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REVIEW ARTICLE

Phenomics, genomics of oil palm (*Elaeis guineensis* Jacq.): way forward for making sustainable and high yielding quality oil palm

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Abstract Oil palm (*Elaeis guineensis* Jacq.) is a heterogeneous, perennial crop having long breeding cycle with a genome size of 1.8 Gb. The demand for vegetable oil is steadily increasing, and expected that nearly 240–250 million tons of vegetable oil may be required by 2050. Genomics and next generation technologies plays crucial role in achieving the sustainable availability of oil palm with good yield and high quality. A successful breeding programme in oil palm depends on the availability of diverse gene pool, ex-situ conservation and their proper utilization for generating elite planting material. The major breeding methods adopted in oil palm are either modified recurrent selection or the modified reciprocal recurrent selection method. The QTLs of yield and related traits are chiefly located on chromosome 4, 10, 12 and 15 which is discussed in the current review. The probable chromosomal regions influencing the less height increment is observed to be on chromosomes 4, 10, 14 and 15. Advanced genomic approaches together with bioinformatics tools were discussed thoroughly for achieving sustainable oil palm where more efforts are needed. Major emphasis is given on oil palm crop improvement using holistic approaches of various genomic tools. Also a road map given on the milestones in the genomics and way forward for making oil palm to high yielding quality oil palm.

Keywords *Elaeis guineensis* · Genomics assisted breeding · Genomic selection · Speed breeding · High yielding quality oil palm

Introduction

Oil palm (*Elaeis guineensis* Jacq.) is a perennial crop with long breeding cycle of 15–18 years with lot of challenges in achieving the sustainable oil palm with good yield and high quality oil palm. After the availability of draft genome sequence in the year 2013, a lot of progress has been made to identify the important genes in oil palm. A focused review is required to summarize the work and to make path for making sustainable and high yielding quality oil palm. In oil palm, few reviews are available (Soh 2017; Parveez et al. 2015; Barcelos et al. 2015; Zulkifli et al. 2017) on various issues like tissue culture and breeding. However, all the reviews discussed only briefly on tissue culture, breeding or transformation. But the present review focused on the role of phenomics and genomics in oil palm improvement programmes to make oil palm as sustainable golden palm. The review focus more on the role of genomic technologies in making successful and sustainable oil palm to meet the world palm oil demands.

Taxonomy

The African oil palm (*Elaeis guineensis* Jacq.) is a major source of edible oil which shares a major contribution of vegetable oils in the world trade. The history of it’s origin and evolution attracts a confusing interpretation based on literature which ends in opposing views and concepts. Though there is documented evidence on African oil palm origin and distribution, however a number of uncertainties exist. Taxonomically, oil palm belongs to the family Aricaceae (formerly known as Palmaceae), sub-family Arecoideae and the genus *Elaeis*. As per the reports, the genus *Elaeis* has four species viz., *Guineensis, Oleifera, Odora*

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and *Madagascariensis*. But this classification has few contradictories like other crops. Based on morphological and molecular distinctness, the genus *Elaeis* is classified into above said four species. However, the genus *Elaeis* mainly classified into two distinct species African and American oil palm. The most commonly accepted oil palm is African oil palm i.e., *E. guineensis*. Various nomenclature have been proposed for oil palm (Schultes 1990). But the commercially grown oil palm is named as African oil palm (*E. guineensis* Jacq.) as proposed initially by Jacquar in the late 1763. The Guinea coast of West Africa was considered as its primary origin and it was found in the late sixteenth century (Lobelius 1581). The second species is known as American oil palm (*E. oleifera* Cortes.) which was initially called as *E. melanococca* and was thought to be part of *E. guineensis*. But it has been placed in a separate genus *Oleifera* due to its several morphological differences with African oil palm like trunk, fronds and inflorescence etc. *E. odora* Traill. and *E. madagascariensis* Becc. were 3rd and 4th species belongs to the genus Elaeis. Later Corley (1976a, b) and Corley and Tinker (2003) opined *Odora* as a separate species due to its minor differences. Similarly Hartley (1977a, b) considered *E. madagascariensis* as a form of *E. guineensis*.

Origin and distribution

The origin and distribution of oil palm having conflict of reports, i.e., either African or American continent (Corley 1976a, b; Hartley 1977a, b; Corley and Tinker 2003). However, most of the researchers opined West Africa as the centre of origin for *E. guineensis* and then distributed to different places due to human interference. Numerous evidences supporting the centre of origin exist, as well as presence of fossil pollen in Miocene strata in Nigeria, shells of oil palm in Uganda (5000BP) and reports by Eurpoean workers (Hartley 1988). An exhaustive study conducted by Rees (1965) opined West Africa is the origin for *E. guineensis*. He ascertained a transparent proof of oil palm in Portuguese voyages before distribution of new world. Currently, oil palm is widely distributed in 34–36 countries with a major share from Indonesia, Malaysia, Nigeria, Thailand, Columbia (accounts for 92% of world CPO) and China and India.

Forms of the genus *Elaeis*

The genus *Elaeis* categorized into various forms based on shell thickness and fruit colour. Based on shell thickness, oil palm has *dura, pisifera, tenera* and *macrocarya* types of fruit forms (Corley 1973). The SHELL gene discovery in oil palm leads to increasing the yield (Beirnaert and Vanderweyen 1941). The thick shelled dura has dominant Sh alleles, shell less pisifera has homozygous sh recessive allele, whereas the hybrid tenera has a lot of mesocarp and high oil content which has alleles (*Shsh*) from each dura and pisifera. Tenera hybrid is commercially accepted variety by all the oil palm growing parts of the world (Hartley 1977a, b). An equilateral triangular pattern is applied for oil palm planting with different densities based on soil fertility, topography and other management factors. The simple tool to differentiate the three fruit forms could be a massive challenge for oil palm breeders and growers. Recently with the availability of gene sequence, few scientific achievements are available on the molecular identification of fruit forms (Babu et al. 2017; Ritter et al. 2016; Reyes et al. 2015). Based on the fruit color, *Nigrescense*, *Virescense* and *Albescense* are the three types available in oil palm. *E. guineensis* has idolatrica and dumpy fruit color. Singh et al. (2013) reported and identified *VIRESCENSE* (VIR) gene which controls fruit color in oil palm. Fruit color is the ripeness indicator in some genotypes of oil palm.

Nutritional importance of palm oil: myths and facts

Palm oil is the world's second largest consumed vegetable oil in facing tons of discussion on the quality and its impact on the cardiovascular diseases (CVD) in humans. The ratio of saturated fatty acids (SFAs) to unsaturated fatty acids (UFAs) is almost equal, that consists of large amount of anti-oxidants, beta carotene and vitamin E (Edem 2002; Skeaff et al. 2009). Studies by Pieters and de Maat (2015) showed reduced cholesterol level after palm oil consumption. However there is no evidence that clearly support cardiovascular guidelines that encourage a high consumption of polyunsaturated fatty acids (PUFAs) and a low consumption of total saturated fats (DiNicolantonio 2014). Recently a meta-analysis (Eilander et al. 2015) also showed that palm oil (PO) may produce both favorable and unfavorable changes as compared to the other dietary SFA, MUFA and PUFA. They observed almost no changes in total cholesterol to high density lipid (HDL) cholesterol, LDL/HDL cholesterol ratios. Recently, Lucci et al. (2015) conducted an exhaustive study on the effect of hybrid palm oil (HPO) and extra virgin olive oil (EVOO) on human plasma lipids related to CVD risk factors, and observed no significant changes in cholesterol, LDL, HDL and tri-acyl glycerols. Their study provided additional support that PO is not harmful as suspected. The crude palm oil (CPO) is a rich source of high carotenoids (500–700 ppm), tocotrienols (600–1200 ppm) and tocopherols (Lee et al. 2001;

Mozaffarian and Clarke 2010). CPO also acts as a good natural antioxidant, acts against reactive axygen species (ROS) which plays key role against aging, CVD and cancer (Eilander et al. 2015). The tocotrienols are reported to be natural inhibitors of cholesterol synthesis. However, several studies found no significant differences when PO compared to Soybean oil, to Olive oil (rich in oleic acid, a MUFA) (Otto et al. 2012), to Sunflower oil (rich in oleic acid and PUFA) and to Canola oil (rich in MUFAs).

