomics to unknot the molecular mechanisms of fatty acid biosynthesis (Wang et al., 2025). Furthermore, modern genome editing technologies such as CRISPR-Cas offer promising roadmap for genetic modifications by altering the key genes controlling the fatty acid composition, potentially over rule the conventional breeding techniques and leading the production of elite oil palm varieties optimized for industrial, nutritional, and biofuel applications (Li et al., 2022). However, publicly acceptance of these modified oil palm varieties must be considerable challenge while implementing these genome editing technologies in commercial level. Continued research efforts should focus on the application of artificial intelligence and machine learning in genetic analysis could offer new insights into complex trait inheritance and optimize breeding decisions.

The integration of gene expression or transcriptomic data with QTL/GWAS studies fundamentally aims to establish a causal pathway from genotype to expression level and ultimately to phenotype (Zhang et al., 2026). This is typically achieved through a sequential analytical framework. First, expression quantitative trait locus (eQTL) mapping is performed to identify genetic variants that regulate mRNA abundance. Subsequently, statistical approaches such as colocalization analysis (e.g., using the COLOC method) or Mendelian randomization are applied to test whether the genetic signals associated with the complex trait of interest share a common causal variant with those influencing gene expression (Dominguez-Alonso et al., 2023). This step is critical for determining if a gene's expression acts as a functional intermediary linking genetic variation to phenotypic outcomes.

In parallel, to refine candidate gene discovery within identified QTL intervals, tissue-specific transcriptomic profiles can be leveraged to prioritize genes whose expression patterns are correlated with the trait. Additionally, constructing gene co-expression networks helps elucidate system-level regulatory modules that may be under genetic control and relevant to the phenotype. Collectively, this multi-omics integration strategy enhances the prioritization of causal genes and elucidates the molecular mechanisms, often involving transcriptional regulation, through which genetic variants shape complex traits, such as oil composition in plants (Yuan et al., 2023).

In conclusion, integration of molecular marker technology, linkage mapping, and QTL analysis represent a significant leap forward in oil palm genetic improvement and in breeding programs will not only enhance oil yield and fatty acid composition but also promote sustainability of palm oil industry. Continued advancements in genetic research and biotechnological innovations will further accelerate the development of oil palm varieties with optimized oil quality, meeting food security, economic growth and environmental sustainability goals in the palm oil industry.

Authors' contribution

Z.Z. Zhao Writing original draft.; B. Alam analysis Data; Q.F. Wu , X.H. Zeng and L.X. Zhou Writing-review and editing. All authors read the final manuscript and have given final approval of the version to be published.

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