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THE OIL PALM GENOME REVOLUTION

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ABSTRACT

Palm oil is a versatile vegetable oil that is a major contributor to the world's edible oil market. The importance of the crop led to the use of biotechnology to better understand and further improve its performance. Initial efforts were focused on the identification of genes and markers associated with specific traits. Although these efforts provided some insights, they were unable to identify the causal genes and mutations relevant to the traits. The major advance came with the introduction of next-generation sequencing, which provided a cost-effective way to sequence the oil palm genome. The publication of the genome sequence in 2013 resulted in the identification of the SHELL, Virescens (VIR) *and* MANTLED *genes. The genome sequence also accelerated the identification of genomic regions influencing other complex traits, such as height and fatty acid composition, and facilitated comparative genomics analyses. This review describes the developments of oil palm biotechnology research, and diagnostic assays for SHELL, VIR and MANTLED traits. The assays have practical applications in improving the efficiency of oil palm breeding and tissue culture. The genomics and epigenomics-based approaches have started to provide the necessary tools that will support the sustainable development of oil palm.*

Keywords: biotechnology, oil palm genome.

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INTRODUCTION

Oil palm, which has the highest yield and produces one of the most affordable vegetable oils, plays an important role in global food security. As the human population growth is expected to continue to increase, albeit at a slower rate (UN DESA, 2017), demand for palm oil will also grow. Traditional breeding techniques, coupled with biotechnology is currently being used in efforts to tackle stagnating yields, control diseases, improve oil quality, and increase versatility and adaptability to climate change (Barcelos *et al.*, 2015; Rival, 2017). The last four decades have seen tremendous progress in the use of biotechnology in oil palm research, beginning with the use of tissue culture for clonal propagation of oil palm, identification of molecular markers and expressed genes, to the eventual sequencing and utilisation of the oil palm genome sequence (*Figure 1*). The use of molecular markers started with the utilisation of restriction fragment length polymorphism (RFLP) markers for DNA fingerprinting (Jack and Mayes, 1993; Mayes *et al.*, 1996). This was followed by research in using genetic or linkage maps to link molecular polymorphisms with phenotypic variation of traits. These studies laid the groundwork for the application of genomics-based tools to improve the selection efficiency in breeding programmes and our understanding of the evolutionary relationships between palms.

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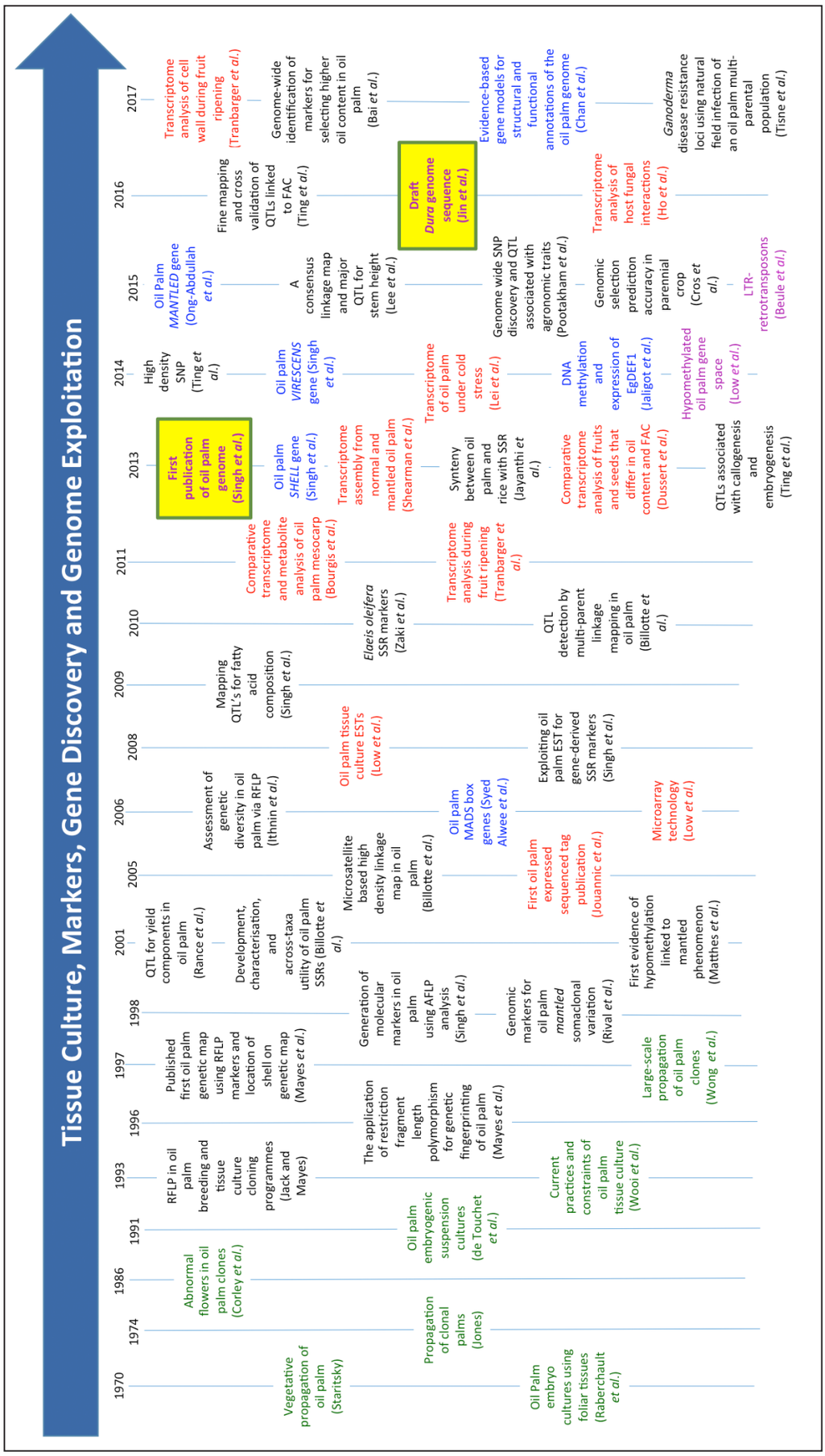

