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HARNESSING THE ROLE OF EPIGENETICS IN OIL PALM IMPROVEMENT

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ABSTRACT

By 2050, the global population will approach 10 billion, placing immense pressure on agriculture to ensure food security amidst stagnant yields, land scarcity and extreme weather events. Enhancing crop improvement for higher productivity per hectare is crucial. Epigenetics, the study of heritable gene expression changes without DNA alteration, presents a promising avenue for crop adaptation and resilience. Plants employ epigenetic modifications to respond to environmental shifts, offering flexibility due to their reversible nature. This review aims to explore the role of epigenetics in oil palm breeding, drawing from insights obtained from other plants with a focus on the heritability and stability of epigenetic modifications, as well as priming strategies to enhance resilience by altering the epigenome. We also highlight key advancements in oil palm epigenetics studies, including the discovery of the Karma *transposable element and its use in the SureSawit™* KARMA *assay to possibly identify plants prone to mantling. Additionally, we discuss the potential of EWAS for marker discovery, integration of CRISPR/dCas9-based epigenome editing for targeted modifications and priming strategies to enhance oil palm resilience. The importance of field-based validation of epigenetic markers and priming approaches is emphasised. These advancements may help promote sustainable agriculture in a changing world.*

Keywords: chromatin, crop improvement, epiallele, priming, stress memory.

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INTRODUCTION

Food demands increase as the human population grows. With limited cultivable lands, intensifying yields per planting area would be sustainable towards securing food availability. Unfortunately, yields of major agronomic crops have been declining due to various environmental stresses. Drought, for example, has led to yield losses of 63%-87% in maize, 57% in wheat, 53%-92% in rice, 45%-69% in chickpea, 46%-71% in soybean and 60% in sunflower (Fahad et al., 2017). Risk assessment of drought and higher temperatures on crop productivity is made possible due to the development of various projection models (Kamali et al., 2022; Leng & Hall, 2019). Global yield losses of grain crops such as wheat, rice and maize due to insect attacks are projected to increase by 10%-25%°C of warming (Deutsch et al., 2018). Crop breeders are urged to create planting materials that can produce higher and stable yields when grown under unpredictable weather conditions involving exposure to various biotic and abiotic threats. Identifying such adaptive traits through epigenetics study could contribute to future crop sustainability. Various studies have implicated the role of epigenetics in conferring adaptive traits, offering an attractive alternative toolkit for crop breeding.

While much attention has been given to staple crops, oil palm (*Elaeis guineensis*), as the world's leading source of vegetable oil, is also vulnerable to both environmental stresses and developmental abnormalities that threaten yields and sustainability. Given the growing demand for sustainable palm oil and the challenges associated with traditional breeding of this perennial crop, this review aims to

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explore the potential of epigenetic mechanisms as a novel tool for oil palm improvement. We provide a concise overview of key epigenetic concepts and mechanisms, and their roles in enhancing crop performance, highlighting relevant studies in other plants. This review also aims to consolidate the current knowledge of epigenetic mechanisms in oil palm, which is mainly related to the mantled abnormality in clones. Furthermore, the potential of epigenetics can be harnessed to enhance oil palm traits, particularly in stress resilience and productivity, offering potentially novel solutions that overcome the limitations of conventional breeding approaches. In relation to this, we discuss the stability of epigenetic changes and the potential of priming strategies for stress resilience.

A search of the Scopus database using the keywords "epigenetics" and "crop" yielded 347 articles published between 2003 and 2025. In contrast, using the keywords "epigenetics" and "oil palm" returned only 15 articles from 2000-2024, limited to English-language journal articles. This suggests that studies on oil palm epigenetics are still in its early stages, presenting opportunities for further exploration and discovery. Author keywords provide insights into the subject focus of articles. Network visualisations were then generated using VOSviewer (Van Eck et al., 2010) based on author keyword co-occurrence for the respective search terms (*Figure 1*). In both datasets, "epigenetics" and "DNA methylation" emerged as the most commonly used keywords.