Steps involved in oil palm improvement through genomics

In the present review, emphasis is given on improvement of oil palm involving holistic approaches of genomic technologies. Also a road map given on the milestones in oil palm genomics and way forward for making oil palm to high yielding quality oil palm. The following steps involved in oil palm improvement, viz., (1) Germplasm exploration, domestication and characterization, (2) gene identification and mapping, (3) genomics assisted breeding, (4) genomic selection and (5) genome editing are discussed below.

Germplasm collection, conservation and characterization

Any successful breeding programme depends on the availability of diverse gene pool, their ex-situ conservation and proper utilization for generating elite planting material. This is particularly more pertinent in the case of oil palm where a narrow genetic base is the major constraint in achieving genetic enhancement. The source of *pisifera* is limited to few palms, where as female (*dura*) was from four bogor palms in the botanical garden of Bogor, Java, Indonesia in 1948 (Rajanaidu et al. 1996).

Oil palm germplasm collection

Countries like Malaysia, Indonesia, and India started exploring the genetic resources of oil palm germplasm. The preliminary exploration was carried out in Congo in the year 1920s. After Second World War, prospection in Congo was started in estates with Yangambi material. The criteria followed for selection of the elite germplasm is palms having $\geq$ 92.5% mesocarp to fruit (MF) and 32% oil to bunch (OB) content. Likewise several collections were made in Ivory Coast, Cameroon, Palm Oil Research Institute of Malaysia (PORIM) from 1940 to 1992. A major collection program was organized jointly by NIFOR and the Malaysian Agricultural Research and Development Institute (MARDI) in 1970s.

African oil palm germplasm resource

The source of the presently cultivated African germplasm was from Deli, AVROS, Yangambe, La Me etc. All these materials are very precious and are the major source of genetic material to the world. All these material has very special characters for yield and oil yield traits. Due to its agronomic potential, a major source of germplasm for good oil quality low height increment and other potential triats which was introduced in 1920s to Africa and in 1950s to Asia. However, major emphasis has been given in the last 40–50 years on *E. Oleifera* germplasm in Malaysia, Ivary Coast, Coastarica, and Brazil (Meunier 1975; Barcelos et al. 2002). It is also being effectively used in interspecific hybrids to introgress valuable *oleifera* germplasm specific traits into *guineensis* (which is commercially cultivated) (Corley and Tinker 2003).

Oil palm germplasm in India

In India, oil palm was first introduced for ornamental purpose in the nineteenth century in the National Botanical Gardens of Kolkata, and then gradually spread to other parts. During 1960s, Department of Agriculture, Kerala introduced dura and tenera from Malaysia and Nigeria for studying the feasibility of oil palm cultivation, along with other plantation in little Andaman. The Indian Council of Agricultural Research-Indian Institute of Oil Palm Research (ICAR-IIOPR) Research Centre, Palode was established as a sub-station of Central Arecanut Research Station during 1959 for taking up research on Arecanut. In order to bring oil palm research under one umbrella, the centre was later merged with ICAR-IIOPR. During VIII Five Year Plan, ICAR established National Research Centre for Oil Palm (NRCOP) at Pedavegi, Andhra Pradesh on February 19, 1995 to strengthen the research on all aspects of oil palm under irrigated conditions. Later it was upgraded as Directorate of Oil Palm Research (DOPR) and then to ICAR-Indian Institute of Oil Palm Research (ICAR-IIOPR) during XII Plan. The details of the germplasm blocks with the number of germplasm and year of planting is in Fig. 1.