Figure 1. Core oil palm publications. Green: tissue culture, black: marker technologies, red: gene expression studies, blue: genes and gene models, purple: oil palm genome research, yellow box: oil palm reference genome.

The first genetic map of oil palm was constructed using RFLP markers (Mayes *et al*., 1997). The study is of particular significance as it resulted in the first publication that reported the mapping of an important monogenic trait, SHELL that is responsible for the *dura*, *tenera* and *pisifera* fruit forms in oil palm. Rance *et al*. (2001) subsequently expanded on the genetic map by Mayes *et al*. (1997) to identify quantitative trait loci (QTL) associated with yield and vegetative parameters. The development of the polymerase chain reaction (PCR) method (Mullis and Fallona, 1987) had a profound impact on the genetic analysis of many organisms, including oil palm. Although the random amplified polymorphic DNA (RAPD) markers were the most popular PCR-based markers initially, the application of RAPD technology in oil palm was not very successful due to problems with reproducibility. However, the Malaysian Palm Oil Board (MPOB) was more successful with the PCR-based marker technique known as amplified fragment length polymorphism (AFLP). The AFLP method was originally developed by Vos *et al*. (1995) and tested on virus, *Acinetobacter*, yeast, human and seven plant specimens. It provided the research community a means to generate huge numbers of dominant markers in any organisms, without any prior sequence information. Although the dominant nature of the AFLP markers suggested it had some limitations, the markers revealed clear Mendellian inheritance (Singh *et al*., 1998). The method was adopted and proved to be useful for map saturation (Billotte *et al*., 2005; Ting *et al*., 2006; 2013; Singh *et al*., 2009; Seng *et al*., 2011). The next DNA-based markers known to molecular scientists are microsatellites or simple sequence repeats (SSR) that are highly variable, co-dominant, chromosome-specific and easy to use. Genomics-based SSR markers were initially reported for oil palm by Billotte *et al*. (2001). Subsequently, the use of a large number of SSR in combination with AFLP markers for oil palm genetic mapping was embarked upon in a collaboration between nine centres of excellence, namely Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), Centre National de Recherche Agronomique (CNRA), University of Montpellier, Centre National de Séquençage (GENOSCOPE), Indonesian Oil Palm Research Institute (IOPRI), NEIKER, Max-Planck Institute, MPOB and SOCFINDO (Billotte *et al*., 2005). SSR had also been used for clonal identification and as a tool for quality control in tissue culture (Singh *et al*., 2007). The availability of the AFLP, RFLP and SSR marker technologies made it possible to construct comprehensive genetic maps that provided a useful means of determining QTL for more complex traits, such as fatty acid composition (Singh *et al*., 2009; Montoya *et al*., 2013), tissue culture amenability (Ting *et al*., 2013) and yield components (Seng *et al*., 2016).

