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Screening and Analysis of Plant Resistant Genes in Secondary Growth Stems of Chlorophyll Deficient Mutants from *Artocarpus heterophyllus*

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Abstract In order to study the changes of plant resistant genes (PRGs) in the secondary growth stems of chlorophyll deficient mutant (CDM) of *A. heterophyllus*, 9 630 PRGs were selected from the transcriptome data. After removing the low abundance (FPKM≤0.5), the differentially expressed genes (DEGs) were screened, and 2 513 DEGs were subjected to weighted gene coexpression network analysis (WGCNA). There are 183 DEGs in the module with high type correlation. The module genes were analyzed for GO function annotation, classification, transcription factors (TFs) and receptor-like kinases (RLKs). The results showed that module genes were mainly annotated in functional groups such as binding, catalytic activity, and metabolic process. TFs analysis showed that there are 7 families, 14 transcription factors. RLKs analysis found that 11 of the 12 DEGs in the RLK-Pelle_DLSV subfamily were up-regulated in CDM, indicating that the subfamily plays an important role in resisting stress of secondary growth stems of *A. heterophyllus* CDM. This study used transcriptome sequencing data to analyze the changes of PRGs in the secondary growth stems of *A. heterophyllus* CDM, providing data for the study of photosynthesis in response to stress of woody plant stems.

Keywords *Artocarpus heterophyllus*; Chlorophyll deficient mutant; Secondary growth stem; Plant resistant genes

Secondary growth of woody plant stems is related to the formation and quality of wood, so it has important economic and scientific research value to study it (Wang and Lu, 2009). In recent years, genome sequencing of woody plants such as *Populus trichocarpa*, *Morus notabilis* and *Eucalyptus grandis* (Dharmawardhana et al., 2010; Novaes et al., 2008) has been completed. Sorce et al. (2013), Rohde and Bhalerao (2007) found that abscisic acid (ABA) changes periodically during the activity of the vascular cambium of *Populus trichocarpa*, and ABA may be involved in regulating the dormancy of the vascular cambium. Metabolic efficacious proteins and resistance proteins produced at the stem base of *Maritime pine* may act as precursors to participate in the secondary growth process of the stem, thus improving the stress resistance of the plant (Paiva et al., 2008).

Photosynthesis is an important indicator of plant biosynthesis, and chlorophyll is the basis of this process. Chlorophyll content in many plants is related to various disease resistance (Ou, 2007, Anhui Agricultural Science Bulletin, 13(6): 134-135). Gu et al. (2004) found that cucumber resistance to downy mildew was positively correlated with chlorophyll content. Zhang et al. (2005) found in the study of *Beta vulgaris* that the chlorophyll content of susceptible species was lower than that of resistant species. However, there is no report on the correlation between chlorophyll content and the resistance to diseases.

Plant defense response is mainly generated through the expression of plant resistant gene (PRGs) (Liu et al., 2008, Anhui Agricultural Sciences, 36(13): 5342-5343, 5417). With the rapid development of molecular biology, the action mechanism and corresponding functions of many PRGs have been confirmed (Sun et al., 2008, Hubei

Agricultural Sciences, 47(5): 598-601). Johal and Briggs (1992) isolated the first PRG: *Hm1* from maize (*Zea mays*) and demonstrated that the HC toxin reductase regulating the expression of this gene could degrade the toxin in the plant and thus make maize resistant. Subsequently, studies on *Arabidopsis thaliana*, *Nicotiana tabacum*, and *Linum usitatissimum* (Weng et al., 2005; Gong, 2014; Song, 2009) found and cloned related PRGs, providing gene resources for subsequent breeding of resistant plants. However, compared with herbaceous plants, these studies were less carried out in woody plants.