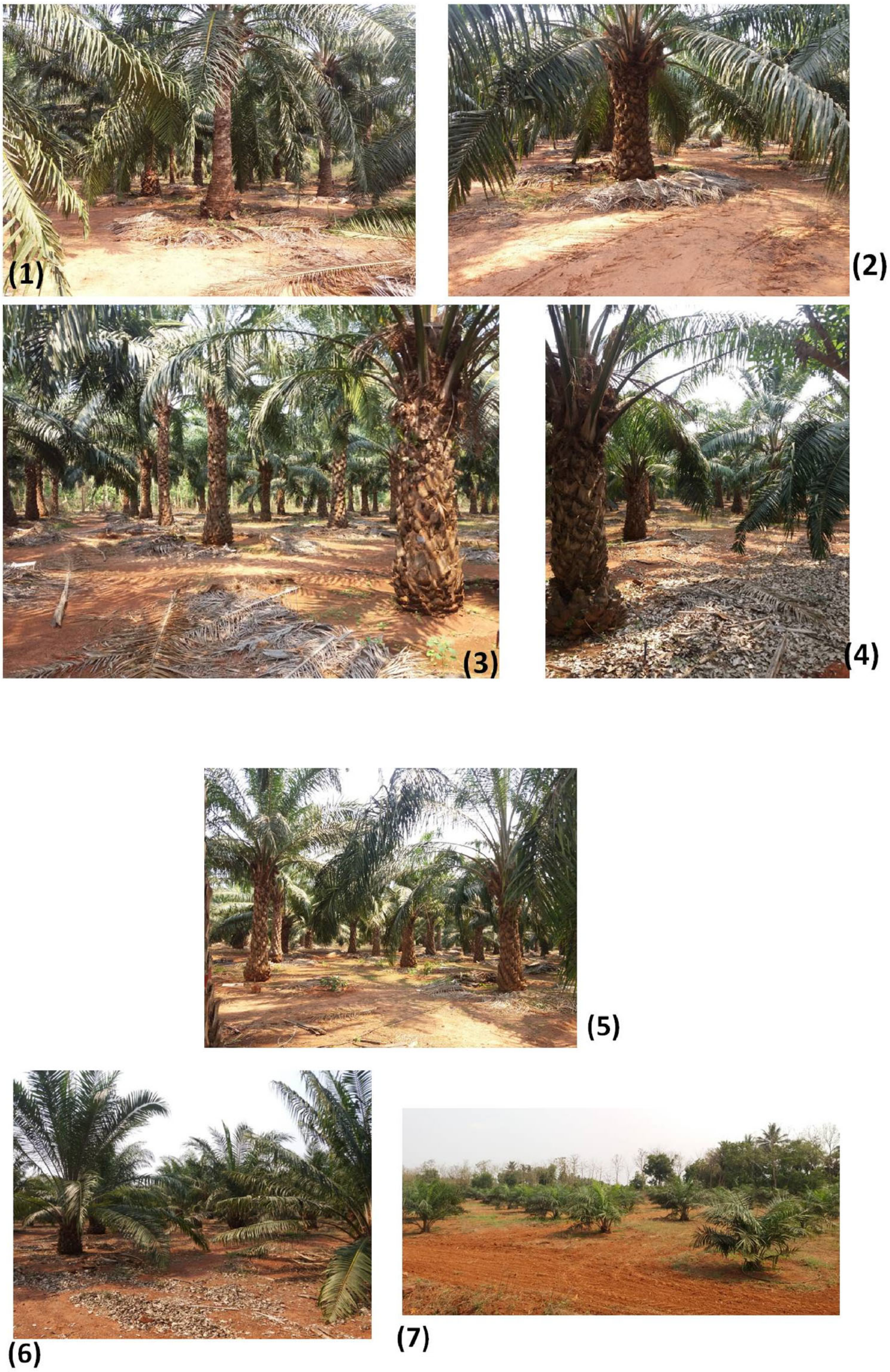


Fig. 1 The germplasm blocks of the institute. (1) germplasm block 1 (06th August, 2004, 130 palms), (2) germplasm block 2 (06th August, 2008, 105 palms), (3) germplasm block 3 (05th October, 2009, 210 palms), (4) germplasm block 4 (13th January, 2010, 53 palms), (5) germplasm block 5 (28th September, 2010, 88 palms), (6) germplasm block 6 (24th July, 2016, 654 palms), and (7) germplasm block 7 (25th June, 2018, 119 palms)

Gene identification and mapping

Genetics and conventional breeding for oil palm improvement

A brief note on genetics and conventional breeding approaches in oil palm improvement given in this section. The four Bogor palms are the basic source of the present commercial plantations across the world (Ooi and Rajanaidu 1979). The major breeding methods adopted are either modified recurrent selection (MRS) method or the modified reciprocal recurrent selection (MRRS) method. First time, Rosenguist (1986) reported MRS in oil palm where the Deli dura parents are selected as commercial hybrid seed production mother palms for further breeding (Corley and Tinker 2003). The advantage of this method is quicker turnover of recurrent crosses and less space required. It exploits only GCA but not SCA (Soh 2017). Pros and cons of the RRS in oil palm have been already discussed (Corley and Tinker 2003). The RRS exploits GCA and SCA and due to this one breeding cycle extends over a long period of time ($\sim$ 20 years), where a high genetic gain has been achieved (Durand-Gasselin et al. 2005). Blup selection was used to integrate unbalanced data from native and experimental designs to get breeding values of parents in oil palm (Wong and Bernardo 2008). Di haploid breeding also tried in oil palm for production of homogeneous F_1 population. It is extremely essential because of long breeding cycle and high inbreeding depression in oil palm.

Milestones in gene identification and mapping

For the convenience of readers, the era of oil palm genomics in oil palm can be divided into two parts viz., genomics before and after sequencing (Fig. 2). The era of biotechnology in oil palm started with RAPD markers (Shah et al. 1994), later the finger printing and genetic mapping studies were conducted using RFLP and AFLP based markers during 1995–2000 period. With the development of species specific, co-dominant simple sequence repeat markers, a major revolution took place in all crops along with oil palm. The first hybridization based SSR marker development and linkage map of oil palm was developed in 2005 (Billotte et al. 2005). The development of SSRs is an expensive task and involves hybridization method which is a laborious method. The major breakthrough in the genomics era of oil palm biotechnology happened with the availability of whole genome sequence of African oil palm (Singh et al. 2013), and draft genome sequence of elite dura palm (Jin et al. 2016). The year 2019 witnessed the first draft genome sequence of Ganoderma fungus which is a causative agent of basal stem rot disease (BSR) in oil palm (Utomo et al. 2018) and also first microsatellite database for all chromosomes made available (Babu et al. 2019a).

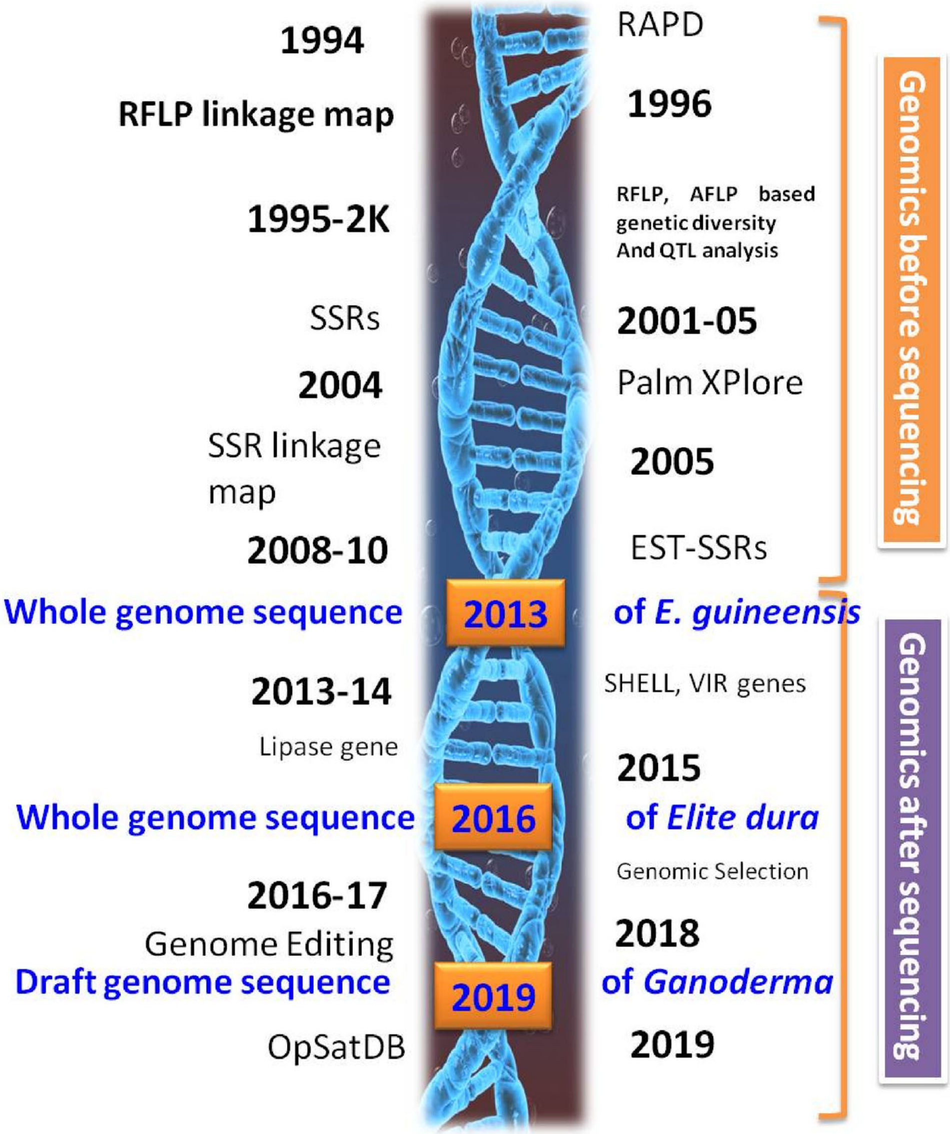
Strategies for making oil palm to golden palm

Here in this review we are suggesting a complete picture on making oil palm to high yielding quality oil palm (HyQOP) also called as golden palm in a sustainable manner. This approach may enhance oil yield with good quality oil parameters along with disease resistance (Fig. 3). This is often the best way where it will solve the many issues related palm oil quality along with feeding the most of the population. This figure depicts steps involved in genomics technologies to improve traits like high fresh fruit bunch (FFB), more oil yield, high iodine value (IV), low phytate and SFs, high oleic acid, linoleic acid and more USFs along with dwarf pattern (less height increment) and BSR resistant. Altogether results in a complete golden palm which will bring revolution in the oil palm especially in the vegetable oil production.