In the past two decades, the process of identifying expressed genes had also improved. Adam *et al*. (1991) showed that as few as 150 to 400 nt complementary DNA fragments were enough to identify expressed genes. The method, known as expressed sequenced tags (EST) became an important tool for rapid gene discovery. Henceforth, Jouannic *et al*. (2005) published the first oil palm EST paper, where they studied genes expressed in five tissues, namely male and female inflorescence, shoot apices from normal and mantled clonal palms, and zygotic embryos. The method was also used to study gene expression in different biological conditions and tissue types (Ho *et al*., 2007; Low *et al*., 2008; Lin *et al*., 2009; Chan *et al*., 2010; Roowi *et al*., 2010). EST were also an important source of molecular markers (Singh *et al*., 2008; Ting *et al*., 2010; Zaki *et al*., 2012). With the advancements in science and technology, EST soon led to the development of the oil palm cDNA microarrays that were used to study gene expression at various stages of oil palm tissue culture (Low *et al*., 2006). The availability of EST allowed Lin *et al*. (2009) and Beulé *et al*. (2011) to develop macroarrays for gene expression studies. The increasing number of EST sequences made it necessary to develop a database system that can be used to manage and share the oil palm EST data. The *PalmGenes* database was a popular resource for *in silico* data mining of SSR in diversity studies (Singh *et al*., 2008; Ting *et al*., 2010) and QTL analysis (Ukoskit *et al*., 2014).

The need to identify new genes and molecular markers, and the desire to identify genes influencing traits of interest resulted in MPOB employing the GeneThresher (GT) technology to preferentially sequence the hypomethylated regions of the oil palm genome (Budiman *et al*., 2005; Low *et al*., 2014). The technique was selected as it was a more cost-effective way to sequence the oil palm genome compared to the conventional Sanger sequencing method. By only sequencing ~7% of the oil palm genome, at least 66% of the oil palm genes were sampled (Low *et al*., 2014). The availability of this data allowed for the bridging of the gap between phenotypic data, genes and whole genome information. The experience in analysing and using the GT data made it possible for MPOB to subsequently undertake a larger task of sequencing, assembling and annotating the oil palm genome (Singh *et al*., 2013a). The most significant results from this endeavour to date are the identification of the *SHELL* gene that is responsible for the formation of *tenera, pisifera* and *dura* fruit forms (*Figure 2*) (Singh *et al*., 2013b), the *Virescens* (*VIR)* gene that affects the colour of the fruit exocarp (*Figure 3*) (Singh *et al*., 2014), and the *MANTLED* gene that causes the