Artocarpus heterophyllus is an excellent tropical cash crop, favored by many scholars and has been studied in many aspects (Ge et al., 2015). Hu et al. (2016) used RNA-seq to analyze the differentially expressed characteristics of genes related to sugar metabolism in the perianth of *Artocarpus heterophyllus*. Fu et al. (2018, Journal of Tropical Crops, 39(6): 1081-1086) studied the characters of chlorophyll deficient mutant (CDM) of *Artocarpus heterophyllus* and found that its overall growth rate was worse than that of normal plants, which may be related to the low content of chlorophyll *in vivo* and the inability to carry out normal photosynthesis. However, what types of PRGs are affected by loss of chlorophyll synthesis is still unknown. In this study, transcriptome sequencing data were used to analyze the changes of PRGs in the secondary growth stems of *Artocarpus heterophyllus* CDM, providing data for the study of photosynthesis in response to stress of woody plant stems.

1 Results and Analysis

1.1 PRGs screening

A total of 9 630 PRGs were screened from the annotated transcriptome data of the secondary growth stems of *Artocarpus heterophyllus*. In addition, the number of PRGs in different expression intervals of control check (CK) and CDM was further counted, 4 267 and 4 189 genes with FPKM less than or equal to 0.5, 1 261 and 1 586 genes with FPKM between 0.5 and 1, respectively. 1 292 and 1 273 were 1~2, 2 810 and 2 582 were larger than 2 (Table 1).

Table 1 The number of PRGs with different expression ranges in CK and CDM

Fragments Per Kilobase Million	Control check	Experimental group
≤0.5	4 267	4 189
0.5~1	1 261	1 586
1~2	1 292	1 273
>2	2 810	2 582

Note: Control check: Normal *A. heterophyllus* secondary growth stems; Experimental group: secondary growth stems of chlorophyll deficient mutants from *A. heterophyllus*

After filtering low abundance (FPKM≤0.5) genes, 2 513 differentially expressed genes (DEGs) were screened. Compared with CK, 1 179 genes were up-regulated and 1 334 genes were down-regulated in CDM (Figure 1A). The 2 513 selected DEGs were divided into four parts: I (Unique gene in CK), II (Common genes of CK and CDM are down-regulated in CDM), III (Common genes of CK and CDM are up-regulated in CDM) and IV (Unique gene in CDM). There were 96 genes in I, 1 238 genes in II, 1 086 genes in III and 93 genes in IV (Figure 1B). In addition, the median gene length in IV was smaller than that in the other three parts (Figure 1C).

1.2 Weighted gene co-expression network analysis

weighted gene coexpression network analysis (WGCNA) was performed on 2 513 DEGs to construct the gene coexpression network. The modules were divided by dynamic shearing method, and 11 modules were obtained after merging. And calculate the eigengenes expression of the module (Figure 2A). After association analysis of the modules with CK and CDM phenotypes in the samples, the correlation between Magenta and Purple modules and phenotypes was 0.99 and -0.95, respectively, and the number of genes in the two modules was 105 and 78, respectively (Figure 2B; Figure 2C; Figure 2D).

