



Identification and Expression Analysis of Transcription Factors in *Carallia Brachiata* Genome

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Abstract

Transcription factors are important regulatory factors in gene expression. To explore the role of transcription factors in the adaptation of *Carallia brachiata* to its environment, this study identified the transcription factor family across the genome and analyzed their expression in eight tissues (roots, stems, leaves, flowers, ovules, fruits, seeds, embryos). The results showed that a total of 2322 transcription factor from 91 families were identified. They were significantly enriched in 12 pathways including plant signal transduction, circadian rhythm, MAPK signaling pathway-plant and plant-pathogen interaction etc. Most genes were involved in environmental information processing and environmental adaptation through signal transduction. The results of expression analysis showed 204 genes were tissue-specific. Genes that were responsible for the signal transduction of cytokinin, auxin, gibberellin, jasmonic acid, salicylic acid were mainly expressed in root, stem, leaf, flower, ovule and fruit while the genes that involve in ethylene and abscisic acid signal transduction were only expressed in seed and embryo. This study suggested that the transcription factors regulated different tissues of *C. brachiata* by participating in different hormone response pathways, so as to regulate plant growth and development.

Keywords *Carallia brachiata* · Transcription factors · Hormone signal transduction · Environmental adaptation

Introduction

The growth and differentiation of organisms are constantly adapted to multiple environmental factors. Environmental factors can vary from moderate to dramatic. They may or may not be biological. Among the many abiotic factors are nutrition, light, oxygen, water, temperature, gravity, wind, etc. Biological agents are other organisms that have symbiotic, pathogenic, or herbivorous interactions with plants. All of these environmental factors are recognized independently and specifically by plants (Liu et al. 2023).

Perception and global response are linked through signal transduction pathways at the cellular, systemic, and inter-biological levels (Kucera et al. 2005; Mostofa et al. 2022). In order to ensure proper adaptation to the environment, the

signals generated after the perception of multiple environmental factors need to be integrated and evaluated according to their importance. This crosstalk between different signal pathways in a network seems to be the basis for assessing the importance of incoming signals. Understanding these complex processes leads to a better understanding of the molecular mechanisms of adaptation. Adjusting the different signal elements can improve the plant's adaptation to its environment.

The regulation of gene transcription level is one of the key factors in plant adaptation to environmental and regional stress, and transcription factors play an important role in this regulation process (Jan et al. 2019; Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). Transcription factors can bind to a specific gene sequence upstream, the 5' end of the gene, thereby controlling how a gene expresses its genetic information at a specific time and space (Jan et al. 2019; Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). Transcription factors generally consist of one or more DNA-binding domains and a transcription regulatory region (Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). It can activate or inhibit the transcription efficiency of multiple

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target genes (Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). Transcription factors are important regulatory factors that activate or inhibit the expression of coding or non-coding genes (Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). It plays multiple functions in plant growth and stress signaling pathways. It is of great biological significance to study the role of transcription factors in plant growth and development. Studies have shown that about 7% of the genes in the genome of vascular plants encode transcription factors (Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). At present, more than 50 transcription factor families of different plant species have been screened and identified through bioinformatics (Li et al. 2016, 2022; Shahzad et al. 2020; Shen 2022; Yin et al. 2021). However, no relevant studies have been reported in Rhizophoraceae plants.

Carallia brachiata is an evergreen tree in the *Carallia* genus of the Rhizophoraceae and distributes in tropical regions of the eastern hemisphere, including China, India, Sri Lanka, Burma, Thailand, Vietnam, Malaysia and northern Australia (Patil and Chavan 2015). *C. brachiata* has the characteristics of barren, drought-resistant, pollution-resistant, etc. (Junejo et al. 2020; Nalinratana et al. 2023; Xiang et al. 2016; Zhou et al. 2015; Qiao et al. 2020). Compared with other genera of Rhizophoraceae growing in marine water, *C. brachiata* grows in inland freshwater environment with salinity close to zero, and even faces drought stress (Junejo et al. 2020; Nalinratana et al. 2023; Xiang et al. 2016; Zhou et al. 2015; Qiao et al. 2020). Studies have shown that *C. brachiata* has strong adaptability to drought conditions, mild drought can promote its growth, and the degree of drought will affect the proportion of its input to above-ground and underground parts (Junejo et al. 2020; Nalinratana et al. 2023; Xiang et al. 2016; Zhou et al. 2015; Qiao et al. 2020). *C. brachiata* could grow well no matter in poor soil or seriously polluted atmospheric environment, so it is also an excellent tree species for transforming forestry, and has the laudatory name of “green diamond” (Junejo et al. 2020; Nalinratana et al. 2023; Xiang et al. 2016; Zhou et al. 2015; Qiao et al. 2020).

In view of the importance of transcription factors in plant growth and development, physiological and biochemical metabolism, as well as their potential application value in improving plant adaptation, this study conducted genome-wide identification and expression analysis of the transcription factor family of *C. brachiata*, in order to provide data support for improving the adaptation of *C. brachiata* and better serving garden optimization.

Materials and Methods

Description of Materials used in this Study

The materials used for genome sequencing were collected in June of 2016 from healthy trees in Gaoqiao Town, Zhanjiang City, Guangdong Province, China where is typical inland area. Eight tissues for transcriptome sequencing were collected from three trees with similar age from June 2016 to May 2017 from the same location. Both the genome and transcriptome data were generated in the article of Qiao et al. 2020.