Yield and oil yield improvement

The demand for vegetable oils is gradually increasing, and is expected that nearly 240–250 million tons of vegetable oil may be required by 2050 in the world (Barcelos et al. 2015). The major oil seed crops in the world are oil palm, soybean, sunflower and canola. Among these, oil palm occupy least area, however contributing highest productivity (MPOB 2017a). Increasing oil palm production by expansion of cultivable area is not a reasonable choice, where boosting the productivity by increasing the yield on existing land is the best one. In these circumstances, genomics assisted oil palm improvement plays key role in yield improvement. The traits like fresh fruit bunch (FFB), oil to bunch (OB), fruit to bunch (FB), mesocarp to fruit (MF), oil to dry mesocarp (ODM), and oil to wet mesocarp (OWM) are the major factors determining the yield of the oil palm. The efforts of conventional breeding methods resulted in an increase of 20–25% yield. However, with the aid of genomics technologies viz., quantitative trait loci (QTL) mapping, marker assisted selection (MAS), genomic selection (GS) and genome editing (GE) will aid in increasing a drastic yield improvement in lesser time. Ukoskit et al. (2014) identified major QTLs influencing sex ratio and shell thickness having small effects on independent loci, but with epistatic interactions. Though several reports available on identification of QTLs influencing important oil yield and yield related traits, but no efforts were carried out in validating those results in a large population of oil palm. This validation is a major lacuna

Fig. 2 The time line of the oil palm genomics before and after the whole genome sequence of oil palm



observed in many crops including oil palm. Recently Jeennor and Volkaert (2014) identified SSRs and genic SSRs for FFB, OB, FB and MF traits. Most of these reports are based on linkage mapping populations (F_1). However linkage based QTL mapping has several disadvantages. The association mapping using natural population offers several advantages like much higher mapping resolution, greater allele number and broader reference population (Mott et al. 2000). Few reports are available on using GWAS for QTL mapping using natural population consisted of diverse germplasm (Babu et al. 2017; Bhagya et al. 2020). The location of QTLs for different yield traits by several workers is given in Table 1.

After the availability of the oil palm genome sequence, the next generation sequencing (NGS) based methodologies took to the new world of oil palm, where the single nucleotide variations playing significant role. Several NGS based techniques like genotyping by sequencing methods have been employed to reveal the location of nucleotides linked to yield and oil yield related traits. Bai et al. (2017) studied GWAS on F_1 population using 1357 SNPs and 123 SSRs and identified QTL for OB and ODM. Pootakham et al. (2015) used GBS for BW and identified candidate genes for DELLA proteins, however few reports are available on GWAS using natural oil palm germplasm (Babu et al. 2019b, c, 2020). All the above results indicated that most of the QTLs of yield and oil yield related traits are located on chromosome 4, 5, 10, 12 and 15. The diagrammatic portrayal of the major QTLs on the five chromosomes is given in Fig. 4. The fruit to bunch QTL linked genes mainly located on chromosomes 4, 10, 12 and 15. Similarly QTLs of oil to bunch were mostly located on

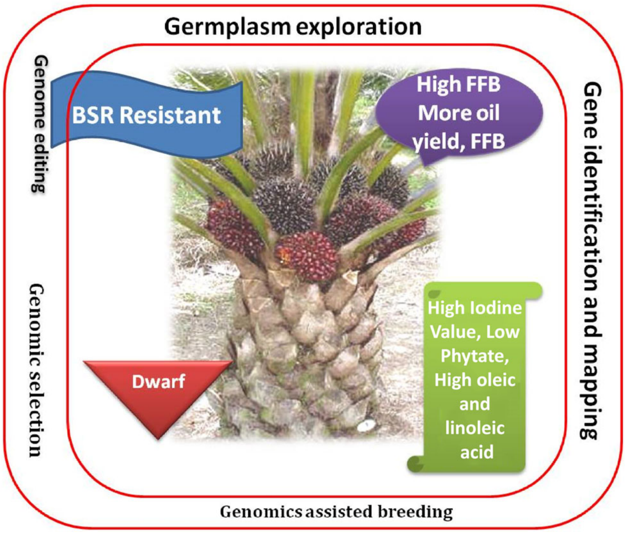


Fig. 3 Approaches for generating elite oil palm germplasm through different technologies

chromosomes 4, 5, 12 and 15. Fine mapping in these regions will enable to identify the key regions responsible for yield and oil yield traits.

Less height increment (Dwarf trait)

After 20–25 years, oil palm trees in general attains a height of 40–45 m which are tall, which is a major problem to harvest the bunches. Genotypes with less height increment or dwarfism is the feasible approach in mitigating the above problem. The dwarf palms offers advantages like it involves less human drudgery, cost, more income by increasing economic life of palm for ten more years. To overcome this problem, molecular technologies plays important role in generating dwarf palms in less time. There were two reports on genome-wide SNP discovery for less height increment in oil palm, where they used the bi-parental mapping population (Pootakham et al. 2015; Lee et al. 2015). Lee et al. (2015) found a major QTL linked to the *asparagine synthase*-related protein (GenBank accession no: AY556420) encoded a protein with 254 amino acids. However, a well structured natural population of oil palm offers several advantages over linkage mapping population. Recently Babu et al. (2019b) used GWAS and identified five significant quantitative trait loci (QTLs) on chromosome 6, 7, and 9. These QTLs were homologous to oil palm B3 domain containing protein (LOC 105,043,719) transcript variant X3, mRNA. The B3 domain containing proteins consisted of families like auxin response factors (ARFs) and abscisic acid insensitive 3 (ABI3). Earlier works showed that ARFs may be playing a major role in less height increment of oil palm which is evident in *Arabidopsis thaliana* and maize (Dietrich et al. 2011; Harpaz and Applebaum 1961). The list of several works on height increment given in Table 2. The probable chromosome region influencing the less height increment is observed to be on chromosomes 4, 10, 14 and 15. At the same time we must always focus on the minor QTLs which also plays major role in selection of desirable palms. The probable candidate genes are *asparagines synthase* related protein and auxin response factors.