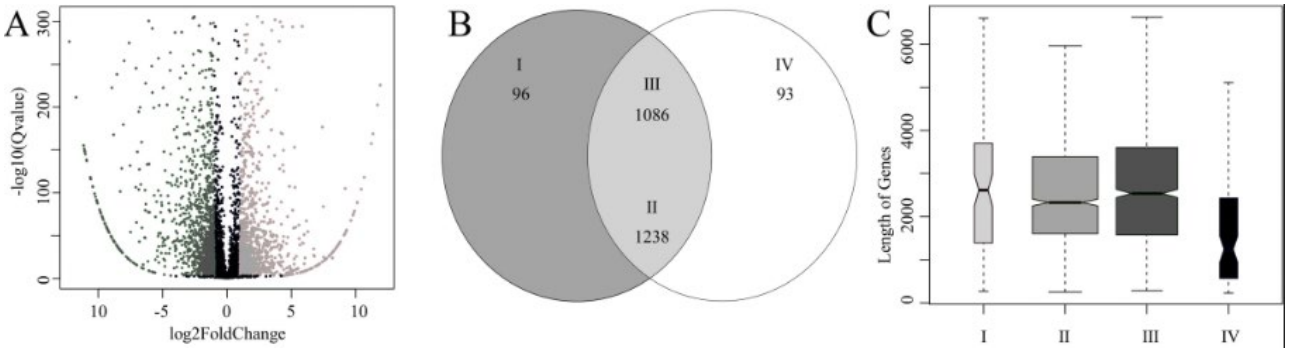

Figure 1 Screening and analysis of DEGs

Note: A: Screening and distribution of DEGs; B: The number of DEGs in each parts; C: Length distribution of DEGs in each parts;I: Unique gene in CK;II: Common genes of CK and CDM are down-regulated in CDM; III: Common genes of CK and CDM are up-regulated in CDM; IV: Unique gene in CDM