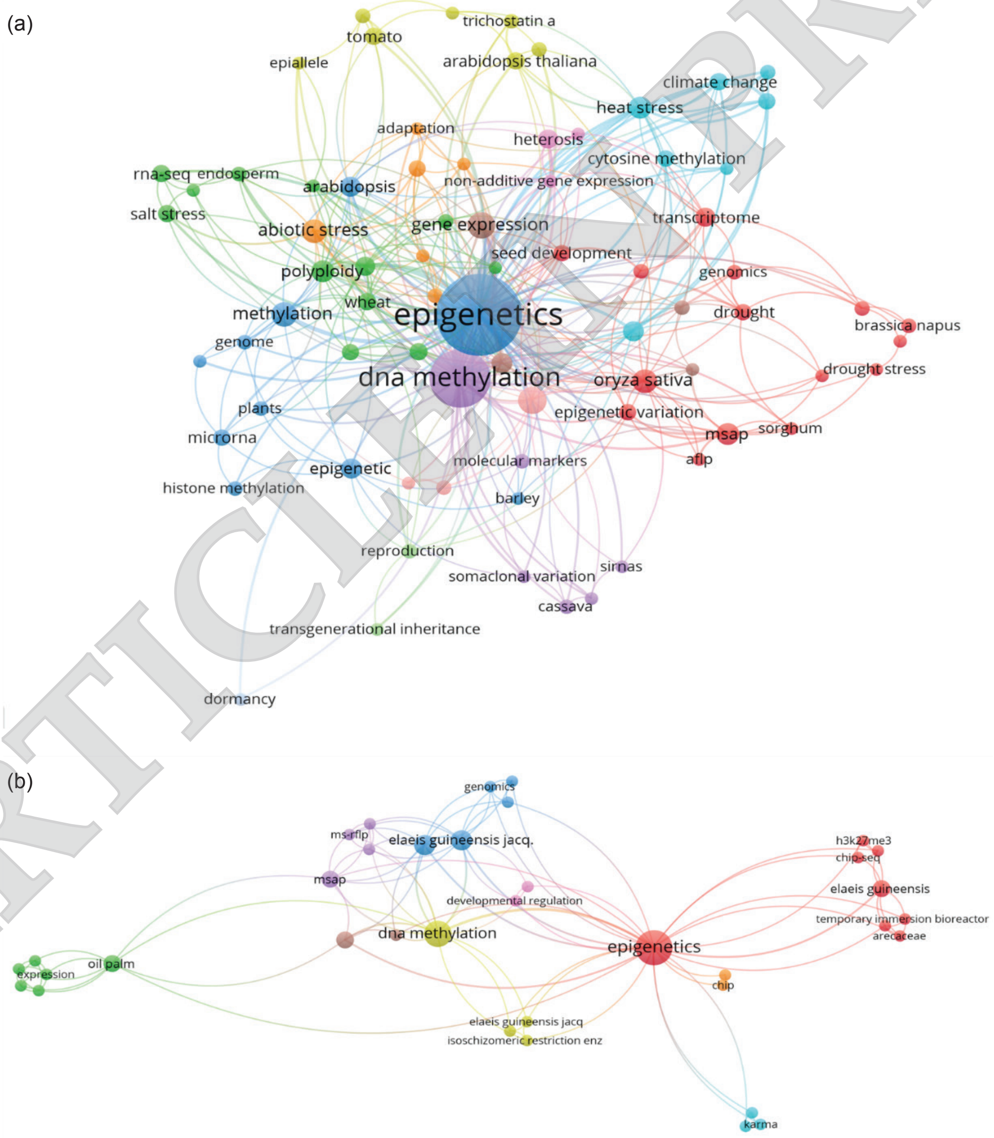


Figure 1. Network visualisation map of authors' keywords. (a) Crop epigenetics studies. Minimum occurrence of a keyword was set at 3 for the threshold. (b) Oil palm epigenetics studies. As there are very few articles associated with these keywords, no threshold was set. However, the network is limited to the parts that have connecting lines. The colour, circle size, font size and thickness of connecting lines represent the strength and frequency of associations among keywords. Keywords frequently grouped share the same colour and cluster.

EPIGENETICS INFLUENCES GENE EXPRESSION

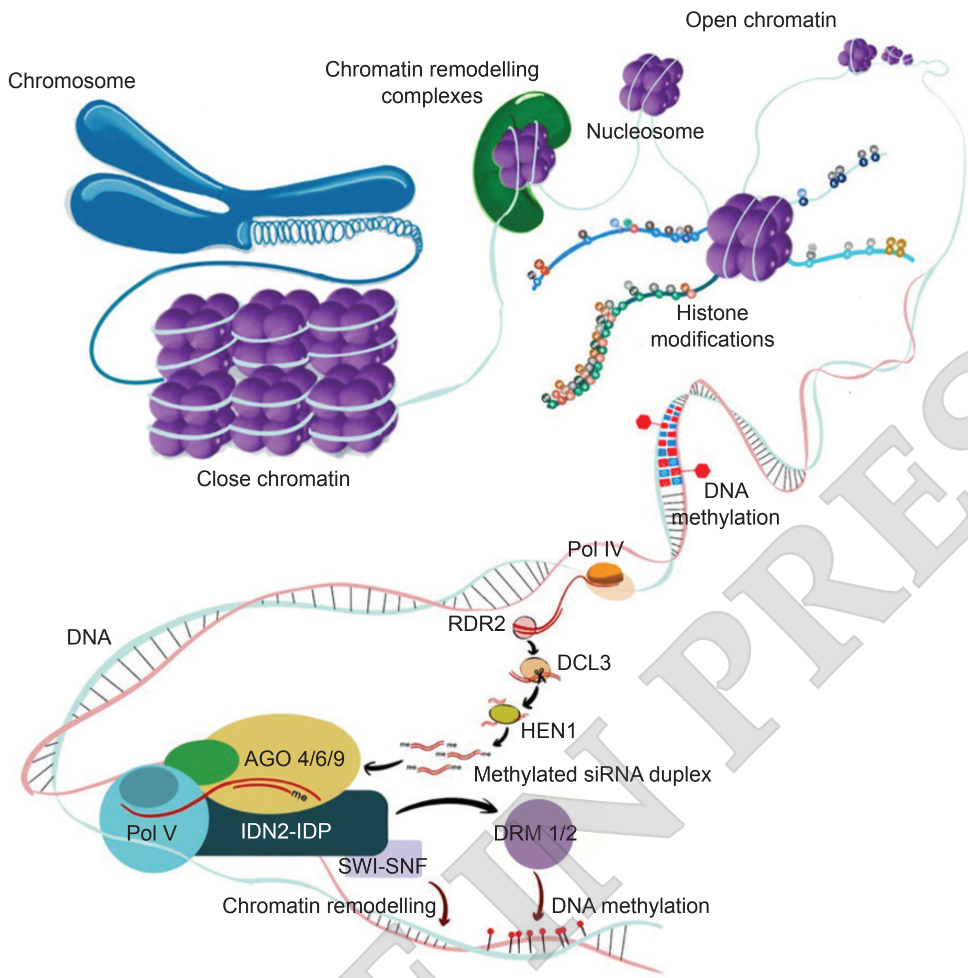
All living organisms, including crop plants, contain DNA that codes for multiple genes. Certain genes will be expressed while others are silenced, but the DNA remains the same throughout the plant's life cycle and development. Gene regulation involves a wide range of mechanisms, including epigenetics. While genetics is the study of DNA and the genes they encode, epigenetics is the study of changes in gene function that do not involve alterations to DNA sequence (Gibney & Nolan, 2010). The term 'epi' comes from a Greek word for 'on top of', thus, 'epigenetics', which was first coined in the early 1940s (Waddington, 1942), could be described as beyond genetics. Unlike the genome, which is represented by a string of A, T, C and G bases that make up the DNA, the epigenome constitutes a collection of biochemical tags attached to the DNA and its associated histone proteins (Agarwal et al., 2020). Epigenetic changes are easily influenced by environmental signals and are potentially reversible (Wright, 2013). Some epigenetic marks could be inherited mitotically, or meiotically, i.e., passed from parents to offspring or transmitted to multiple generations.