Oil quality parameters

The major debated issue in oil palm cultivation is its oil quality parameters. There are several reports where it was discussed on pros and cons of palm oil quality issues. The benefits and its effects on human health were discussed in the earlier section. However, the genomic technologies are suitable tools to produce elite oil palm germplasm with good oil quality parameters. Concerted efforts have been made so far in identification of pathways for fatty acid regulation and key candidate genes involved. Singh et al. (2009) used AFLP, RFLP and SSR markers to construct a map in an inter-specific cross involving a Columbian *E. oleifera* and a Nigerian *E. guineesis*. They found significant QTLs for Iodine value (IV), myristic acid (C14:0), palmitic acid (C16:0), palmitoleic acid (18:0), oleic acid (18:1), and linoleic acid (18:2) content. The mesocarp lipase activity causes consequential oil losses and requires costly measures to limit free fatty acid (FFA) levels. Montoya et al. (2013) identified key genes related to oleic acid C18:1 underlying enzyme FATA and SAD, using intra-gene SNPs. The FATA enzyme could be a smart candidate gene to export C18:1 from plastid to endoplasmic reticulum (ER). The KASI candidate gene also seems to be a candidate gene for C14:0 on LG 15. In the same location they also found KAS II candidate gene which plays role in conversion of C10:0 to C14:0. They also studied comparative genomics using bioinformatics tools to identify the orthologs and homologs in oil palm influencing fatty acid composition. Common genomic regions across populations, involving QTLs of interest, facilitate positional cloning and marker-assisted selection of agronomic genes. The literature showed that very less work was done on fatty acid composition of oil palm and identification of the candidate genes. Hence, more focus needs to be given in identifying germplasm with good oil quality parameters and identifying the genomic loci using SSR and SNP markers. It is also observed that most of the QTLs were located on chromosomes 1, 3, 4 and 5. The elaborated list of the mapping studies for different fatty acid compositions using different marker systems given in Table 3.

Table 1 The QTLs identified for yield and oil yield traits using SSRs, SNPs and DArT markers and their linked candidate genes

References	Traits	Marker	Population	Chromosome	Candidate genes	R^2
Teh et al (2016)	ODM	200 K SNP array	F_1 (132*)	5 and 11	Pyruvate kinase	–
Jeennor and Volkaert (2014)	FFB, ABW, OF, OB, ODM, FB, OWM, ODM/OWM, SF, KF, KB	SSRs (211#)	F_1 (52)	FFB-1 BW-15 OF-4, 6 and 12 OB-4, 12 ODM-10 FB-12 SF-4 KF-4	Indole 3-glycerol phosphate synthase gene for lyase enzyme (OB, OF, SF, KF) ACX gene oxidation pathway (BN, BW)	12.4 – 56.8%
Ithnin et al. (2017)	13 traits	SNPs (4451)	MPOB (422) Multiparental population	KB-7 MF-3, 4, 7, 11, 15 MFW-4, 5, 6 OY-3, 7, 8 RL-2,4,10,16	–	–
Bai et al. (2017)	OB ODM	SSRs (123) SNPs (1357)	F_1 (177)	OB-1 ODM-8, 10	–	7.6–13.3%
Pootakham et al. (2015)	BW	SNPs (3417)	F_2 (108)	BW-3	DELLA protein GA11 Gibberellin 2-oxidase 2	17–19%
Kwong et al. (2017)	SH Shell thickness	SNPs (70,804)	F_1 (132)	2, 5, 10	STK, C GBF4, FAD3, COX, CPC, ITPK1	1–18%
Ukoskit et al. (2014)	Sex ratio	SSRs (292)	F_1 (208)	SR-1, 8, 11 FFB-7, 10, 15	–	8.1–13.1%
Seng et al. (2011)	21 oil yield traits	SSRs and AFLP	F_1	164 QTLs	–	–
Arolu et al. (2016)	FFB BN ABW MF, SF, KF, SF, OB, KB, OF, OY, KY	–	F_1	–	–	–
Rance et al. (2001)	KF, SF, MF, RL, PCS, FW, BN, BW, FFB, OB, LA	RFLP	F_2	KF-11 SF-3 MF-11 RL-14 PCS-5, FW-16, BN-4, BW-14, FFB-4, OB-7, LA-5	–	8.2–44%
Babu et al. (2020)	OB, ABW, KF, FB, OWM, ODM, SF, BI, FFB, BN	SNP (4031)	Association mapping using 96 African germplasm	OB-2, 3, 4, 5, 12, 13, 15, 16 KF-3, 5 FB-4, 6, 8, 10, 15 OWM-3, 11, 13, 15 ODM-6, 15 SF-9, 10 BI-5, 10 ABW-1, 2, 4, 7, 8, 16 FFB-1 BN-3, 6	OB-mitogen activated protein kinase-5 (MAPK-5) protein OWM-betaglucosidase/Alpha L-arabino furanosidase-2 bunch weight-cysteine desulfurase 1 protein	7–25.3%

Table 1 continued

References	Traits	Marker	Population	Chromosome	Candidate genes	R^2
Babu et al. (2017)	OB, FB, ODM, SF	SSRs (100)	Association mapping using 96 African germplasm	OB, SF-2 FB, ODM-14	–	5.1–9.6%
Babu et al. (2019c)	LA RL, TDW	SNPs	Association mapping using 96 African germplasm	LA-1, 4 RL-1, 16 TDW-2, 14	–	11–18%
Chuenpoma and Volkaert (2016)	BN ABW FFB	SNPs (40)	Association mapping using natural population	–	–	–
Bhagya et al. (2020)	12 oil yield and yield traits	SSRs (50)	Association mapping using natural population	FFB-5 ABW, TDM-8 BI-5 LA-3, 8, 12	–	14–17%
Astorkia et al. (2019)	BN BW, BY, OWM, ODM, OB SFA MUFs PUFs IV	SNP (115)	F_1 (198) Interspecific oil palm hybrids from five different origins			8.9–26% 6.1–28%
Guarín et al. (2019)	LDW, LA RL Yield BN BW	SNP (3776)	F_1 (378) Interspecific oil palm hybrids	LDW-3 LA-15 RL-13 Yield BN-5 BW-10	RL-Guanine nucleotide-binding protein subunit gamma (AGC3)	5–10%

*Numbers in brackets is the number of genotypes

#number of markers

Biotic stress

In comparison to other crops, oil palm is less prone to pests and diseases except few diseases like basal stem rot (BSR) caused by *Ganoderma* sp. in tropical countries like Malaysia, Indonesia, Nigeria and other Asian countries (Kinge and Mih 2011; Sariah et al. 2011). The diseases include stem wet rot, leaf spot, bud rot and basal stem rot etc. However in Malaysia and other Asian countries, BSR causing a major loss to the palm oil yield even some times up to 80–90%. This much yield loss can't be compromised by the countries like Malaysia and Indonesia, where oil palm is the main economy role player. Though few BSR resistant varieties developed by some organizations in Malaysia and Indonesia, they are not fully open to the scientific community to utilize that germplasm in further breeding programmes. The mechanism of Ganoderma infection is elaborately discussed in oil palm by Sahebi et al. (2015). Several options are available to control the BSR disease in oil palm like better cultivation practices, effective fungicides, and some bio-control agents. However, they have little effect on controlling BSR, due to environmental factors, stages of infection and several other factors (Breton et al. 2006). Till today, no proper control measures are available to tackle the menace of BSR disease. Few oil palm germplasm found to show moderate resistant and tolerance to *Ganoderma* (Idris et al. 2004; Durand-Gasselin et al. 2005). Some researchers attempted to reveal the genes linked to *Ganoderma*, where they identified SAD1 as well as SAD2 genes are highly expressed in oil palm roots and leaves (Alizadeh et al. 2011). Another study by Tan et al. (2013) identified two candidate genes EgEMLP1 and EgMT with respect to *G. boninense* that were suggested as biomarkers for detection of *G. bionense* early infection. Later, the whole genome sequence of *Ganoderma boninense* published by Utomo et al. (2018). Tisné et al. (2017) identified two SNP loci in the initial stages of infection of Ganoderma sp. and few haplotypes were identified. Very few mapping studies have been conducted in oil palm for BSR. Putranto et al. (2017) studied differential gene expression of susceptibility and tolerance in oil palm, suggested six genes like EgCH1, EgVIR-1, EgVIR-2, EgIFR-2, EgMT1 and EgSPI-2 which were unregulated can be used as biomarkers. Genome editing tools for these genes may be appropriate way to create genetically stable oil palm germplasm against BSR.