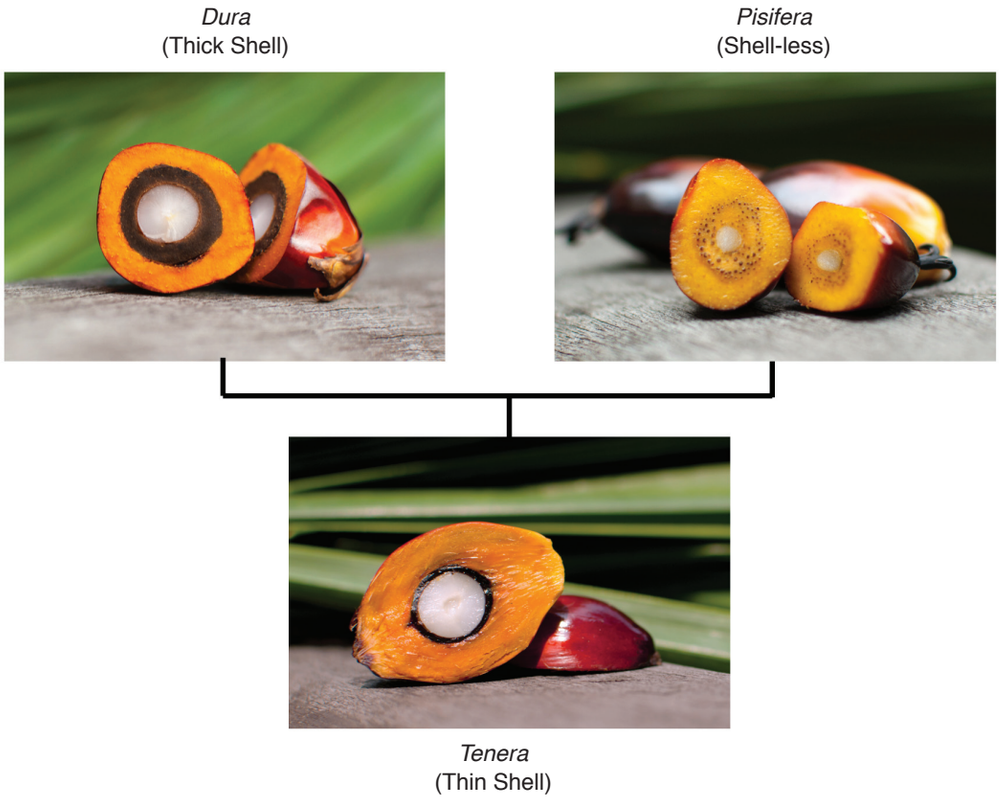

Figure 2. Dura, tenera *and* pisifera *fruit forms.*

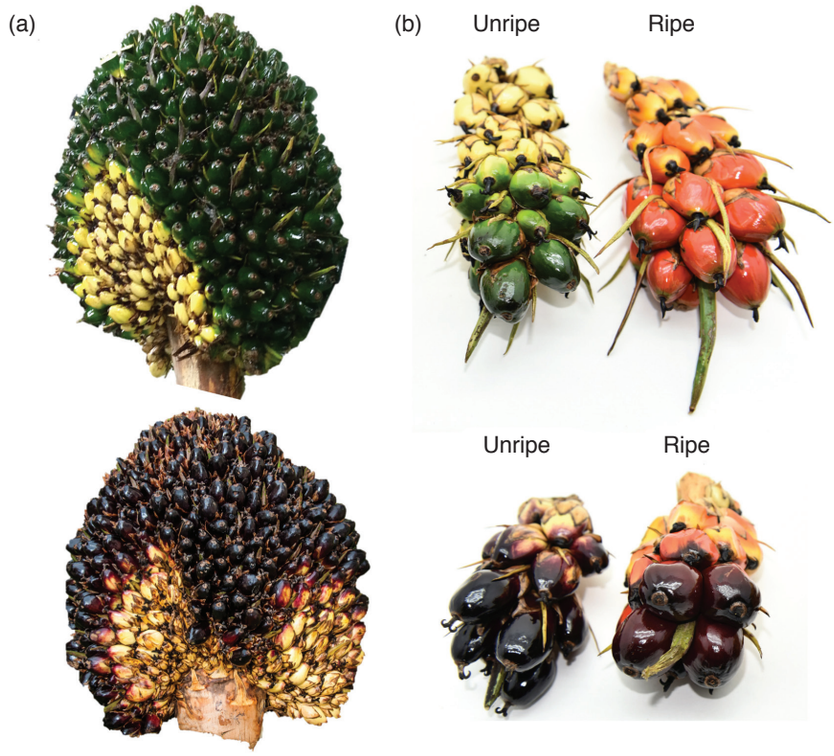

Figure 3. Oil palm virescens *and* nigrescens *fruits. (a) Unripe* virescens *(top) and* nigrescens *(bottom) fruit bunch, (b) unripe and ripe* virescens *and* nigrescens *fruit spikelets.*