Exhibition and improvement of traits, therefore do not rely exclusively on the DNA encoding the traits, but also on the epigenetic state of the DNA in enabling the traits to be expressed. The expression of genes leading to phenotype expression is regulated by several interconnected epigenetic mechanisms, including chromatin accessibility, DNA methylation, histone modifications and non-coding RNAs. These elements influence how tightly or loosely the chromatin structure harbouring the genes is packed, whether the genes are turned on or off and how their regulation responds to environmental and developmental signals. Genetic information stored in the DNA strand is packed in a compact hierarchical chromatin structure within the nucleus (*Figure 2*). The primary structural unit of chromatin consists of DNA and histone proteins, called nucleosomes. A nucleosome is composed of 146-147 bp of DNA, which is tightly wrapped around a histone octamer (two each of H2A, H2B, H3 and H4). Two adjacent nucleosomes are linked by 10-80 bp of linker DNA, and the H1 histone binds to the linker DNA to stabilise the entire complex (Agarwal et al., 2020). The chromatin can exist in a relaxed (euchromatin) or condensed (heterochromatin) state, which determines how easily genes can be transcribed. Chromatin remodelling complexes such as switch/sucrose non-fermentable (SWI/SNF), chromodomain helicase DNA-binding (CHD), inositol requiring 80 (INO80) and imitation switch (ISWI) complexes, utilise the energy from ATP hydrolysis to restructure nucleosomes, affecting chromatin packaging and accessibility (Clapier & Cairns, 2009). In addition to physical restructuring, post-translational modifications of histone tails such as acetylation, methylation, phosphorylation and ubiquitination further influence how tightly DNA is wound around the histones (Bowman & Poirier, 2015).

At the DNA sequence level, transcriptional activity of associated genes can be altered by DNA methylation, a type of epigenetic modification that involves the addition of a methyl group to the fifth position of the pyrimidine ring of the cytosine base, also referred to as 5-methylcytosine (5mC). DNA methylation, which occurs in three sequence contexts in plants: CG, CHG and CHH (where H = A, T or C), helps to regulate gene expression, transposon silencing, and chromatin interactions (Zhang et al., 2018). Non-coding RNAs (ncRNAs) are clusters of RNAs that do not encode for functional proteins. ncRNAs are categorised into housekeeping and regulatory types, with regulatory ncRNAs further classified by their lengths: Small RNAs (18-30 nucleotides [nt]), medium-sized ncRNAs (31-200 nt), and long ncRNAs (>200 nt) (Collins et al., 2011; Wei et al., 2017). Small RNAs are grouped into micro RNAs (miRNAs), transposable element (TE)-derived small interfering RNAs (siRNAs) and phased siRNAs (phasiRNAs). miRNAs mediate transcript cleavage and translation repression, while siRNAs are involved in transcriptional gene silencing by directing DNA methylation and/or histone methylation through a process known as RNA-directed DNA methylation (RdDM) (Yu et al., 2019). The best characterised phasiRNAs known as *trans*-acting siRNAs (tasiRNAs) regulate target coding genes via mRNA cleavage in *trans* (Deng et al., 2018). Long ncRNAs (lncRNAs) are characterised based on the region they derive from, e.g., intergenic regions (long intergenic ncRNAs [lincRNAs]), intronic regions (intronic ncRNAs [incRNAs]), and coding regions (natural antisense transcripts [NATs]). LncRNAs interact with histone-modified complexes or enzymes to regulate histone modifications and regulate DNA methylation through the RdDM process (Zhang et al., 2019b). Due to its stability and the availability of various detection tools, DNA methylation is thus by far the most extensively studied epigenetic modification.

EXPLOITING EPIGENETICS FOR CROP BREEDING

Conventional crop breeding has long relied on selecting and crossing plants with desirable traits, followed by evaluating the offspring over several generations to achieve improved varieties. This process, although successful, is often time-consuming and dependent on the



Note: All elements in the figure were drawn from scratch, and the RdDM illustration part was adapted from Frost et al. (2024).

Figure 2. Schematic representation of chromatin organisation and epigenetic regulation. DNA wrapped around the histone proteins makes up the basic chromatin organisation called the nucleosome. Epigenetic regulators that influence gene expression include chromatin accessibility, post-translational histone modifications, DNA methylation and non-coding RNAs. Chromatin accessibility is modulated by chromatin remodelling complexes that reposition or evict nucleosomes. Histone tails can undergo post-translational modifications; for example, trimethylation at histone H3 lysine 4 (H3K4me3) and acetylation (e.g., H3K4ac) are generally associated with active transcription. DNA methylation involves the addition of a methyl group to cytosine residues, typically leading to transcriptional repression. Non-coding RNAs, such as small interfering RNAs (siRNAs), participate in RNA-directed DNA methylation (RdDM). In this pathway, RNA polymerase IV (Pol IV) transcribes single-stranded RNAs, which are converted to double-stranded RNAs by RNA-DEPENDENT RNA POLYMERASE 2 (RDR2). These are processed into 24-nucleotide siRNAs by DICER-LIKE 3 (DCL3) and stabilised by methylation at the 3′ end by HUA ENHANCER 1 (HEN1). The 24-nt siRNAs are loaded onto ARGONAUTE proteins (primarily AGO4, AGO6 and AGO9) to form the RNA-induced silencing complex (RISC). This complex interacts with transcripts produced by RNA polymerase V (Pol V) and recruits DOMAINS REARRANGED METHYLTRANSFERASE 1 and 2 (DRM1/2), which catalyse de novo cytosine methylation, thereby silencing specific genomic regions.

natural occurrence of beneficial traits in the gene pool. Advances in genomics have contributed to a deeper understanding of the relationships between genotype and phenotype for numerous genes and traits. A significant accomplishment in the use of genomics for crop breeding comes from the marker-assisted selection (MAS) approach, which relies on the linkage between a marker and a gene or the quantitative trait loci (QTL) of interest (Collard & Mackill, 2008). The use of DNA markers to screen for allelic variation in genes underlying the traits helps to increase the efficiency and precision of crop breeding (Nadeem et al., 2018).

