Identification and expression analysis of histone modification gene (HM) family during somatic embryogenesis of oil palm

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Abstract

Background: Oil palm (Elaeis guineensis, Jacq.) is an important vegetable oil-yielding plant. Somatic embryogenesis is a promising method to produce large-scale elite clones to meet the demand for palm oil. The epigenetic mechanisms such as histone modifications have emerged as critical factors during somatic embryogenesis. These histone modifications are associated with the regulation of various genes controlling somatic embryogenesis. To date, none of the information is available on the histone modification gene (HM) family in oil palm.

Results: We reported the identification of 109 HM gene family members including 48 HMTs, 27 HDMs, 13 HATs, and 21 HDACs in the oil palm genome. Gene structural and motif analysis of EgHMs showed varied exon–intron organization and with conserved motifs among them. The identified 109 EgHMs were distributed unevenly across 16 chromosomes and displayed tandem duplication in oil palm genome. Furthermore, relative expression analysis showed the differential expressional pattern of 99 candidate EgHM genes at different stages (non-embryogenic, embryogenic, somatic embryo) of somatic embryogenesis process in oil palm, suggesting the EgHMs play vital roles in somatic embryogenesis. Our study laid a foundation to understand the regulatory roles of several EgHM genes during somatic embryogenesis.

Conclusions: A total of 109 histone modification gene family members were identified in the oil palm genome via genome-wide analysis. The present study provides insightful information regarding HM gene's structure, their distribution, duplication in oil palm genome, and also their evolutionary relationship with other HM gene family members in Arabidopsis and rice. Finally, our study provided an essential role of oil palm HM genes during somatic embryogenesis process.

Keywords: HMs, Somatic embryogenesis, Oil palm, Real-time PCR

Background

Histone modifications gene family (HMs) play a vital role in plant growth and developmental processes by histone modification processes (methylation, demethylation, acetylation, and deacetylation) either by activating or silencing the gene expression. These four different histone modification processes are regulated by four different HM gene family members such as HMTs (histone methyltransferases), HDMs (histone demethylases), HATs (histone acetylases), and HDACs (histone deacetylases) [1, 2]. Each of the HM gene family members also consisted of a varied number of subfamilies with different domain structures. The HMTs contained SDG (set domain group) and PRMT (protein arginine methyltransferases) sub-families. The HDMs contained HDMA (SWIRM and C-terminal domain) and...
**Results**

### Identification of HM gene family in oil palm genome

In this investigation, a total of 109 EgHMs gene family members such as 48 HMTs (histone methyltransferases); 27 of HDMs (histone demethylases); 13 of HATs (histone acetylases), and 21 HDACs (histone deacetylases) were successfully identified in the oil palm genome via genome-wide analysis. All the EgHMs family members are categorized into 11 subfamilies (SDG, PRMT, HDMA, JMJ, HAG, HAM, HAC, HAF, HAD, SRT & HDT) based on their protein domain architecture. The HMT family is included with 39 SDGs and 9 PRMTs; HDM family is contained with 3 HDMs and 24 JMJs; HAT family is included with 4 HAGs, 2 HAMs, 6 HACs, and 1 HAF; HDAC family included with 15 HADs, 3 SRTs, and 3 HDT sub-families. All of the gene IDs of EgHMs family members were provided in Supplementary Table 1. The pI and Molecular weight of the oil palm HMs family members were ranged from 4.57 to 9.95 and 12.3 to 273.3 respectively (Supplementary Table 1). The EgHMs are predominantly localized to the cytoplasmic regions (Supplementary Table 2).

### Gene structure and conserved motif analysis of EgHMs family members

We analyzed the gene structure of all EgHMs gene family members using the Gene Structure Display Server tool 2.0 (http://gsds.chi.pku.edu.cn/). We found the occurrence of varied numbers (2–34) of exons among the HMs gene family members (Fig. 1). The highest number (34) of exons was observed in EgHMT members i.e. EgSDG18 and the least number (2) of exons were observed in EgSDG39 (Fig. 1). We found 10 conserved motifs among the 109 HM gene family of oil palm (Fig. 2).
Fig. 1 Gene structural organization of 109 EgHMs. Coding sequences (CDS) are represented by orange color blocks; 3’ & 5’ UTRs are regions represented by blue color blocks; intron regions are represented by black color blocks in the diagram.
The chromosomal distribution of 109 EgHM gene family members was also examined across the 16 chromosomes of the African oil palm genome. The EgHM gene family members were unevenly distributed across the chromosomes.
on the chromosomes (Fig. 3). Among the identified 109 EgHMs, only 86 were mapped across the 16 chromosomes (Fig. 3). We have not observed the mapping of 26 EgHM members on any of the chromosomes. Chromosomes 1 and 9 had the highest number (9) of EgHM family genes, whereas chromosome 14 had only one EgHM family gene (Fig. 3). Apart from chromosome 14, all of the remaining chromosomes at least contained 3 or more EgHM family genes.