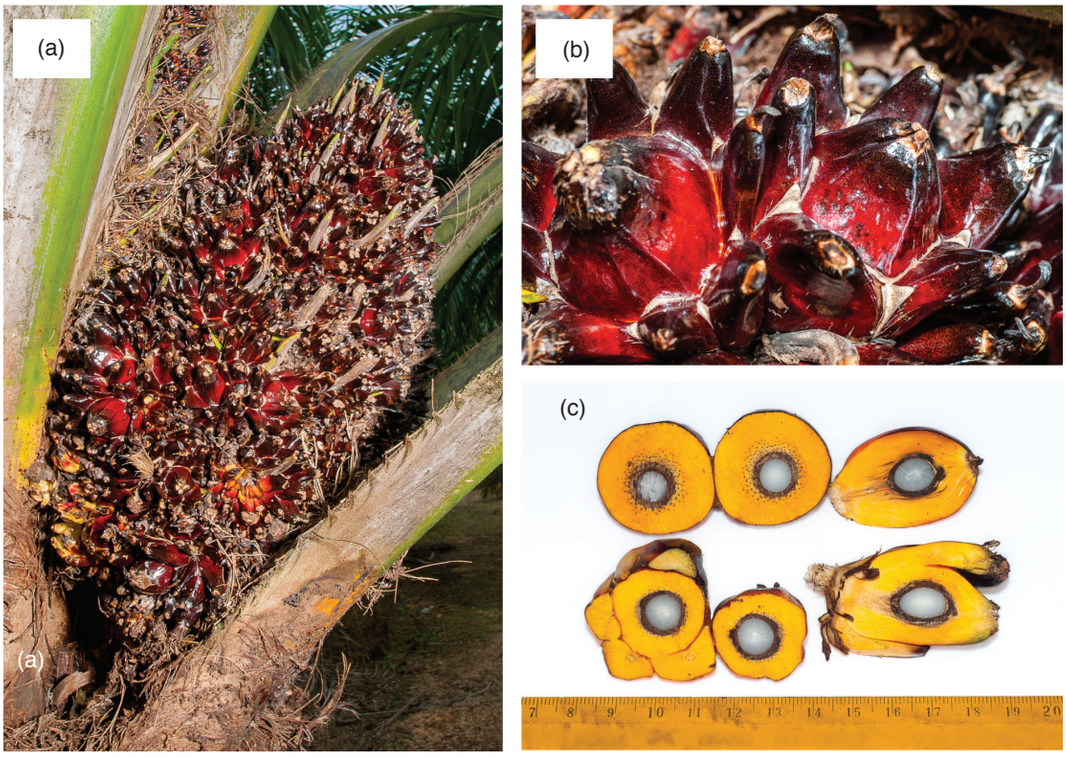

Figure 4. Mantled fruits. (a) Mantled fruit bunch, (b) mantled fruits, (c) cross and longitudinal sections of normal (top) and mantled (bottom) fruits.

mantled fruit somaclonal variant (*Figure 4*) (Ong-Abdullah *et al*., 2015). This shows the importance of the oil palm genome as a tool to drive oil palm biotechnology research to new heights.

OIL PALM GENOME

The *E. guineensis* [AVROS (Algemene Vereniging van Rubberplanter ter Oostkust van Sumatra) *pisifera* fruit form] genome was sequenced and published by MPOB in 2013 (Singh *et al*., 2013a). A total of ~1.5 Gb sequence of the 1.8 Gb genome with N50 size of 1.05 Mb was released to the public domain, of which ~660 Mb were linked as pseudochromosomes using two genetic maps, T128-selfed and P2. In 2016, the *dura* elite palm from Wilmar International Ltd Plantation, Indonesia was sequenced. The statistics of the assembled draft *dura* genome sequence were similar to the *pisifera* genome: 1.7 Gb with N50 size of 0.76 Mb and ~86% of the *dura* genome sequences are identical to the *pisifera* genome sequences (Jin *et al*., 2016). A total of 30 752 and 36 105 gene models were identified by Singh *et al*. (2013a) and Jin *et al*. (2016), respectively. A revised version of gene models for the *pisifera* genome was subsequently published (Chan *et al*., 2017a). The revised gene models were predicted using an integrated workflow of two independent gene-prediction pipelines, Fgenesh++ (Solovyev *et al*., 2006) and Seqping (Chan *et al*., 2017b), resulting in the identification of 26 059 high-quality protein-coding genes with transcriptome and RefSeq evidence. The completeness of the revised gene models was assessed using BUSCO (Benchmarking Universal Single-Copy Orthologs) (Simao *et al*., 2015). The 26 059 predicted genes in the *pisifera* genome contained ~90% and ~86% of BUSCO's eukaryotic and embryophyta profiles. The annotations and sequence information of the revised gene models are available in the PalmXplore Database System at http://palmxplore.mpob.gov.my or via a link in the Genomsawit website (http://genomsawit.mpob.gov.my). The gene information can also be visualised in the MyPalmViewer Genome Browser at http://gbrowse.mpob.gov.my.