Epigenomics open up new possibilities in crop breeding by tuning a trait's expression up or down. Breeding for climate-resilient crops requires epigenetics-linked traits to be incorporated in breeding programmes, as adaptability and survival also relate to epigenetic mechanisms. Manipulation of the epigenome for breeding purposes or so-called epigenetics-mediated crop breeding (epi-breeding), relies on the epiallele, a gene variant based on epigenetic marks associated with traits of interest. In the same fashion that QTLs progress to utilisation as genomic markers, a stable epiallele can be linked to a QTL (epiQTL) and can therefore be potentially developed into reliable epimarkers and used as a complement to genomic markers in tagging of the traits (Gahlaut et al., 2020). EpiQTLs associated with potential agronomic traits have been found, such as traits related to height, seed quality, and development in *Brassica napus* (Long et al., 2011), flowering time and primary root length in *Arabidopsis* (Cortijo et al., 2014), and growth and wood properties in *Populus* (Lu et al., 2020). In the future, epimarkers would likely be useful for epigenomic editing as a way to introduce specific epimutations associated with improved phenotypes.

Epialleles contribute to phenotypic differences and can thus be used as an additional source of variation for breeding. These variants often arise from modifications in epigenetic marks that influence gene expression. A classic example of a naturally occurring epiallele is the *Lcyc* (*Linaria cycliodea*) gene in toadflax (*Linaria vulgaris*), where an altered epigenetic state leads to a shift from bilateral to radial flower symmetry (Cubas et al., 1999). In tomato, changes in epigenetic regulation of *CNR* (colorless non-ripening) and *VTE3* (vitamin E3) genes result in colourless fruits and increased tocopherol levels, respectively (Manning et al., 2006; Quadrana et al., 2014). Similarly, altered epigenetic control of the *CmWIP1* gene in melon affects sex determination and promotes the development of female flowers (Martin et al., 2009). Epialleles can also be artificially induced to produce epigenetic variants (Dalakouras & Vlachostergios, 2021; Srikant & Tri Wibowo, 2021). Such epialleles were reported in *Arabidopsis* epigenetic recombinant inbred lines (epiRILs) derived from an initial cross between DNA hypomethylated mutants and wild-type plants, which were then found to be stably inherited for many generations (Johannes et al., 2009). However, the creation of such lines would be very challenging in crops due to the unavailability of hypomethylated mutants.

Environmental conditions, including biotic and abiotic stresses, can influence the epigenome as well, with examples reported in rice under drought (Zheng et al., 2017) and maize planted in zinc deficiency conditions (Mager et al., 2018). Tissue culture has also been associated with shifts in epigenetic states, as seen in maize regenerants (Han et al., 2018) and the floral abnormality in clonal oil palm (Ong-Abdullah et al., 2015).

THE UNDESIRABLE *BAD KARMA* EPIALLELE OF MANTLED CLONAL OIL PALMS

With limited arable land, oil palm cloning is an important and attractive alternative for the vegetative propagation of elite planting material towards the goal of increasing oil yields per hectare. Somaclonal variation, however, occurs during the clonal propagation of many plants (Krishna et al., 2016). In oil palm clones, the mantled somaclonal variant was hypothesised to be an epigenetic anomaly due to the characteristics of its phenotype (Adam et al., 2007a). Mantled clonal palms display feminisation of the male floral organs in their male and female inflorescences at various degrees of severity. Mild phenotypes involve the development of a few pseudocarpels on the fruit bunch, which can still ripen and provide oil. Severely mantled palms, though, can exhibit six pseudocarpels on their parthenocarpic fruit bunches, with feminisation of all six male floral organs on a female inflorescence, leading to abortive fruit bunches and therefore oil loss from these palms (Adam et al., 2005). Mantled clonal palms are usually only identified at 2-3 years after field planting, when mantled fruit bunches are visible.

Although oil palm cloning was successfully achieved 50 years ago, large-scale commercial planting was halted in 1986 following public disclosure of the mantling floral abnormality. Initial investigations ruled out ploidy changes as a contributing factor (Rival et al., 1997), and molecular markers such as RAPD and AFLP revealed no DNA polymorphisms associated with the mantled phenotype (Rival et al., 1998), suggesting that a genetic defect was unlikely to be the underlying cause. The unpredictable nature of mantling, including variations between genotypes and occasionally reverting to normal, prompted consideration of an epigenetic mechanism. Early studies supported this hypothesis with global DNA hypomethylation detected in abnormal tissues such as fast-growing callus, mantled inflorescences and leaves from mantled palms (Jaligot et al., 2000). However, attempts to establish universal methylation thresholds or consistent sequence-specific methylation markers were challenged by genotype-specific background variations. Consequently, research shifted towards candidate gene analyses, particularly focusing on the MADS-box genes involved in floral organ development as described in the ABCDE model. Misregulation of the B-class genes such as *DEFICIENS* (*DEF*) and *GLOBOSA* (*GLO*) was proposed as a potential cause of mantling due to the important roles of these genes in stamen development. In 2014, Jaligot et al. first reported the possible involvement of *DEF* methylation changes in the mantled phenotype, along with the methylation profiles of *Koala* and *Rider* transposable elements residing in *DEF*.

After many years of research following the public disclosure of mantling (*Table 1*), an epigenetic mark on *Karma*, another transposable element located in the *DEF* gene (called *EgDEF1*), was strongly associated with the mantled phenotype (Ong-

Abdullah et al., 2015), representing a significant step in understanding the underlying cause of mantling. *EgDEF1* is a B-type MADS-box gene that is important for the development of male floral organs in oil palm inflorescences (Adam et al., 2006). In mantled female inflorescences, reduced expression of *EgDEF1* was detected especially in the abnormal staminodes or pseudocarpel initials (Adam et al., 2007b; Ooi et al., 2019). This may be due to feedback regulation from the expression of *kDEF1*, an alternatively spliced transcript isoform of *EgDEF1* in mantled inflorescences, as *kDEF1* expression is almost absent in normal inflorescences (Ong-Abdullah et al., 2015). Therefore, misregulation of *EgDEF1* isoforms' expression due to the hypomethylated *Karma* element in inflorescences leads to the feminisation of male floral organs and subsequently, mantled fruit development and oil yield loss thereafter.