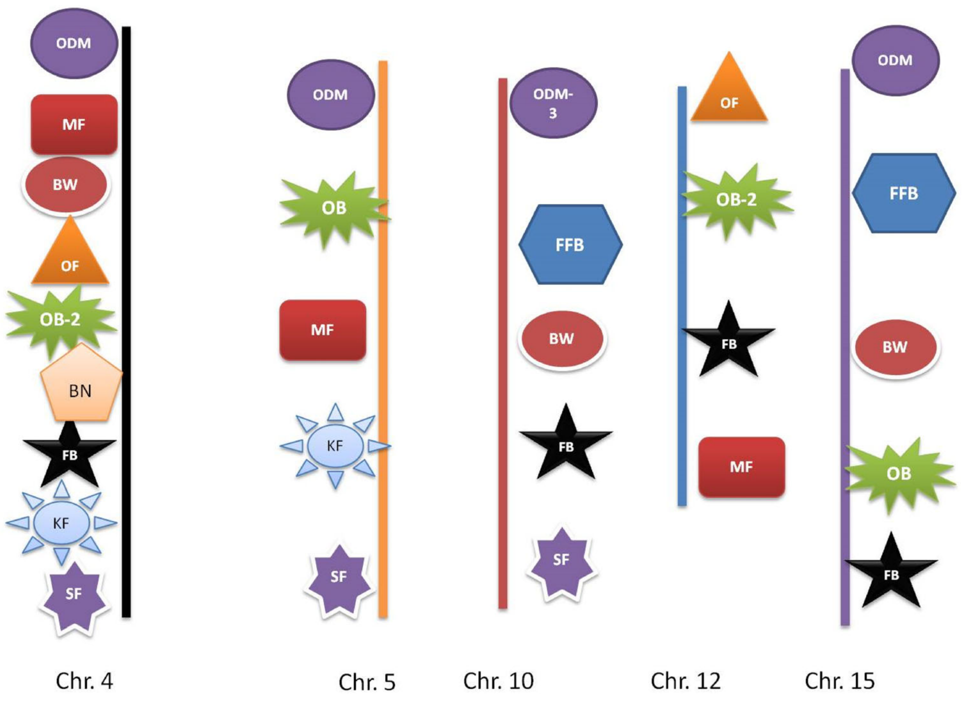


Fig. 4 The chromosomal location of the major QTLs for yield and oil yield traits in oil palm

Abiotic stress

Oil palm is more suitable to the temperature range of 22–35 °C and is widely grown in temperate countries where it is successfully cultivated. However, it is sensitive to low temperatures (below 10 °C) and high temperatures (more than 37 °C) and salty soils. However, till now no reports on the experimental evidence of yield losses due to the extreme temperatures. In India, during summer temperature goes up to 45–48 °C where oil palm is being cultivated mostly under irrigated conditions It is visually examined that deficit stress minimizes FFB of 5 tons per ha with significant reduction of 26% in vegetative growth (Murugesan et al. 2017). Identifying and validating the genes responsible for low cold conditions and salt tolerance will assist in breeding cultivars suitable for cold regions and salt affected areas. Xiao et al. (2017) first time identified EgWRKY genes with the *E. guineensis* for abiotic stresses like cold and salt. Similar transcription factors were also reported to be associated with abiotic stress in Arabidopsis (Scarpeci et al. 2013), rice (Raineri et al. 2015) and other crops (Rabara et al. 2012). Lei et al. (2014) conducted RNA-Seq analysis of cold tolerant oil palm germplasm. They observed C-repeat binding factors (CBFs) expressed high level in the cold stress conditions. Also showed that mutation and absence of DRE core motifs in the promoters of six CORs suggested may not be induced via cold stress in *E. guineensis*. Till now no reports on identification of genes/QTLs for abiotic stress related traits.

Genomic assisted selection

Genomic assisted selection or marker assisted breeding is most common in the cereal crops and is being widely utilized. In case of rice, marker assisted breeding has been used in generating new generation lines with improved traits like submergence tolerance (Septiningsih et al. 2009), *Xanthomonas* resistance (Davierwala et al. 2001), and leaf blast resistance. In maize, the quality protein maize (QPM) was successful in introgression of *opaque2* genes (Babu et al. 2005, 2012) into locally well adapted germplasm through MAS. However, in oil palm it is not possible, since the breeding cycle for one generation is 15–18 years. The possible application of marker technology in oil palm is selection of germplasm with highly effective linked markers which takes less time without involving any segregating populations. There are very few cases where MAS can be effectively used in oil palm are discussed below. Along with below cases, identification major QTLs for important traits and their validation in large population allows researchers in selecting oil palm germplasm with desired economic traits.

SHELL gene influencing shell thickness

The SHELL thickness gene (*Sh* gene) was discovered long back during 1940s, which led to increase in the oil palm production by 20–25% (Beirnaert and Vanderweyen 1941). The dura (D) germplasm had thick shell (Sh/Sh), pisifera (P) with shell less having recessive homozygous sh/sh

Table 2 The details of QTLs linked to height increment in oil palm along with chromosomes and R^2 values

References	Traits	Marker	Population	Chromosome	Candidate genes	R^2
Lee et al. (2015)	Height	SSRs and SNPs	F1 (192*)	1 and 16 (LG5)	Asparagine synthase related protein	51% by SSR EgEMS0023
Chuenpoma and Volkaert (2016)	Height	SNPs (40#)	Association mapping using natural population	–	–	–
Arolu et al. (2016)	HI		F1			
Pootakham et al. (2015)	HT	SNPs (3417)	F2 (108)	HT-10, 14, 15	DELLA protein GA11 Gibberellin 2-oxidase 2	17–19%
Kwong et al. (2017)	HI	SSRs, SNPs	Association mapping using natural population	4, 8, 10, 11, 14, 15	Indole 3 acetic acid Amydosynthetase gene	
Billotte et al. (2010)	HI	SSR SNP		1, 2, 4, 10		
Guarin et al. (2019)	Trunk diameter height	SNPs (3776)	F_1 (378) OXG	TD-15 HT-15	Nucleic acid binding protein	5–10%
Babu et al. (2019a)	HI	SNPs	Association mapping using African germplasm	6, 7, 9	Auxin response factors (ARFs) and abscisic acid insensitive 3 (ABI3) calcium-dependent protein kinase 8 and U box domain-containing protein	11–15%
Guarín et al. (2019)	TD HT FA	SNP (3776)	F_1 (378) Interspecific oil palm hybrids	TD, HT, FA-15	HT-Paired amphipathic helix protein (PAH)	5–10%
Bhagya et al. (2020)	HT, palm girth	SSRs	Association mapping using indigeneous population	8 and 10		

*Numbers in brackets is the number of genotypes

#number of markers

allele (Corley and Tinker 2003). The discovery of SHELL gene, homologue of SEEDSTICK gene was a major turning point in oil palm research and development (Singh et al. 2013). This lead to identification of molecular markers to identify the fruit forms at an early stage, which greatly helps breeders, and farmers. This technology saved lot of time, space, labour, and cost. Babu et al. (2017) identified cleaved amplified polymorphic site (CAPS) marker for differentiation of oil palm fruit type. Allele specific bi-directional PCR tool was designed (Reyes et al. 2015) to identify dura, pisifera and tenera varieties. All the above studies were pertaining to *E. guineensis* varieties. However, recently Astorkia et al. (2020) identified homologue of *SHELL* gene in *E. oleifera* germplasm. They detected seven SNPs, out of that SNP NK2 was specific to *E. oleifera* alleles and absent in *E. guineensis* and designed species specific markers. As per earlier reports SHELL gene is monogenic, but shell thickness is varied to a great extent in dura and also in tenera accessions. Still there are some discrepancies as reported by Teh et al. (2016) where they found five genotype–phenotype discrepancies using the reported mutations (sh AVROS, sh MPOB, shMPOB2, sh MPOB3 and shMPOB4). These works suggested a further need of identifications of some more mutations like cis-compounded mutations.