Analysis of the *pisifera* genome sequence revealed several interesting characteristics. The GC_3 content, *i.e.* the number of guanines and cytosines in the third position of codons among coding genes, showed that oil palm has a unimodal GC_3 distribution with a long tail towards high values of GC_3 (Clement *et al*., 2014; Chan *et al*., 2017a). This is in contrary to grasses that usually have bimodal GC_3 distributions (Clement *et al*., 2014; McKain *et al*., 2016) and the bimodal GC_3 evolved before the ancestor of all commelinids (Clement *et al*., 2014). Clement *et al*. (2014) suggested that the ancestor of

oil palm and banana, which also has unimodal GC_3 distribution may have lost bimodality gradually.

The oil palm genome has high levels of repeats, estimated to be ~57% (Singh *et al*., 2013a). Analysis of the retroelements in the genome showed that *Copia* elements are more prevalent in the gene-rich regions, while *Gypsy* elements are found more widely distributed thoughout the genome (Beule *et al*., 2015). Telomeric repeats analysis showed that oil palm chromosomes 2 and 14 were the result of Robertsonian fusions of two telomeric chromosome ends, explaining why oil palm has 16 chromosomes while its closest sequenced relative, the date palm has 18 chromosomes (Singh *et al*., 2013a). This theory is supported by Mathew *et al*. (2014), where the mapping of markers from a date palm genetic map to the oil palm genome revealed that the oil palm chromosome 2 is the fusion of date palm chromosomes 1 and 10.

The oil palm has also gone through whole-genome duplication (WGD) (Singh *et al*., 2013a; Jiao *et al*., 2014). Comparison with date palm, banana and *Arabidopsis* showed that date palm shared the highest amount of segmental duplications (Singh *et al*., 2013a). This is because date palm and oil palm experienced two paleopolyploidy events, of which the first *tau* WGD occurred early in the evolutionary history of monocots (Jiao *et al*., 2014). The second event happened only in palms. Banana and grass lineages had three and two additional duplications respectively after the shared ancestral *tau* WGD (Jiao *et al*., 2014; McKain *et al*., 2016). Comparison of *tau* synteny blocks showed that pairs of oil palm putative ancestral regions were lined up with single eudicot sacred lotus (eudicot; *Nelumbo nucifera*) putative ancestral regions (McKain *et al*., 2016). Oil palm retained ~16 092 out of 32 225 of its pre-*tau* paralogs while rice maintained 10 887 out of 39 049 pre-*tau* paralogs. This shows that oil palm evolved at a much slower rate, as rice had higher paleoparalog loss (Jiao *et al*., 2014). This was probably due to the fact that oil palm has a much longer generation time. These studies are important as oil palm researchers can benefit from the myriad of research findings from other monocot crops. They can use ortholog information and syntenic regions from other crops to infer regions in the oil palm genome that may control the same agronomic traits. A preliminary study by Jayanthi *et al*. (2013) showed that it was possible to use the rice genome to select oil palm markers for genetic mapping.

One important discovery that demonstrates this is the dominant wild-type *VIR* gene which plays a regulatory role in determining the colour of the fruit exocarp during ripening. *VIR* fruits shows a profound colour change from green to orange while *Nigrescens* fruits, commonly used as commercial material in South-east Asia produces fruits that are deep violet at the apex and do not have major changes in colour during ripening. The *VIR* locus was identified in the selfed-T128 mapping population. Markers flanking the *VIR* locus were mapped by sequence similarity to the oil palm genome. Using information from other organisms, the list of genes between the flanking markers was narrowed down to four, and mutation(s) in one of these genes, a R2R4-Myb gene, resulted in the absence of anthocyanins in the *VIR* fruits (Singh *et al*., 2014). The discovery in oil palm has had an impact in date palm research. The ortholog of *VIR* in date palm is also responsible for yellow fruits in the *Khalas* variety of date palm (Hazzouri *et al*., 2015). Since date palm and oil palm share high level of synteny (Mathew *et al*., 2014), it is not surprising that the genes that influence an important oil palm trait also influence a similar trait in date palm. Similarly, genes that influence traits in other crops can also provide important leads for oil palm research. For example, researchers working on the dioecious date palm found evidence that date palm uses an XY system of gender inheritance (Al-Dous *et al*., 2011) and were able to localise the sex determination region on a putative date palm sex chromosome (Mathew *et al*., 2014). The information is relevant as oil palm is a temporal dioecious species (Cruden, 1988). It has alternate male and female flowering cycles that are influenced by both genetic and environmental factors, such as abiotic stress. Water stress has been shown to promote the formation of male flowers in oil palm (Adam *et al*., 2011). This has implications on the impact of climate change to oil palm cultivation. The date palm data may help us shed some light on the genetic loci and mechanism associated with sex determination in oil palm.