The discovery of this epigenetic mark on *Karma-EgDEF1* led to the development of a screening assay for the early culling of potentially mantled ramets before they reach reproductive maturity (Hashim et al., 2018; Ong-Abdullah et al., 2016). Plants that are tested with this assay would provide planters with a greater assurance of the lower mantling risk of these plants. This assay, currently available as the SureSawit™ *KARMA* assay (Orion Biosains, 2024), involves just sampling of a leaf disc from a nursery or juvenile stage plantlet using the SureSawit™ Sample Collection Kit. This probe-based quantitative PCR test provides a prediction on the risk of mantling for the sampled palm. Implementation of the SureSawit™ *KARMA* screening test in the quality control procedures of clones will undoubtedly increase the cost price of clonal planting material (Weckx et al., 2019). However, this may potentially offset the higher costs encountered with planting of unknowingly mantled palms in the field. Nevertheless, due to the dynamic nature of epigenetic marks, the predictive power of *Karma* hypomethylation in young ramets has yet to be comprehensively assessed.

While the SureSawit™ *KARMA* assay generally employs bisulfite conversion followed by real-time quantitative PCR (Ong-Abdullah et al., 2016), improvements in next-generation long-read sequencing technologies from PacBio and Oxford Nanopore now allow the detection of methylated DNA on native DNA, eliminating the need for bisulfite conversion. This is particularly advantageous for analysing the whole ~3 kb *Karma* retrotransposon, as long reads can span its length and potentially resolve mapping ambiguities arising from its repetitive nature. Alternatively, targeted methylation arrays or panels coupled with sequencing offer a potentially cost-effective approach for single-base resolution methylation analysis of specific regions, such as *Karma*. For example, methylation arrays designed based on specific DNA methylation biomarkers have been used for noninvasive detection of lung cancers in humans (Wei et al., 2021).

Furthermore, additional cytosine sites within the *Karma* element have been associated with the mantling risk of ortets (Ooi et al., 2024, 2023). However, these findings require further investigation and validation in a larger sample size from more diverse genotypes. Importantly, this association was detected in the mother palms used for cloning, suggesting that if these methylation differences are consistent, it might be possible to even predict mantling risk before initiating tissue culture.

TABLE 1. KEY FINDINGS FROM EPIGENETICS STUDIES OF OIL PALM MANTLING (2000-PRESENT)

References	Key findings
Jaligot et al. (2000)	HPLC quantification and SssI-methylase accepting assay revealed global hypomethylation in leaf DNA of abnormal regenerants and abnormal fast-growing callus as compared to the respective normal tissues.
Matthes et al. (2001)	An amplified fragment length polymorphism (AFLP) analysis using methylation-insensitive enzymes showed no polymorphisms between the ortets and their tissue culture-derived regenerants (ramets), but AFLP with methylation-sensitive enzymes revealed polymorphisms, although none of the polymorphic bands were common to all ramets.
Jaligot et al. (2002)	A band shift towards lower molecular weight DNA revealed reduced methylation in the abnormal (fast-growing) callus type compared to the normal (nodular compact) callus type.
Kubis et al. (2003)	No genomic organisation differences in transposable DNA elements were observed between ortet and mantled-regenerated palms. A genome-wide decrease in DNA methylation levels occurred during tissue culture, which was restored in regenerated trees, though methylation levels remained slightly lower than in the ortet.
Jaligot et al. (2004)	A methylation-sensitive amplification polymorphism analysis of CCGG sites in normal and mantled revealed limited methylation differences, with several methylated markers showing genotype-specific discrimination.
Sianipar et al. (2008)	Changes in methylcytosine content between normal and abnormal somatic embryo cotyledons, and between plantlets and the normal mother oil palm, were attributed to hypomethylation.
Rival et al. (2013)	*In vitro* proliferation induces time-dependent DNA hypermethylation across several clonal lines, while loss of methylation in one line was associated with its inability to produce somatic embryos.

TABLE 1. KEY FINDINGS FROM EPIGENETICS STUDIES OF OIL PALM MANTLING (2000-PRESENT) (continued)

References	Key findings
Yaacob et al. (2013)	Higher histone deacetylase activity was observed in leaf samples from mantled palms, along with distinct banding patterns in fruits and florets compared to normal tissues.
Jaligot et al. (2014)	*Gypsy* and *Copia* retrotransposons are heavily methylated, and alternative splicing of the *EgDEF1* gene generates an alternate transcript during inflorescence development, potentially contributing to the mantled phenotype.
Ong-Abdullah et al. (2015)	The hypomethylation state of a *Karma* retrotransposon within the *DEFICIENS* gene is associated with the mantled abnormal phenotype of clones.
Ong-Abdullah et al. (2016)	The SureSawit^{TM} *KARMA* assay was developed to evaluate *Karma* hypomethylation for the identification and subsequent culling of high-risk ramets at the nursery stage prior to field planting.
Sarpan et al. (2018)	An optimised ChIP-seq protocol was reported for histone modification studies in oil palm, including chromatin isolation, shearing, and immunoprecipitation.
Sarpan et al. (2020)	WGBS analysis revealed that several CHG hypomethylated sites within *Karma-EgDEF1* and hypomethylated hotspot regions in several chromosomes were associated with mantling.
Sarpan et al. (2022)	Histone modification profiles for H3K4me3 and H3K27me3 in oil palm were identified near putative transcription start sites, consistent with other plants.
Ooi et al. (2023)	Three sRNA clusters were identified as differentially regulated in ortets that gave rise to high mantling outcomes. In these ortets, CHH hypomethylation was predominantly detected at specific regions in *Karma* and its surrounding regions.
Ooi et al. (2024)	Hypomethylation at the mid-*Karma* region in phenotypically normal clonal ortets is associated with high-mantling outcomes in their reclones.

STABILITY OF EPIGENETIC VARIANTS

Issues on stability and heritability of epigenetic variants need to be first addressed for the practical implementation of epi-breeding. In many plants, various biotic and abiotic stresses can lead to a wide range of epigenetic changes (Srikant & Tri Wibowo, 2021). These epigenetic changes are part of the stress memory acquisition in plants, which may lead to improved stress tolerance response (Crisp et al., 2016). This memory is retained by plants after a stress exposure. Depending on the duration and level of stress exposure, plants may or may not retain the stress memory. Subsequent generations of non-stressed *Arabidopsis* plants were found to lose the salt stress tolerance inherited through a multigenerational exposure to salt stress (Wibowo et al., 2016). However, some genome modifications due to environmental stress were found to be stable and may be inherited into the next generation (Bruce et al., 2007; Kinoshita & Seki, 2014; Thiebaut et al., 2019).