EgHM gene duplication in oil palm genome
To know the expansion of the HM gene family in oil palm genome, we generated a gene duplication event diagram for duplicated blocks using a Circos algorithm. In a total, 37 pairs of EgHMs were identified from 16 chromosomes of oil palm, including 14 pairs of EgSDGs; 4 pairs of EgPRMTs; 6 pairs of EgJMJfs; 2 pairs of EgHAMs; 1 pair of EgHACs; 9 pairs of EgH-DAs, and 1 pair of EgSRTs (Fig. 4). The paired EgHM duplicated genes were all located in different chromosome blocks of oil palm genome (Fig. 4). Moreover, Chromosome 1 and Chromosome 6 had 6 and 5 number of duplicated genes respectively. However, chromosome 14 block had no duplicated HM genes (Fig. 4). These results demonstrated the expansion of EgHM gene family that occurred through these duplicated regions.

Phylogenetic analysis between oil palm, rice, and Arabidopsis HM gene family
To elucidate the evolutionary relationship between oil palm, rice, Arabidopsis, we generated the rooted phylogenetic trees for each HM gene family (HAT, HDAC, HDM, and HMT) (Figs. 5, 6, 7 and 8). The phylogenetic tree for subfamilies of each HM gene family was classified and clustered into diverse trends. The phylogenetic tree of HAT family showed that all the HAG, HAM, HAC, and HAFs of oil palm, rice, and Arabidopsis were not clustered together and they clustered in a species-specific manner and also in mixed type (Fig. 5). For HDAC family, HDTs and SRTs clustered in a species-specific manner, whereas HDAs clustered together (Fig. 6). The phylogenetic tree of HDM family showed a different trend with a species-specific type of clustering (Fig. 7). The phylogenetic tree of HMT family revealed that all the SDGs and PRMTs genes were clustered together (Fig. 8). Altogether, our results indicated that there is a clear evolutionary relationship and diversification between oil palm, rice, and Arabidopsis HM gene family members.

Expression levels of EgHMs in different somatic embryogenic stages (Embryogenic calli, Non-embryogenic calli, and somatic embryos)
Based on the available transcriptome data of oil palm EC, NEC, and SE (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA699335) stages were downloaded from the NCBI.
website and analyzed the expression levels of all identified 109 *EgHM* gene family members. The transcript abundance of *EgHM*s in various stages of oil palm somatic embryogenesis was analyzed by generating the heatmap with the help of FPKM values. As shown in Fig. 9, *EgHM* gene members showed differential expression in different stages of somatic embryogenesis of oil palm. However, most of the genes were down-regulated in all three stages of somatic embryogenesis (Fig. 9). Moreover, six members of *HMTs* (*EgSDG*13, *EgSDG*26, *EgSDG*30, *EgSDG*34, *EgPRMT1* and *EgPRMT4*), two members of *HDMs* (*EgJMJ*15 and *EgJMJ*17); on member of *HATs* (*EgHAM*1); and four members of *HDACs* (*EgHDA*5, *EgHDT1*, *EgHDT2*, *EgHDT3*) are expressed during both EC and NEC stages (Fig. 9). The *HDAC* genes *EgHDT1* and *EgHDT2* were showed expression in all three stages.
of somatic embryogenesis. A total of seven HM members including EgJMJ24, EgHAG4, EgSDG12, EgSDG25, EgSDG28, EgPRMT3 and EgHDA4 were only expressed in SE stage. Though EgHDA15 expressed in all three stages of somatic embryogenesis, it is highly upregulated in SE stage. None of the HM members were highly and specifically expressed either in EC or NEC stage. EgHDT1 is highly expressed in EC and NEC stages of somatic embryogenesis (Fig. 9). Our results elucidated the role of specific EgHMs during the conversion of NEC to SE during oil palm somatic embryogenesis.