The genome data has also accelerated other research programmes, such as marker-assisted selection. The first foray into developing a diagnostic assay for oil palm materials for field plantings was achieved with the discovery of the *SHELL* gene (Singh *et al*., 2013b). The discovery led to the development of a diagnostic assay that can distinguish *dura, tenera* and *pisifera* fruit forms. The assay is an important quality control tool that can ensure only *tenera* plants are planted in commercial fields. This allows for more yield to be produced on the same land area as *tenera*, which is the commercial planting material in South-east Asia has ~30% and ~100% more oil yield than *dura* and *pisifera*, respectively. The tool is valuable as a survey published in 2016 showed that the weighted average non-*tenera* contamination rate of 10 224 mature palms or seedlings from 57 independent planting sites and nurseries in Malaysia was 10.9%, with 20 sites having contamination rates of >10% (Ooi *et al*., 2016). The SHELL diagnostic assay can also be used to specifically select *dura*, *tenera* and/or *pisifera* palms for breeding programmes, depending on the

final objectives of the study (Low *et al*., 2016). After the discovery of *SHELL* and *VIR* genes, the gene that causes the mantled fruit somaclonal variant was also identified (Ong-Abdullah *et al*., 2015). Characterisation of the *MANTLED* gene revealed the molecular mechanism associated with the mantled phenotype in clonal palms. To date, three diagnostic assays, namely for SHELL (Ooi *et al*., 2016; Low *et al*., 2016), VIR and MANTLED (Ong-Abdullah *et al*., 2016) have been developed. The VIR assay has important implications in breeding for homozygous *virescens* palms which can facilitate harvesting and hence improve yield, while the SHELL and MANTLED assays are actively being used by the oil palm industry to screen materials for field plantings.

With the identification of the genes that control the two most important monogenic traits (SHELL and VIR), oil palm researchers have now focused their attention towards using the genome data to identify markers or genes that control polygenic traits, such as low height increment, resistance to diseases, high yield, more liquid oil and resilience to climate change. Towards this end, a number of new and important developments have taken place. In 2015, two groups using the oil palm genome sequences were able to identify QTL related to height (Lee *et al*., 2015; Pootakham *et al*., 2015). Lee *et al*. (2015) identified one likely candidate gene in the QTL region while Pootakham *et al*. (2015) identified two genes in the 0.5-LOD (logarithm of the odds) support interval that may be involved in determination of plant height. Pootakham *et al*. (2015) was also able to identify a QTL linked to bunch weight. The genome sequences also allowed researchers to use markers identified from next-generation sequencing (NGS) data of restriction-site-associated DNA (RAD) libraries to study oil content. Two QTL for oil content and markers linked to higher oil content in the populations tested were identified (Bai *et al*., 2017). As for oil quality, several structural genes in fatty acid and oil biosynthesis pathways, and a transcription factor were identified in the QTL interval linked to fatty acid composition (Ting *et al*., 2016).

The availability of the genome data enabled multi-locus genome-wide association studies (GWAS) to be conducted. A GWAS effort conducted by Ithnin *et al*. (2017) was able to identify 13 QTL influencing bunch components and six QTL linked to vegetative parameters. Another interesting study published in 2017 relates to the devastating basal stem rot disease caused by *Ganoderma boninense*. The study used the infection status of 1200 individual palms in the field over 25 years and genotyped 757 palms from this population. The authors were able to associate two QTL linked to occurrence of first *Ganoderma* symptoms and two to the death of the palm (Tisne *et al*., 2017). All these studies have provided many possible leads that can help make marker-assisted selection of the ideal oil palm a reality. Nevertheless, further studies need to be carried out to identify the causal genes and/or mutations linked to traits of interest. Gene expression analysis will also provide a better understanding of the underlying genes involved in the control of the traits and their regulatory networks.