Stress memory can be divided into two categories, short-term and long-term memories (Sun et al., 2021). Short-term memory involves retaining tolerance to that particular stress for several days, mainly attributed to temporary changes in morphology and metabolite composition (Crisp et al., 2016). Long-term stress memory, which involves epigenetic changes, can last the entire lifespan of the plant and may even be transferred to its offspring (Bilichak & Kovalchuk, 2016; Zheng et al., 2017). Drought-induced DNA methylation changes could be maintained in successive generations of rice plants that were exposed to drought stress from the tillering to grain filling stages (Zheng et al., 2017). A moderate temperature increase treatment in *Arabidopsis* led to a transgenerational epigenetic memory involving small RNA biogenesis and gene silencing, and this memory was retained for at least three generations, though with a gradual decline in strength over the next generations (Zhong et al., 2013).

DNA methylation in epialleles can be transmitted in a Mendelian manner during meiosis (Schmitz et al., 2013). Chromatin modifications associated with abiotic stress response or pathogen attack are usually transiently retained as somatic stress memory that lasts only a small portion of the plant's lifespan (Kumar, 2018; Lämke & Bäurle, 2017). Reports on transgenerational inheritance of histone modifications are rather limited (Zhi & Chang, 2021). As histone modifications may be transmitted through mitosis, clonal propagation may be an avenue to maintain this transmission. This approach is likely applicable for over 60% of crops, such as potato, yam, taro, sorghum, cassava (Zhi & Chang, 2021) and oil palm.

DNA methylation and histone modifications are often reset during meiosis and therefore, inheritance of certain epigenetic modifications marks through meiosis may be a problem (Danchin et al., 2019). For clonally propagated crops such as potato, however, transfer of epigenetic marks through mitosis is stable (Sun et al., 2021). Some epigenetic changes can be stably transmitted through many mitotic or meiotic cycles and inherited in the progenies (Quadrana & Colot, 2016; Zhang et al., 2018), though it is unclear why some methylation marks are erased while others can be inherited into the next generation (Srikant & Tri Wibowo, 2021). Heritability of induced epialleles appears to be influenced by three factors: The magnitude of the initial epigenetic change, the genetic landscape of the particular locus and the local chromatin environment. The frequency, duration and magnitude of applied stresses may affect the heritability of the epigenetic changes (Srikant & Drost, 2021). Stable and heritable epialleles usually emerge from regions with a high CG content and lower repeat density or high levels of H3K4me3 and H3K18ac euchromatin marks (Srikant & Tri Wibowo, 2021).

As various stresses implicate various molecular pathways via cross-talk of the pathways, exposure of plants to one type of stress may promote cross-resistance to other stresses (Foyer et al., 2016; Lämke & Bäurle, 2017). Biotic and abiotic stresses in plants involve common types of biological pathways and signals (Atkinson & Urwin, 2012). Stress exposure may confer stress priming and provide plants with improved stress response in future (Hilker & Schmülling, 2019; Leuendorf et al., 2020; Molinier et al., 2006; Wang et al., 2014). Breeding using genetic diversity has become limited for some crops due to intensive breeding, but epigenetic variation is an attractive avenue to provide an alternative source for crop improvement (Gallusci et al., 2017). For example, continuous screening under drought stress of *B. napus* for three generations provided plants with not only strong drought resistance but also high nitrogen utilisation efficiency (Verkest et al., 2015). Improvements in stress resistance may also involve the regulation of small RNAs (Banerjee et al., 2017; Zhang et al., 2019a).

PRIMING CROPS TO IMPROVE STRESS RESILIENCE

Crop production is sensitive to climate change. Adaptation of crop species to withstand multiple stresses without yield reduction is required to sustain food security. Priming, by pre-exposure of plants to low or non-lethal stress factors, could train plants to be self-prepared for the recurring stresses (Wang et al., 2017). Following the first stress exposure, plants acquire a stress memory to retain the initial stress response, which then primes for a quicker and stronger response to the subsequent stress (Hilker et al., 2015; Lämke & Bäurle, 2017), thereby enhancing stress tolerance in primed plants as compared to the unprimed. Many reports have suggested that stress memory and adaptation are heavily epigenetics based (Crisp et al., 2016; Lämke & Bäurle, 2017; Liu et al., 2022). Depending on the types of priming and subsequent triggering stresses, priming can be categorised as *cis-* or *trans*-priming. *Cis*-priming occurs when similar stresses are involved, for example, tomato plants primed with mycorrhizal colonisation acquired resistance to both fungal and a virulent bacterial pathogen (Fujita et al., 2022). *Trans*-priming refers to different initial and subsequent stress types, for example, cold priming increased salt tolerance in Bermuda grass (Fan et al., 2019), which also indicates cross-tolerance events.

A wide range of priming research has been conducted in plants encompassing various priming stimuli such as abiotic factors, biological agents and chemical compounds. Priming can be applied to seedlings (Bahuguna et al., 2018; Wang et al., 2015) or specific plant parts (He et al., 2019) at various developmental stages. In addition to increasing stress tolerance, priming generally results in other growth-promoting effects. In rice, priming with mild drought not only significantly reduced oxidative damage but also increased photosynthesis, stomatal conductance and enzymatic activity, thereby improving sink strength and significantly reducing seed set and grain yield losses (Bahuguna et al., 2018). In silicone-primed maize seedlings, detrimental effects of drought stress were alleviated with enhanced shoot and root lengths, biomass and improved levels of photosynthetic pigments (Parveen et al., 2019).