Real time-PCR expression analysis of candidate EgHM family genes

A total of 99 EgHM genes were selected and analyzed their relative expression levels during different stages (NEC, EC & SE) of somatic embryogenesis of oil palm through q-RTPCR. Our results revealed the varied expression levels of selected EgHMs during various stages of somatic embryogenesis. The relative expression of HMTs (PRMTs & SDGs) was significantly higher in EC and SE stages than NEC stage (Fig. 10). EgPRMT2 is highly expressed in EC and SE stages, whereas EgPRMT8 has shown the highest expression in SE stages of somatic embryogenesis (Fig. 10). EgPRMT2 & 5 have shown similar expression in all three stages of somatic embryogenesis. EgSDG24, 28, 35 were highly expressed in SE stage and EgSDG18 has shown the highest level of expression in NEC stage. EgSDG19, 20, and 37 have shown significantly higher expression in EC stage (Fig. 10). The relative expression of HDMs (HDMAs & JMJs) was significantly higher in EC and SE stages, whereas EgJMJ20 has shown the highest expression in NEC stage and also in SE stage (Fig. 10). The relative expression of HATs was also significantly higher in both EC and SE stages. Some of them have shown the highest expression in specific stages (either in EC or SE) (Fig. 10). The relative expression of a majority of HDACs is also higher in EC and SE stages than NEC. EgSRT1 and EgHDA15 were highly expressed in SE stage (Fig. 10). Taken together, all these results indicate the potential role of some EgHMs in somatic embryogenesis of oil palm.

Discussion

Somatic embryogenesis is an important tissue culture approach for plant regeneration and it incites various epigenetic changes such as histone modifications (methylation, demethylation, acetylation, and deacetylation [27, 28]. During the somatic embryogenesis process, various histone modifications are potentially regulated [27, 29].
The histone modifications activity leads to the altered gene expression of somatic embryogenesis process [27]. These histone modification changes regulated by various genes during somatic embryos potentially affect the development of somatic embryos. It’s necessary to know the information of various genes that regulate the histone modifications during somatic embryogenesis. To date, none of the studies provided brief information on histone modification genes of oil palm during somatic embryogenesis process. To the best of our knowledge, this is the first report on the identification and characterization of HM genes in oil palm during somatic embryogenesis process. In our study, we identified a total of 109 HM genes including 48 of HMTs (histone methyltransferases); 27 of HDMs (histone demethylases); 13 of HATs (histone acetylases), and 21 of HDACs (histone deacetylases) through genome-wide analysis and analyzed their expression patterns during different stages (NEC, EC,
and SE) of somatic embryogenesis process of oil palm. We reported a comprehensive study including gene structural organization, motif composition, and location on chromosomes, duplication events, and phylogenetic analysis of all of identified 109 EgHMs.

The number (109) of identified HMs in oil palm genome were neither more nor lesser than the identified
Fig. 8 Phylogenetic analysis of EgHMTs with rice and Arabidopsis HMT genes. Domain composition and gene structure of oil palm, rice and Arabidopsis HMT members were also shown in the middle and right sides respectively. Domains were represented by different colours. Exon(s) and intron(s) were shown in orange boxes and black lines respectively. The UTR regions (5' & 3') were represented by blue boxes.
HM gene family members in other crops including *Malus domestica* (198 HMs) [8]; *Lycopersicum esculentum* (125 HMs) [17]; in *Citrus sinensis* (136 HMs) [18]; *Litchi chinensis* (87 HMs) [9], indicating that the variance in occurrence of several HM genes is not related with the genome size of species. The identified EgHM gene family members were divided into four categories and then 11 sub-families, which is similar to the classification of HM genes published previously in other crops [8, 9, 17, 18].

The diversification of the gene family is majorly associated with the intron–exon organization (gain or loss) of genes [30]. Our study also demonstrated that the EgHM genes with similar structural organization were clustered together, whereas others with different structural organizations were grouped distantly. Our findings have coincided with the previous studies genome-wide identification studies of HM gene families in the apple and citrus genome [8, 18]. The typical domains in gene clusters of HM gene families are conserved in most of the crops [8, 17, 18]. Moreover, oil palm HM family genes also contained the same typical domain structure as similar to other plant HM gene families [8, 17, 18].