GENE IDENTIFICATION AND EXPRESSION STUDIES

With the availability of NGS technology, RNA sequencing (RNA-Seq) has become increasingly popular in oil palm research. This is due to the fact that gene expression studies using RNA-Seq are easier and more comprehensive than previously available methods, such as the EST approach. As reported by Bourgis *et al*. (2011) and Tranbarger *et al*. (2011), RNA-Seq can help improve our understanding of genes that are involved in important biological processes and regulatory networks. Bourgis *et al*. (2011) were able to identify key enzymes of plastidial carbon metabolism, synthesis of fatty acids and triacylglycerol assembly by comparative transcriptome and metabolite analysis between oil palm and date palm. Fatty acid biosynthesis genes showed major differences in expression with distinct increases during oil palm ripening. This could explain why oil palm accumulates up to 90% oil in its mesocarp, while date palm accumulates mainly sugars. Tranbarger *et al*. (2011) examined the transcriptional basis of lipid and carotenoid metabolism to study the regulatory mechanisms involved in the developmental phases preceding and during maturation, and ripening. Comparison of the compositions of lipids and transcripts in *dura, pisifera* and *tenera* mesocarp and endosperm tissues showed that a transcription factor, *WRINKLED1*, was upregulated in *tenera* compared to their parental palms. This may explain the high expression of lipid biosynthesis pathway genes in *tenera* (Jin *et al*., 2017). These datasets provide information for breeders to identify candidate genes involved in high oil synthesis and tackle the issue of stagnating yields in oil palm. Other transcriptome studies of interest include the study by Shearman *et al*. (2013) on normal and mantled oil palm fruits, and cell wall development during fruit ripening by Tranbarger *et al*. (2017).

Together with the release of the oil palm genome sequence in 2013, MPOB also made available transcriptome data, including those from leaf, flower, pollen, mesocarp, kernel, roots and shoot to the oil palm research community. The 19 transcriptome libraries were assembled from sequences generated from the Roche 454 sequencing platform (Singh *et al*., 2013a) while 10 transcriptome libraries from

kernel and mesocarp were constructed and deep sequenced using Illumina HiSeq (Singh *et al*., 2013a; 2014). RNA datasets from a wide range of tissue types support better quality gene model predictions and allow for comparison of genes and pathways in different tissues.

A transcriptome study was also performed to improve our understanding on *Ganoderma* infection. Differential gene expression analysis of root transcriptomes of untreated oil palm seedlings with those inoculated with *G. boninense* and *Trichoderma harzianum* suggested that jasmonate, salicylate and ethylene signalling pathways may partly determine the downstream defence responses against *G. boninense* (Ho *et al*., 2016). The data also showed that endophytic *T. harzianum* improved the nutrition status and nutrient transportation in host plants. The study is an important first step at the efforts to enhance our understanding on the molecular interactions of oil palm and diseases. This will eventually be used to develop future strategies for disease prevention and treatment, and for development of disease resistant varieties.

By exploiting transcriptome data, a series of SSR markers were developed based on differentially expressed genes in response to cold stress (Xiao *et al*., 2014). Sequenced cold-treated samples of oil palm indicated that C-repeat binding factor may play a central role in cold tolerance (Lei *et al*., 2014). Effects of future climate change on growth and yield of oil palm have always been a major concern to the industry. Enhancing our understanding of genes that are impacted by temperature change will help improve the versatility and adaptability of the crop to climate change and help develop tools to enhance oil productivity of this tropical species. Xiao *et al*. (2014) identified an EST-SSR loci that was expressed in response to low temperature, which may have potential application in breeding for palms that can withstand significant drop in temperature.

CONCLUSION

The last few years has witnessed the oil palm scientific community making great progress in deciphering and exploring the genome, using new and improved technologies. This has facilitated interesting new discoveries that will have a significant impact on improving oil palm breeding and tissue culture. We have witnessed empowering and exciting results from the discovery of *VIR*, *SHELL* and *MANTLED* genes. The genomics age has also produced significant advancements in our understanding of oil palm fruit development and fatty acid biosynthesis, defence response against diseases, and cold resistant. However, to produce the ideal palm of the future, considerable effort is still needed to hunt for the genetic factors that can overcome stagnating yields, control diseases, improve oil quality, reduce height increment, increase compactness, and enhance versatility and adaptability to climate and environment change. The oil palm genome data has shown that it can open new and important research opportunities that will eventually lead to higher yielding disease resistant palms that are amenable to mechanisation. Palms having these traits, coupled with the ability to withstand climate change and have increased nutrient uptake efficiency will help ensure that the oil palm industry is a sustainable agribusiness.

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