VIR gene influencing VIRESCENCE fruit color

Based on the oil palm fruit exocarp colour, it is divided into two types, viz., *Nigrescense* and *Viruscense* type. In case of *Nigrescense* palms, harvesting of the bunch is possible only predicted on the presence of detached fruits on the ground. Sometimes harvesters harvesting bunches at inappropriate stage due to lack of knowledge on harvesting skills. This leads to reduction of oil yield extraction, where ultimately farmers loosing the net income. But this is not in the *Viruscense* type of palms where matured/ ripened palms easily identified by the change of color from green to orange. This

Table 3 The details of QTLs linked to fatty acid components in oil palm along with chromosomes and R^2 values

References	Traits	Marker	Population	Chromosome	Candidate genes	R^2
Singh et al. (2009)	Fatty acid composition IV, myristic acid, palmitic acid, palmitoleic, stearic acid	RFLP AFLP SSR	F_1 inter-specific *E. oleifera* × *E. guineensis* (118*)	1, 3, 15		13.1–55.8%
Montoya et al. (2013)	Fatty acid composition	SSRs (384#) EST-SSRs (113) Coconut SSRs (21)	F_1 inter-specific cross (134 full sibs)	C14:0–2 C16:0, C18:1, C18:2–3, 5 C18:1, C16:0, C14:0, C18:3–4 C16:1, C18:0, IV-6 C16:0, IV, C14:0–15	FATA SAD genes KASI, II FATB	
Montoya et al. (2014)	FA	SSRs	LM2TXDA10D (116 full sibs)	16 QTLs		
Astorkia et al. (2019)	SFA MUFs PUFs IV	SNP (115)	F_1 (198) Interspecific oil palm hybrids from five different origins			6.1–28%

*Numbers in brackets is the number of genotypes

#number of markers

change is due to degradation of chlorophyll and accumulation of high carotenoids. The color differentiation of unripe and ripe bunches of both *Nigrescense* and *Virus-cense* given in Fig. 5. A gene conferring *VIRESCENSE* which encode R2R3-MYB transcription factors was discovered (Singh et al. 2013). Introgression of this fruit color trait into nigrescence without compromising the yield and oil quality will greatly help the oil palm researchers and farming community to reduce the harvesting losses.

Speed breeding

From the above discussion, we know that oil palm has long breeding cycle and it obstructs the development of elite breeding materials. The only possible way to produce elite germplasm to hurry up the breeding cycle by different speed breeding methods. In case of cereals (Ghosh et al. 2018) speed breeding involves changes in the environmental conditions to reduce the breeding cycle. But in oil palm, it is not so easy in practical. Therefore, molecular technology together with tissue culture techniques will speed up the breeding cycle of oil palm, which results in developing elite oil palm germplasm with all the desirable traits in a short period of time. Hence, in this review we are here with proposing the following model of speed breeding which may allow oil palm researchers to put more efforts on speed breeding (Fig. 6). It is an integration of molecular marker technologies, tissue culture and breeding activities. Detailed review on speed breeding approaches in horticultural crops is elaborately discussed in (Nocker and Gardiner 2014).

Genomic selection (GS)

The genomic selection (GS) is initially being developed for animal systems to accelerate genetic gain in the breeding programmes, later widely utilized in plant systems. The main challenge faced by the oil palm breeders and molecular breeders is the accuracy, efficiency and handling immense populations for getting better results. In such cases, GS is very useful in oil palm, still suitable models for GS is under investigations. GS is considered to be very important in perennial crops rather than other crops like cereals and annual crops (Robertsenb et al. 2019). In perennial crops, GS shortens breeding cycles and efficiency in selection procedures will be increased.

The GS in oil palm was discussed thoroughly by Wong and Bernardo (2008) followed by Cros et al. (2015) where they used different training sets and statistical methods for estimating breeding values (EBVs). Results showed that

Fig. 5 The color differentiation of unripe and ripe bunches of both nigrescens and virescense. **a** Nigriscence bunch palm, **b** virescence bunch bearing palm, **c** ripened bunch of virescence type and **d** ripened bunch of nigrescence type

GS has given more statistical strength in terms of mendelian algorithms compared to pedigree based model. Kwong et al. (2017) used RR-BLUP, Bayesian A, B, Cπ, LASSO, Ridge Regression and two machine learning methods (SVM and Random Forest) using SSR and SNP markers. The advantages of GS over RRS were very well discussed in an elaborative review given by Cros et al. (2015) in oil palm. They suggested GS along with efficient design and breeding strategies might be better option for traits like FFB, BN and ABW. The genetic diversity within the available germplasm is a key point for enhancing long term progress in GS. Invariably GS in perennial crops differs from other annual crops on several aspects from breeding. Though in some perennial crops GS is reported (Barthólomé et al. 2016; Isik et al. 2017; Lenz et al. 2013; Resende et al. 2012), practical implementation is yet to foreseen. By increasing the selection intensity and shortening the breeding cycle, GS could exacerbate this phenomenon, at the expense of the long-term one. This is even more relevant for oil palm where the base population is very narrow.

Genome editing (GE) using CRISPR/Cas9

The approach of genome editing involves random mutagenesis, cleavage and rejoining of DNA molecules at specific sites to modify the genetic material for specialty traits like grain yield. It was initially used for improving milk production in dairy cows (Bovine HapMap Consortium 2009; Riquet et al. 1999). A unique genome editing tool *CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)/*CRISPR associated (Cas) protein system with the CRISPR/Cas9 has been known as powerful GE tool. The GE technology was widely used in several applications to improve fatty acid composition in *Camelina sativa* seeds oil (Jiang et al. 2014), which become more beneficial to human health. Applications of CRISPR/Cas9 system have been reported in *Arabidopsis thaliana*, *Nicotiana benthamiana*, *Oryza sativa*, *Triticum aestivum*, *Solanum lycopersicum*, and *Sorghum bicolour*. So far, there have been few reports on the application of CRISPR/Cas9 on genome editing of oil palm. Budiani et al. (2018)