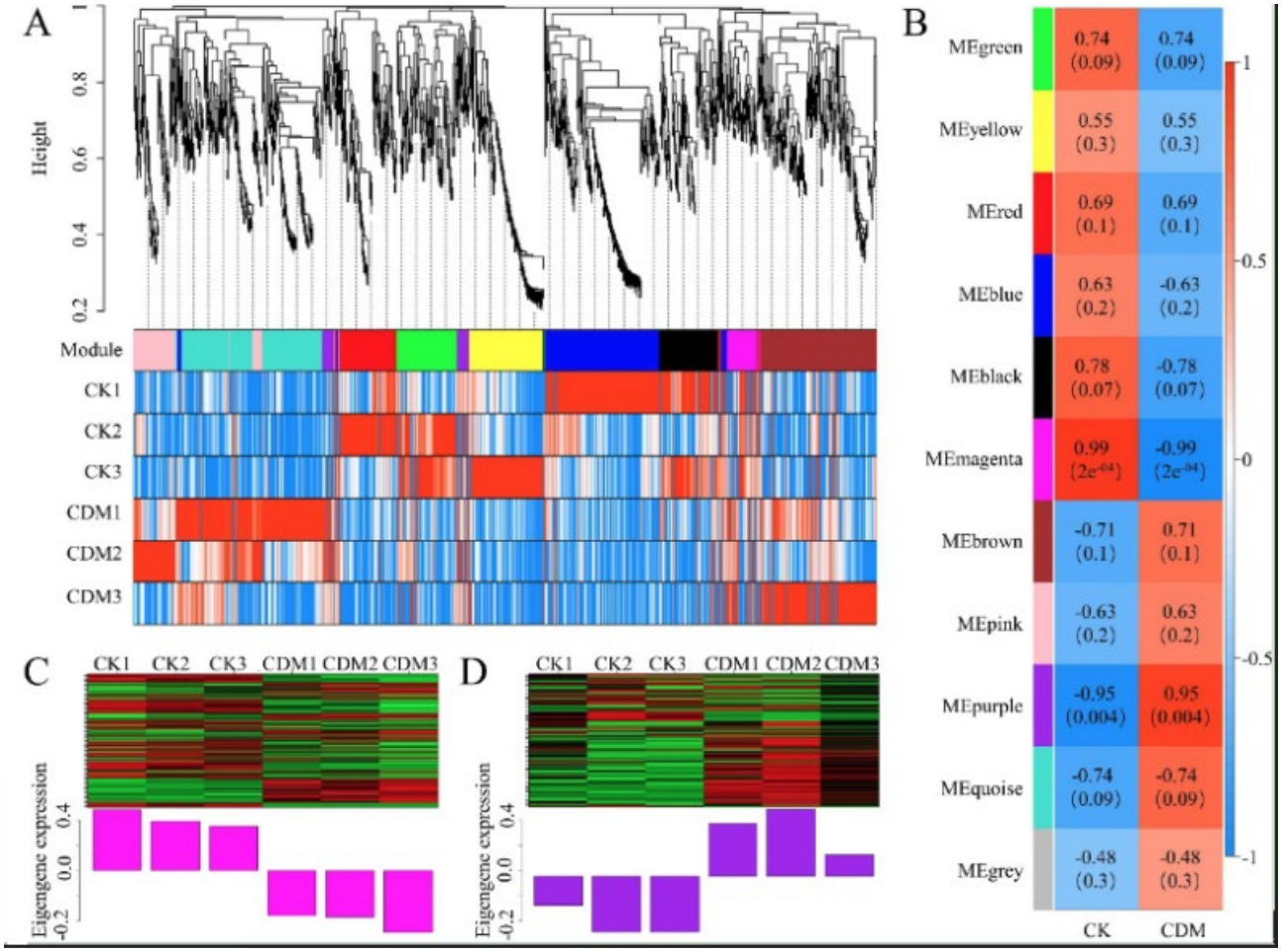

Figure 2 Weighted gene coexpression network analysis of DEGs

Note: A: Gene cluster tree and its module; B: Correlation analysis between module and phenotype; C: Heat map and feature vector of DEGs in magenta module; D: Heat map and feature vector of DEGs in purple module

1.3 GO annotation

Merge 183 DEGs from Magenta and Purple modules for GO annotation and classification. The results showed that 149 DEGs were annotated. Among them, DEGs annotated molecular function accounted for the highest proportion (135, 78.03%), followed by biological process (124, 71.68%). Cellular component was the least (105, 60.69%). In addition, GO enrichment analysis is conducted on DEGs, and significant enrichment nodes are displayed in the GO system in a hierarchical relationship. The lower the hierarchy is, the more detailed the function represented by nodes,

and the Nodescore value of each node is represented by the color depth of the box. The darker the color is, the higher the Nodescore value is, and vice versa. In cellular component, a total of 105 DEGs were annotated. Compared with CK, 60 genes in CDM were up-regulated and 45 genes were down-regulated, and the biological functions of DEGs were mainly reflected in cell and membrane pathways. In addition, molecular function was the category with the largest number of annotated genes, and DEGs binding pathway was the largest (102, 75.56%). In the biological process, a total of 124 DEGs were annotated. Compared with CK, 70 genes in CDM were up-regulated and 54 genes were down-regulated. Metabolic process and cellular process accounted for 69.35% (86) and 75.81% (94), respectively (Figure 3).

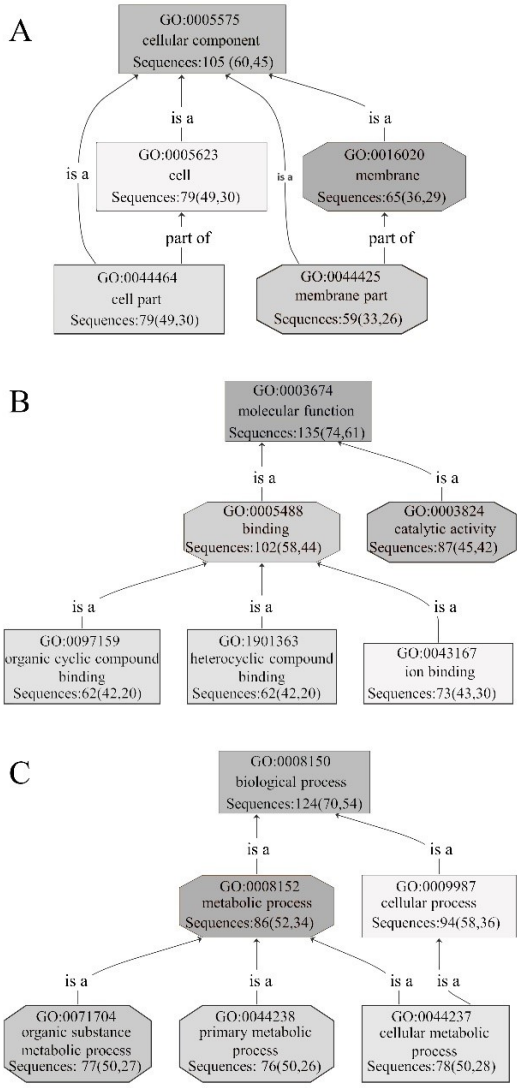

Figure 3 GO annotation and classification of magenta and purple module genes

Note: A: Cellular component; B: Molecular function; C: Biological process; The number after GO in the box is the unique comment number for each node; The number in parentheses in the box represents the number of annotated genes, the number of genes up-regulated in the CDM on the left, and the number of genes down-regulated on the right