The phylogenetic analysis of oil palm HM gene family with *Arabidopsis* and rice was analyzed for each family (HMT, HDM, HAT, and HDAC). They were clustered in a species-specific manner which was slightly different from the previous reports on HM gene families in various crops [8, 17]. Our results support the diversification of oil palm HM gene family from other crops, however, future phylogenetic studies are needed to know the evolutionary relationship with other closely related palm plants. The chromosomal distribution of all 109 HM genes was uneven across 16 chromosomes of oil palm and our results are coinciding with the previous reports on HM gene family distribution on apple and citrus genome [8, 17]. Gene duplication plays an essential role in making the complexity of genomes and also in evolutionary lineages [31–33]. Our results also demonstrated the tandem duplication of EgHMs in oil palm genome during the evolutionary process. These findings are consistent with the expansion of HM gene families during the evolution of the apple genome [8].

The epigenetic events trigger the expression of a specific set of genes that are responsible for cellular totipotency [34]. The histone modifications modulate the expression of genes responsible for somatic embryogenesis [29, 34].
In our study, several genes encoding histone methylation, demethylation, histone acetylation, and histone deacetylation were identified through genome-wide study and analyzed their expression analysis during different stages (NEC, EC & SE) of somatic embryogenesis. In this study, several EgHMs displayed their differential expression between different stages of somatic embryogenesis as shown in Fig. 10. Based on qPCR data, EgPRMT2, EgPRMT3, EgPRMT5, EgPRMT6, EgSDG1, EgSDG3, EgSDG15, EgSDG16, EgSDG21, EgSDG23, EgSDG26, EgSDG27, EgSDG33, EgHMA2, EgJM2, EgJM5, EgJM6, EgJM8, EgJM12, EgJM13, EgJM19, EgJM24, EgHAM1, EgHAC3, EgHAC5, EgHAC6, EgHAG1, EgHAG2, EgHAG3, EgHDT1, EgHDT2, EgHDT3, EgHDA11 & EgHDA14 showed their expression levels during both embryogenic calli and somatic embryo stages, revealed their prominent role in somatic embryogenesis. These identified EgHMs may provide insightful information to elucidate the molecular mechanisms associated with the somatic embryogenesis of oil palm.

**Material and methods**

**EgHMs identification in oil palm genome**

The pfam database was used to identify the EgHM gene family members using the Hidden Markov Model profiles of published IDs of each type (HMT, HDM, HAT & HDAC) of HM genes [17, 18]. The pfam IDs belongs each type of HM genes were used as a query to search for HM gene members in oil palm genome database [35] using HMMER3.0 tool. Further, we also retrieved the unavailable sequences of EgHMs using the known HM gene sequences of Arabidopsis (http://www.arabidopsis.org/) and Oryza sativa (http://rice.plantbiology.msu.edu/) through blast search in oil palm genome database (http://palmxplore.mpob.gov.my/palmxplore/).

We also predicted the coding sequence length of each HM gene family member using Blastn search against oil palm genome database. The identified putative oil palm HMs genes, such as HMTs (SDGs and PRMTs), HDMs (HDMAs and JMJs), HATs (HAGs, HAMs, HACs, and HAFs), and HDACs (HDAs, SRTs, and HDTs) were identified finally based on the highly conserved domains. Additionally, the M.wt, pl values of oil palm HM gene members were also determined with the help of ExPASy (https://web.expasy.org/compute_pi/). The online tool “CELLO” (http://cello.life.nctu.edu.tw/) was further used to predict the subcellular localization of all oil palm HM gene family members.

**Gene structure, Conserved motifs analysis of EgHMs**

The 109 EgHM genes structural analysis (intron–exon organization) was analyzed by the Gene Structure Display Server (http://gsds.cbi.pku.edu.cn/). The conserved motifs analysis of all identified EgHM proteins were...
EgHM gene duplications, phylogenetic relationships, and their distribution on chromosomes

We explored the duplications of 109 EgHM gene family members in oil palm genome using the MCScanX tool with default parameters [36, 37]. Further, we mapped the location of all 109 EgHMs across 16 chromosomes of oil palm from the available genome database of oil palm. We also generated the phylogenetic tree for each type (HMT, HDM, HAT & HDAC) of oil palm HMs with HM genes Arabidopsis and Oryza sativa using MEGA 7.0 [38] by Maximum Likelihood method, with a bootstrap value of 1000 replications.