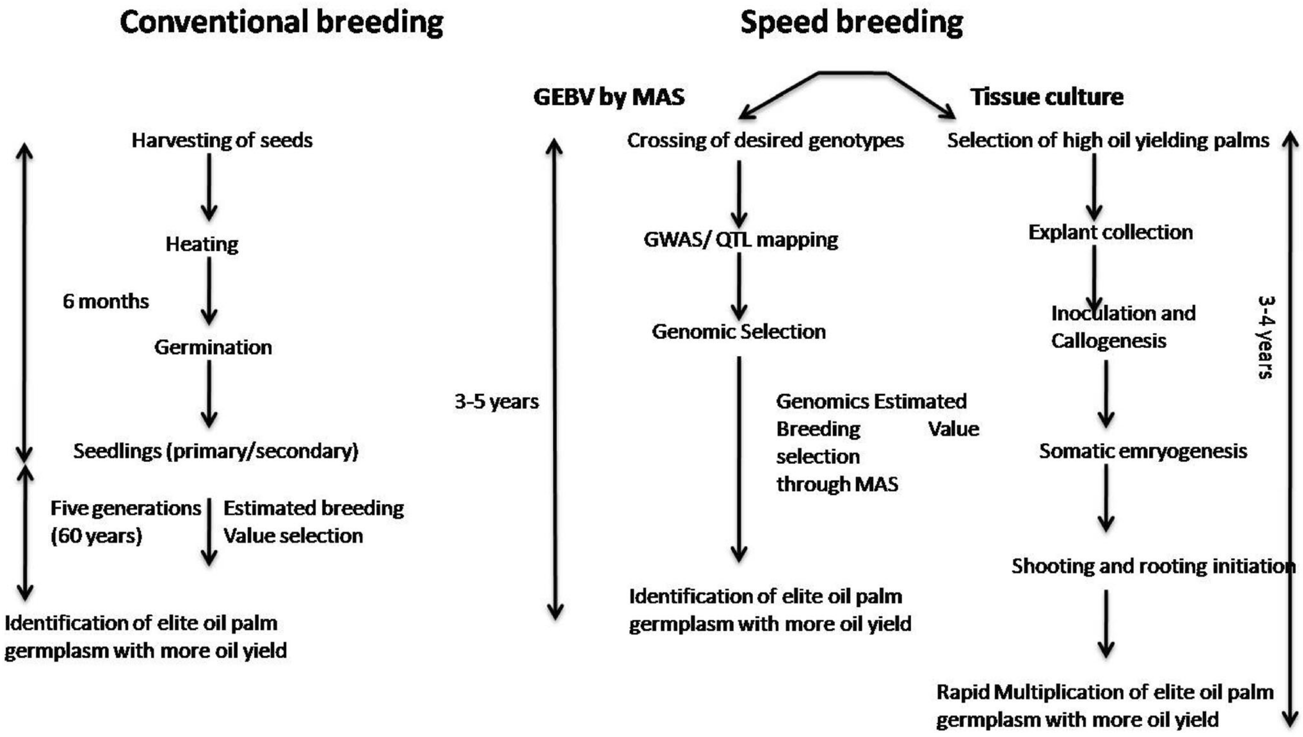


Fig. 6 Speed breeding approaches for enhancing oil yield of oil palm

transformed oil palm calli using CRISPR/Cas9 construct containing sgRNA against the Ganoderma disease which is a major problem in oil palm plantations. Two genes isoflavone reductase (IFR) and methallothionine like protein (MT) were used as target genes. In order to determine universal efficiency of CRISPR/Cas9, extensive research needs to be performed in oil palm. The CRISPR/Cas9 mediated non-transgenic mutants may be a challenging task in perennial crops like oil palm, but is highly desirable. High throughput sequencing will help in selecting the transformed calli from non-mutant lines. The methodology used by Chen et al. (2018) in tobacco may be applicable to oil palm which may be used to generate desired oil palm genotypes.

Bioinformatics

A huge data generated by next generation sequencing technologies made researchers to think beyond the omics applications like bioinformatics to utilize and apply in-silico models for locating gene structures and pathway models in crops like oil palm. Now it is possible to identify the orthologs and paralogs by comparing the relevant crop genome databases. The high similarity existing between closely related species like date palm and oil palm was already studied by Mathew et al. (2014). It showed that oil palm chromosome 2 constitutes a fusion of date palm chromosomes 1 and 10. These results help in finding the orthologs and paralogs between species. However, our results found high synteny between oil palm with rice. Rice is a model crop and monocotyledon which may serve to identify important genes related to some useful traits like dwarfness. High syntenic relations were determined between oil palm and rice. Oil palm chromosome 7 was found to be fusion of 1st, 2nd and 3rd chromosomes of rice. Oil palm chromosome 1 showed synteny with rice chromosome 1 and with less syntenic with chromosome 3 and 12. The diagrammatic representation of synteny between oil palm and rice chromosomes is given in Fig. 7.

Riju and Arunachalam (2007) did mining of EST sequences, later Ting et al. (2010) also mined EST based SSR markers which were used for genetic diversity studies. The main use of EST based SSR or genic SSRs is easy to identify, no hybridization required and large number of SSRs can be identified. An exhaustive study by Babu et al. (2019a) designed whole genome microsatellite database of oil palm i.e., OpSatdB. It is the first microsatellite database of oil palm, using PHP and MySQL database (www.ssr.icar.gov.in). Similarly, few other databases also available in oil palm like Tropgene (Ruiz et al. 2014) and PalmXplore (Sanusi et al. 2018). The Tropgene database contains only the genomic SSRs which were developed through hybridization and are very less number (around 400). The PalmXplore database is additionally a comprehensive

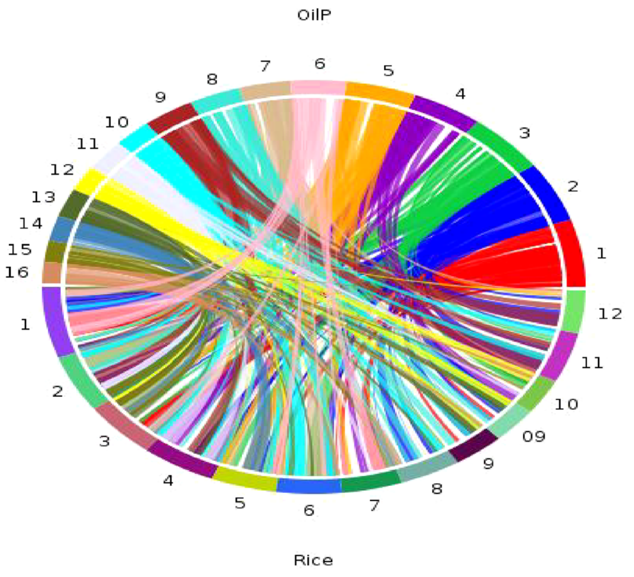


Fig. 7 The circos plot showing the synteny observed between oil palm and rice chromosomes

database which contains full gene information, EST sequences.

Conclusion

Palm oil is the major source of global vegetable oils, where it contributes 70% of the total vegetable oil demand. Hence, in the present review, we suggested various breeding and molecular approaches and future strategies to enhance the yield, oil yield along with biotic and abiotic stress tolerant traits to produce a sustainable high yielding quality oil palm. Advances in genomics and next generation technologies were discussed in detail for improvement of oil yield, biotic stress and abiotic stress traits. These approaches will help in bringing elite oil palm germplasm which is able to solve the issues of stakeholders like farmers, processing units and researchers.

Author's contribution Conceptualization: BK, RKM, Writing: BK, RKM, GR, PA, Reviewing and editing: BK, RKM, HPB.

Declarations

Conflict of interest The authors declare that they have no conflict of interests.

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