The seed is frequently used in priming methods. Seed priming is a pre-sowing treatment where seeds are soaked with priming agents that can induce a range of biochemical changes resulting in enhanced germination and boosting stress tolerance (Paparella et al., 2015). Various seed priming technologies have been developed, including treating seeds with water (hydro-priming), salt (halo-priming), osmotic agents (osmo-priming), plant hormonal solution (hormonal priming), a solution containing a solid carrier (solid matrix priming), magnetic field (magneto-priming), valuable microbe solutions (bio-priming) and solutions with nano-particles (nano-priming). It is well documented that primed seeds could mitigate the adverse effects of environmental stresses. Water-, KNO3- and urea-primed Chinese cabbage seeds displayed increased germination traits at various levels of drought stress, whereby such enhanced tolerance was associated with increased antioxidant enzyme activities and osmolyte concentrations (Yan, 2015). Nano-priming of maize seeds with titanium dioxide enhanced seed germination and seedling growth under salinity stress and mitigates the deleterious impact of such stress by enhancing antioxidant enzyme activities, leaf water content, proline and total phenolics content while reducing lipid peroxidation products and membrane relative electrolytes (Shah et al., 2021). In both cases, the fact that seedlings conferred tolerance when priming was done at the seed stage demonstrates that priming imprints were carried over into different stages of the plant's life cycle.

Among the different seed priming methods, bio-priming is the only approach that tackles both biotic and abiotic stress management (Mitra et al., 2021; Prasad et al., 2016). Bio-priming has been recognised as an inexpensive and eco-friendly technology over conventional seed priming, which uses chemical treatments. Beneficial microbes identified as plant growth-promoting rhizobacteria (PGPR) such as *Pseudomonas* spp. (Elsharkawy et al., 2022) and *Bacillus* spp. (Yildirim et al., 2021), as well as fungi such as the *Phanerochaete* spp. (Dief et al., 2021), have been used as bio-inoculants. Bio-primed seeds with PGPR contribute to induced systemic resistance to a wide range of plant pathogens (Pieterse et al., 2014), leading to an improved defence ability. Seed bio-priming also contributes to overall plant growth and higher productivity when planted under stress conditions. Bio-priming with a mixture of *Pseudomonas fluorescens* and *Rhizobium phaseoli* strains in mungbean (*Vigna radiata* L.) showed an 8%-12% increment in yield and yield components compared to non-bioprimed plants under terminal drought stress, which resulted from a strong antioxidant defense system and improved nutrient uptake (Nawaz et al., 2021). With the potential of these beneficial impacts, seed biopriming has indeed much to offer towards the sustainable agriculture of crops such as the oil palm.

FUTURE OUTLOOK FOR OIL PALM EPIGENETICS

Strengthening crop improvement programmes is crucial to attain food security goals. Advances in epigenetics research could help in the development of crop varieties with higher yield, enhanced nutritional values and better stress adaptation. In oil palm, where the long generation time presents a challenge for rapid genetic gains, epigenetics offers a strategic opportunity other than genetic approaches. By manipulating the epigenome, it is possible to bring about beneficial changes in gene expression, both naturally and through targeted interventions, without altering the DNA sequence. This is beneficial to improve crops with long-breeding cycles like the oil palm, targeting traits that are epigenetically regulated through prior discovery of epialleles or when a desired trait is needed temporarily. It provides an approach to fine-tune characteristics with the possibility of reversion to their original state depending on whether it is a mitotically or meiotically-heritable modification.

Enhancing oil palm traits can be achieved through several epigenomic approaches (*Figure 3*). The Epigenome-Wide Association Study (EWAS) has emerged as a promising approach to identify epigenetic markers associated with key agronomic traits. Conceptually similar to Genome-Wide Association Studies (GWAS), EWAS links phenotypic traits not to genetic variants like SNPs, but to epigenetic variations such as DNA methylation, histone modifications, or non-coding RNAs. Early EWAS efforts focused more on human studies where array-based platforms such as the Illumina Infinium HumanMethylation27 and 450K arrays were used to examine DNA methylation at pre-defined CG sites across the genome (Flanagan, 2015). However, the limited coverage and reliance on known regions restricted the discovery of novel epigenetic marks. The advent of high-throughput methylation sequencing technologies, particularly Whole-Genome Bisulfite Sequencing (WGBS), has since revolutionised EWAS by enabling unbiased, genome-wide methylation profiling at single-base resolution.

In oil palm, the potential of EWAS was demonstrated by the discovery of the *Karma* epiallele, which provided important insights into the epigenetic basis of the mantling abnormality in clones. This shows how EWAS can uncover epialleles associated with key traits by providing information that can be applied to epi-breeding to help breeders select superior individuals with desirable epigenetic states that might be missed by purely genetic approaches. Additionally, since epigenetic marks are responsive to environmental cues, epi-breeding also offers the possibility of selecting for traits with greater plasticity or adaptation to specific environments.

Integrating EWAS into breeding programs could start with selecting populations that exhibit variations in traits of interest and followed by sampling tissues that are relevant to the trait's expression. Then, profiling their epigenomes can be done using various tools such as WGBS for comprehensive coverage, reduced representation bisulfite sequencing (RRBS) for CG-rich regions, or methylation arrays and targeted bisulfite sequencing for known loci. The next steps include identifying differentially methylated regions (DMRs), linking these to phenotype data and validating the stability of candidate epigenetic markers by monitoring methylation levels across multiple developmental stages and a broader set of genotypes. Applying epigenetic tools in large-scale breeding programs can be costly and technically demanding for routine use due to the risk of epigenetic instability in field environments,