Plant materials

The Oil palm (Elaeis guineensis; pisifera, thin-shelled African oil palm) plants were grown in the coconut field of Coconut Research Institute, Chinese Academy of Tropical Agricultural Sciences, Wenchang, China. All the plants were grown under institutional regulatory issues. All the plant materials are collected by the corresponding author of this research work. The immature zygotic embryos were selected as explants for oil palm tissue culture and followed the method as described by Silva et al. (2012) [39] with few modifications. The calli (non-embryogenic or embryogenic) was induced from immature zygotic embryos on callus induction media (CIM). The explants were cultured on CIM: (1/2 MS medium supplemented with 30 mg/l picloram, 100 mg/l casein hydrolysate, 500 mg/l L-glutamine, 200 mg/l asparagine, 200 mg/l arginine, 2 mg/l glycine, 100 mg/l adenine sulfate, 100 mg/l citric acid, 100 mg/l ascorbic acid, 30,000 mg/l sucrose, and 3,000 mg/l Phytagel). The EC and NEC were induced after 3 months of repeated subcultures. The Somatic embryogenesis (SE) was induced by transferring EC to somatic embryo induction medium (SIM: CIM without picloram). The somatic embryo was induced in SIM after four months of culture. The EC, NEC, and SEs (torpedo) were collected at their stages and then quickly frozen in liquid nitrogen followed by the storage of -70 °C for subsequent RNA extraction.

EgHMs expression analysis from available transcriptome data

We downloaded the transcriptome data of oil palm somatic embryogenesis stages (EC, NEC, and SE; Accession number: PRJNA699335) from the Sequence Read Archive (SRA) database of NCBI. The heatmap (http://www.omicsshare.com/tools) was generated to calculate EgHMs expression levels in three different stages of somatic embryogenesis using RPKM values (RPKM= \( \frac{10^C_C}{NL/10^p} \) [32].

EgHMs gene expression analysis by quantitative real-time PCR

Total RNA was extracted from the different stages of calli (NEC, EC, and SE) during somatic embryogenesis using RNAprep pure Plant Kit (Tiangen, Beijing, China) by following the manufacturer’s instructions. The first-strand cDNA was synthesized using EasyScript® First-Strand cDNA Synthesis SuperMix (TransGen, Beijing, China) kit. The relative expression analysis of the 99 EgHMs genes from the 109 identified HM genes was carried out by using the real-time qPCR method. The real-time qPCR was performed with SYBR® Select Master Mix (Thermo Fisher Scientific, Waltham, USA). The ABI QuantStudio™ 6 Flex quantitative real-time PCR instrument (Thermo Fisher, Waltham, USA) was used to analyze the data. The relative expression levels of 99 HM genes at different stages of somatic embryogenesis were calculated via 2\(^{-\Delta\Delta Ct}\) method. The qPCR primers for analyzing the expression of 99 HM genes were designed using QuantPrime qPCR primer designing tool (https://quantprime.mpg.de/) and listed in Supplementary Table 3. All the qPCR reactions were performed with three biological and three technical replications. The oil palm actin gene (EgActin1) was used as an internal control to check the expression of EgHMs. The statistical significance at \( p < 0.05 \) was determined by using One-Way ANOVA.

Conclusions

In conclusion, this is the first report on genome-wide analysis of histone modification genes (HMT, HDM, HAT, and HDAC) in oil palm. From this study, a total of 109 EgHMs were identified and analyzed candidate genes expression patterns during somatic embryogenesis of oil palm. Moreover, comprehensive information regarding their gene structure, motif, composition, chromosomal distribution, duplication events, evolutionary relationship with rice, and Arabidopsis was also reported. Furthermore, differential expression of various EgHMs at different stages of somatic embryogenesis was also elucidated through real-time PCR analysis indicating their potential involvement during the somatic embryogenesis of oil palm.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12864-021-08245-2.

Additional file 1: Table 1. List of EgHMs in oil palm genome.
Additional file 2: Table 2. Subcellular localization prediction of 109
EgHM gene family.
Additional file 3: Table 3. List of qRT-PCR primer pairs used for real-time
expression of EgHM gene family members in oil palm during somatic
embryogenesis.

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Authors’ contributions
LZ assessed the conceptualization of research. LZ and RY conceived and
designed the methodology. LZ, RY, LJ, YY, HC, and ZZ analyzed the data. RY
prepared and wrote original manuscript draft. LZ supervised the research. All
authors have read and approved.

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Availability of data and materials
The transcriptome data used in this study are available in the NCBI Sequence
Read Archive (SRA) with BioProject accession number PRJNA699335. All data
sets analyzed during this research are provided as Supplementary files and
also included in the article. The data sets generated during this study are also
available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
All methods in this research were carried out in accordance with relevant
guidelines and regulations of Coconut Research Institute, Wenchang, China.

Consent for publication
Not applicable

Competing interests
The authors declare that they have no competing interest.

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