1.4 Analysis of transcription factors and receptor-like protein kinases

There were a total of 14 transcription factors (TFs) in 183 DEGs of the two modules, among which 12 were up-regulated and 2 down-regulated in CDM (Figure 4A). These DEGs were distributed in 7 TFs families. The 5 CDM families with all up-regulated DEGs were B3, BES1, C3H, CAMTA and NAC, with 2, 2, 1, 1 and 3 DEGs, respectively. However, DEGs of AP2/ERF-ERF and C2C2-Gata families were not all up-regulated in CDM. Two of the three DEGs of the AP2/ERF-ERF family were up-regulated and one down-regulated in CDM. In the C2C2-GATA family, one DEGs was up-regulated and one down-regulated in CDM.

In addition, 21 of 183 DEGs are receptor-like kinases (RLKs), which can be divided into 8 subfamilies (Figure 4B). RLK-Pelle_DLSV subfamily contained the most DEGs. 11 of its 12 DEGs were up-regulated and one down-regulated in CDM. However, the number of DEGs in LRR-RLK-III, LRR-RLK-Xb-1 and RLCK-IXb subfamilies was relatively small.

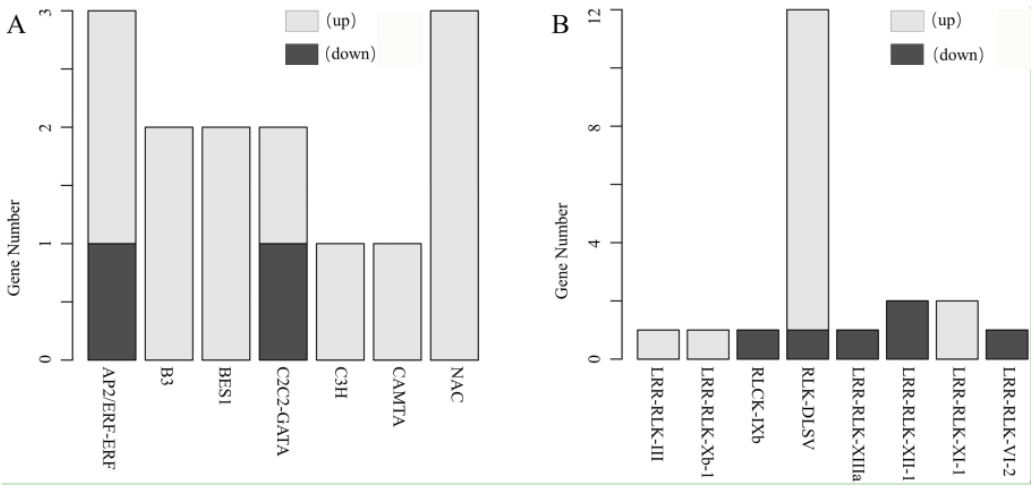

Figure 4 TFs and RLKs family analysis of magenta and purple module genes

Note: A: Transcription factor family and number of module genes; B: Receptor-like protein kinase family and number of module genes

1.5 Analysis of RLK-Pelle_DLSV subfamily

In order to further study the expression patterns of 12 DEGs in RLK-Pelle_DLSV subfamily, cluster analysis was conducted according to the expression quantity. The results showed that only CL19237. Contig33 was down-regulated in CDM, and the other 11 DEGs were up-regulated (Figure 5A). In addition, phylogenetic trees of 12 DEGs in RLK-Pelle_DLSV subfamily were constructed. The Bootstrap values of CL18233.Contig17 and Unigene20220 branches were lower than 75, while the Bootstrap values of the rest branches were higher than 75 (Figure 5B). In addition, CL326.Contig13 and CL326.Contig24 were highly homologous, CL1710.Contig3 and CL1710. Contig6 were highly homologous, while CL19237.Contig33 and Unigene32980 clustered in the same branch, but the relationship is longer.