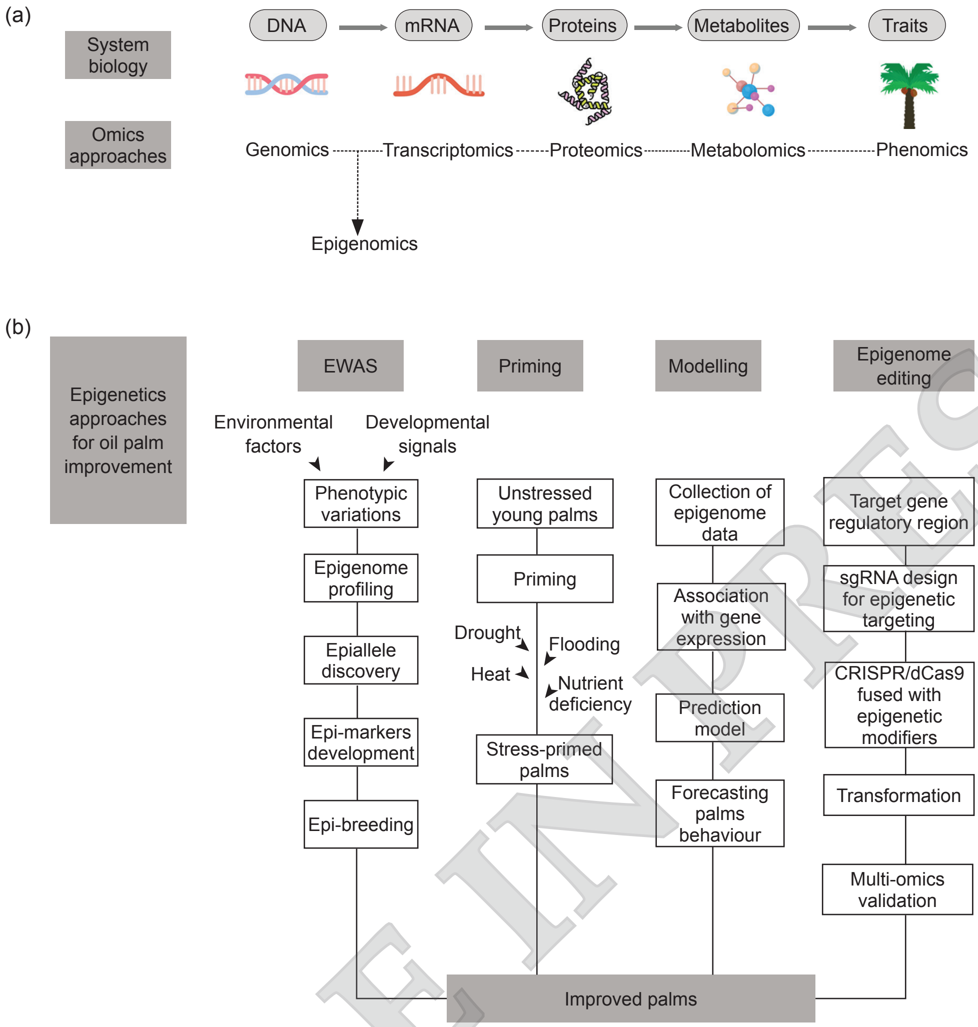


Figure 3. Integration of epigenomics approaches for oil palm improvement, (a) the foundational molecular layers in plant biology progress from the most basic (DNA) to the most complex (traits), highlighting the stages where epigenetics may play a role and (b) epigenetics approaches can be leveraged to improve oil palm phenotypes through epiallele discovery, which can be developed into epi-markers for breeding programs. Additional strategies include priming palms with stress treatments to enhance resilience, epigenomic data mining to develop predictive models for forecasting palm behaviour and epigenome editing to directly manipulate epigenetic marks for targeted phenotype improvement.

which could lead to reversion. Nevertheless, further validating stable markers and simplifying profiling methods would help to effectively capitalise on epigenetic applications for oil palm improvement.

The use of CRISPR/dCas9-based epigenome editing offers a targeted approach to improve oil palm traits. While EWAS provides a genome-wide associative approach to identify DMRs linked to desirable traits, CRISPR/dCas9-based epigenome editing offers a precise and targeted method to functionally modify these regions, without changing the DNA sequence. Specifically, once EWAS identifies stable epigenetic markers such as hypomethylated or hypermethylated regions associated with traits of interest, CRISPR/dCas9 fused with epigenetic modifiers (e.g., *TET1* for demethylation or *DNMT3A* for methylation) can be directed to these loci to intentionally alter methylation status. This targeted approach might be useful to address epigenetic instabilities in clonal propagation. For instance, re-establishing proper methylation at the *Karma* element using CRISPR/dCas9-DNMT3A could help mitigate the mantling abnormality in oil palm clones.

Plant priming also offers a practical and field-applicable approach to enhance oil palm performance. Leveraging on the growing concept of stress memory, priming prepares plants for improved adaptation to subsequent stress events. In the oil palm, the application of priming could begin by identifying the specific stress or trait targeted for enhancement. Based on this, an appropriate priming agent is then selected and applied to the plant material, which may vary depending on the developmental stage, such as seeds or juvenile plants. Initial evaluation of these strategies can be conducted on treated and non-treated plants in controlled environments. DNA methylation profiling can then be performed, with transcriptomics and phenotypic assessments, to evaluate the persistence and heritability of the induced stress memory. Plants are then transferred to the field for further evaluation, with periodic monitoring of their epigenetic profiles. At this stage, greater care is required as the plants are exposed to natural environmental variations, which may influence the epigenome. This stepwise strategy outlines how priming can be systematically implemented in the oil palm. Recent studies have demonstrated improved plant performance through priming, supported by methylome profiling. In *Medicago ruthenica*, priming through two cycles of drought exposure with rehydration in between resulted in reduced wilting and increased root size after the final drought period, compared to unprimed plants (Zi et al., 2024). In addition, genomic DNA methylation levels decreased following the two drought exposures, which may have triggered stress response mechanisms. This is supported by the increased expression of *P5CS* and *ABA2*, genes involved in the biosynthesis of proline and abscisic acid (ABA), both of which play key roles in drought response. In wheat, drought priming led to the accumulation of osmolytes such as proline and betaine, with their biosynthesis linked to promoter demethylation of the *TaP5CS* and *TaBADH* genes, thereby enhancing drought tolerance (Li et al., 2023).

Precision breeding thus represents a promising way to enhance desirable traits in oil palm by integrating advanced molecular insights into selection and improvement strategies. A key component of this approach would be the development of a comprehensive epigenome database that links epigenetic features with other molecular components such as transcriptomes, proteomes and metabolomes, in order to better understand how specific traits are regulated. Such integration also helps to identify which genomic regions are under epigenetic control (Sarpan et al., 2022). Associations between epigenetic marks and gene expression across large sample sets can provide information on meaningful relationships, leading to the construction of predictive models that forecast trait expression or developmental outcomes based on epigenetic signatures. This approach could ultimately aid in predicting oil palm performance and guide strategic breeding decisions. Achieving high predictive accuracy relies on high-quality data, large sample sizes and robust bioinformatics pipelines, which are valuable investments toward realising the full potential of epigenetic-based precision breeding.

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