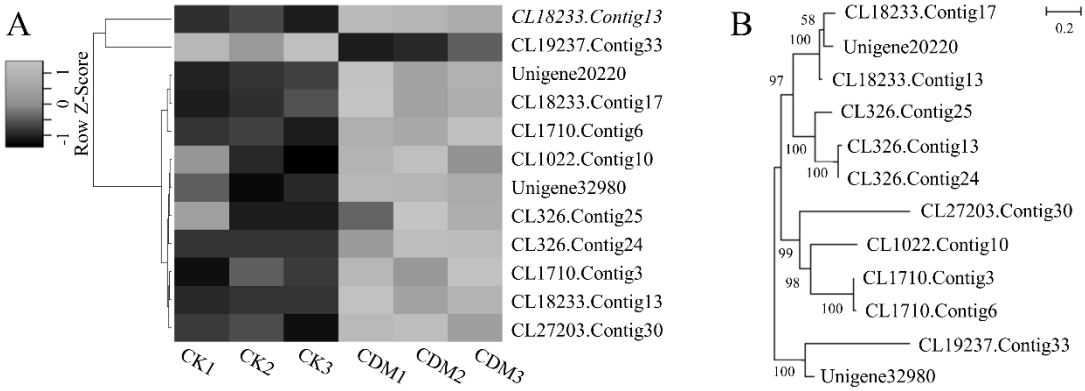

Figure 5 Analysis of RLK-Pelle_DLSV subfamily

Note: A: Expression pattern of RLK-Pelle_DLSV subfamily members; B: RLK-Pelle_DLSV subfamily evolutionary tree construction

2 Discussion

Currently, plant PRGs are widely studied in rice (*Oryza sativa*), wheat (*Triticum aestivum*) and tomato (*Lycopersicon esculentum*) (Zhang et al., 2008; Luo et al., 2002; Song et al., 2012). There are no related reports about PRGs of CDM secondary growth stem of *Artocarpus heterophyllus*. In this study, transcriptome sequencing data were used to explore the changes of PRGs in the secondary growth stems of *A. heterophyllus* CDM, providing basic data for the study of resistance breeding of woody plants.

Carbon is an important component of organic matter, and secondary xylem is one of the important storage pools of carbon (Li et al., 2017). Green plants convert light energy into chemical energy through photosynthesis and store it in organic matter to maintain normal growth and development of plants and energy supply (Fromme et al., 2003). The CDM of *Artocarpus heterophyllus* is unable to carry out photosynthesis and can only rely on endosperm to provide nutrients for it (Zhu et al., 2012). Studies have shown that in order to adapt to stress conditions, plants accumulate a large amount of organic matter in their cells to survive the adverse environment (Yu and Xu, 2003). In this study, 27 organic substance metabolic process down-regulated PRGs pathways were identified by GO annotation and classification. These results may indicate that the secondary growth stem of *Artocarpus heterophyllus* CDM is trying to reduce the degree of stress injury by slowing down the metabolic rate of organic substances.

Calcium and Titanium plasma play an important role in plant growth and development and stress conditions (Zhang et al., 2007; Wei et al., 2019). The great difference in intracellular calcium ion concentration in plants under stress generates calcium signals, which then trigger a series of defense mechanisms to guide calcium ions to bind to corresponding calcium proteins and resist environmental damage (Du and Duan, 2010). In this study, 73 DEGs annotations were found in the ion binding pathway by GO classification, and compared with CK, 40 genes in CDM were up-regulated and 33 genes were down-regulated. It is speculated that there are still ions in the cells of the secondary growth stem of *Artocarpus heterophyllus* CDM that bind to the corresponding target protein to resist stress. The specific regulation process of these ions in the secondary growth stem of *Artocarpus heterophyllus* is a question that can be discussed in the follow-up study.

RLKs play a key role in the regulation network of plant resistance to adversity (Cao et al., 2014). In this study, the RLKs of PRGs secondary growth stem of *Artocarpus heterophyllus* CDM were analyzed, and it was found that the number of RLK-PELle_DLSV subfamily members was much higher than other members, and 11 out of 12 members were up-regulated in CDM. Liu et al. (2015) found that the RLK-PELLE_DLSV subfamily showed considerable differential expansion in soybean, and it may represent a specific adaptive ability to detect and respond to developmental signals and environmental stimuli by changing cell metabolism, gene expression or growth and development. Therefore, it is speculated that the RLK-PELle_DLSV subfamily may play an important role in the response of secondary growth stems of *Artocarpus heterophyllus* CDM to stress. Therefore, understanding the specific mechanism of RLKs in the stress resistance process of the secondary growth stems of *Artocarpus heterophyllus* may provide ideas for the study of the stress resistance of woody plants.

3 Materials and Methods

3.1 Experimental material

In this study, the secondary growth stems of *Artocarpus heterophyllus* CDM were cultured for 40 days in Danzhou Campus of Hainan University, Danzhou City, Hainan Province. Normal secondary growth stems were used as the control and stored in liquid nitrogen for quick freezing. The samples were sent to BGI for RNA extraction, cDNA library construction, quality control and sequencing.

The transcriptome data of secondary growth stems of *Artocarpus heterophyllus* used in this experiment were from the results of our research group (https://www.ncbi.nlm.nih.gov/sra/SRX8296522; https://www.ncbi.nlm.nih.gov/sra/SRX8296523; https://www.ncbi.nlm.nih.gov/sra/SRX8296524; https://www.ncbi.nlm.nih.gov/sra/SRX8296525; https://www.ncbi.nlm.nih.gov/sra/SRX8296526; https://www.ncbi.nlm.nih.gov/sra/SRX8296527).

3.2 DEGs screening and analysis

The genes with low abundance (FPKM≤0.5) were removed from transcriptome annotation data of secondary growth stems of *Artocarpus heterophyllus*, and all DEGs were screened under the conditions of P-value<0.001 and $\log_2$|Fold change|≥1.

3.3 WGCNA analysis

The WGCNA program package in R language was used to cluster the DEGs with similar expression patterns and analyze the significant association between modules and phenotypes (Langfelder and Horvath, 2008). Softpowr was set to 30 and MergeCutHeight was set to 0.20. Correlation analysis was conducted between the obtained modules and phenotypes, and modules with greater correlation with phenotypes were selected for subsequent analysis.

3.4 GO analysis

The amino acid sequences of Magenta and Purple were saved in FASTA format using Blast2GO (v5.1) software (https://www.balst2go.com). blastp (E-value≤$1.0E^{-3}$) was compared with Nr database in NCBI, and the process of mapping and annotation was completed to predict the biological functions involved in module genes and classify them (Altschul et al., 1990; Conesa et al., 2005).

3.5 TFs and RLKs analysis

The amino acid sequences of Magenta and Purple were identified by TFs and RLKs using itak website (itak.feilab.net) (Zheng et al., 2016). PF00847 from Pfam database was used for identification of TFs, while PF07714 and PF00069 domains were used for RLKs, and Melissa was used for its classification (Lehti-Shiu and Shiu, 2012). The TFs and RLKs that completed classification were analyzed by histogram to analyze the up-regulation number of each family member.

3.6 Phylogenetic tree construction of RLK-Pelle DLSV subfamily

Based on the multiple alignment data of amino acid sequences, MEGA5.1 software was used to construct phylogenetic tree (Jiang and Chen, 2010). Neighbor-joining (NJ) was adopted to run the corresponding parameters (Wang et al., 2011): bootstrap=1000, with Poisson model, and the gap was set as Pairwise deletion.

Authors' contributions

ZLT and YXD were the experimental designers and executors of this study. ZLT and CZP completed data analysis and wrote the first draft of the paper. XLQ, CZP, DJN, WFH and LJJ participated in experimental design and result analysis. CZP is the architect and principal of the project, directing experimental design, data analysis, paper writing and revision. All the authors read and approved to the final manuscript.

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