Data Preparation

Genome and transcriptome data (roots, stems, leaves, flowers, ovules, fruits, seeds, embryos) of *C. brachiata* were downloaded from NCBI official website. The accession number was PRJNA632974 (*C. brachiata*) (Qiao et al. 2020).

Data Analysis

Transcription Factors Identification on the Genome

XMM analysis (Finn et al. 2011) was performed using PFAM search tool (Punta et al. 2012) to obtain protein domain information of all genes. All transcription factors were identified and predicted according to DNA binding Domain (DBD), the structural features contained in transcription factors. Finally, all PFAM search domains conforming to the above criteria were obtained according to the information on PlantTFDB and PlnTFDB websites (<http://plntfdb.bio.uni-potsdam.de/v3.0/>).

Quality Control of Transcriptome Data

Save the original data in FASTQ format, and use FastQC (version 0.11.2) (<http://www.bioinformatics.babraham.ac.uk/projects/fastqc>) for data quality control. Remove the connector with TrimGalore (version 0.4.0) (https://www.bioinformatics.babraham.ac.uk/projects/trim_galore/).

Reference Sequence Alignment Analysis

The quality-controlled reads were compared to the reference genome using the default parameter settings in HISAT2 software (Kim et al. 2015).

Analysis of Gene Expression Level

FPKM (expected number of Fragments Per Kilobase of transcript sequence per Millions base pairs sequenced) was used to represent gene expression. HTSeq software (Anders et al. 2015) was used to calculate the gene expression level of each sample, and whether FPKM was greater than 1 was used to characterize the gene expression (Brooks et al. 2011). The final expression of the same gene is the average of the repeats.

Differential Gene Expression Analysis

The number of reads was standardized using edgeR packages (Robinson et al. 2010). The DESeq R (1.20.0) (Wang et al. 2010) package was then used for differential gene analysis between different tissues, and the *P*-values were corrected using Benjamini & Hochberg's method (Benjamini and Hochberg 2000). $P < 0.05$ and absolute value of $\log_2(\text{reads multiple}) \geq 1$ were the threshold for significant difference. The expression of a gene in a certain tissue was greater than 80% of the sum of the expression of the gene in all tissues, which was considered as tissue-specific gene.

GO (Gene Ontology) Enrichment Analysis

GO enrichment is the most direct visual method to help us understand the gene function. This study used the free analysis platform (<http://www.omicshare.com/tools>) for enrichment of different expression genes. Significant enrichment is defined as a GO term with a probability $P \leq 0.05$.

KEGG (Kyoto Encyclopedia of Genes and Genomes) Enrichment Analysis

Pathway enrichment analysis is the most direct and simplest way to accurately understand which metabolic pathways and signal transduction pathways genes are involved in, and it is also one of the important methods to target key genes. This analysis was done on the free platform (<http://www.omicshare.com/tools>). If $P \leq 0.05$, it indicates that genes are significantly enriched in this pathway.

RT-qPCR Validation

To verify the expression level of key genes of *C. brachiata*, we used RT-qPCR method. For reverse transcription, the first-strand cDNA was synthesized using a 5X All-In-One RT MasterMix (ABM, Canada). The relative quantification was done by ChamQTM Universal SYBR® qPCR Master Mix (Vazyme, China) from three biological replications, normalized to the reference actin gene from two species

respectively and calculated by the $2^{-\Delta\Delta Ct}$ method. Primer sequences are shown in Table S1.

Results

Transcription Factors Identification

2322 transcription factors were identified on *C. brachiata* genome. According to the homology of the DNA binding domain, all transcription factors can be divided into 91 families. Among them, the five families with the most members are *MYB*, *C2H2*, *bHLH*, *AP2/ERF-ERF* and *NAC*. The number of them were 146, 135, 131, 114 and 109 (Table 1).

KEGG and GO Enrichment Analysis of Transcription Factors

The results of enrichment analysis of 2322 transcription factors showed that they were enriched in 15 pathways and the first 12 were significantly enriched (Fig. 1a). Among 15 pathways, eight and three of them are divided into metabolism and genetic information processing classes respectively (Fig. 1b). Of the remaining four pathways, two belong to environmental adaptation processing and two to organismal systems (Fig. 1b). They are plant hormone signal transduction, circadian rhythm-plant, plant-pathogen interaction, MAPK signaling pathway-plant (Fig. 1a). Meanwhile, these four pathways also have the highest number of enriched genes. The gene numbers of them are 323, 125, 93 and 89 respectively (Fig. 1a). The annotation of KEGG pathways showed that there are 373 and 218 genes are involved in signal transduction and environmental adaptation respectively (Fig. 1c). We list fifteen significantly enriched Go terms. Twelve of them are biological processes. The other three are belong to the molecular function (Fig. 2).

Tissues Specific Expression (TSE) Analysis of Transcription Factors

The expression profiles of 2322 transcription factors showed that 200 TFs were tissue specifically expressed (Figure S1). The number of them in eight tissues were 34 (root), four (stem), 20 (leaf), 48 (flower), 42 (ovule), 32 (fruit), 13 (seed) and 11 (embryo) respectively (Table 2). 204 TFs belonged to 40 families. 25, five, nine and seven genes were annotated in the plant hormone signal transduction, circadian rhythm-plant, plant-pathogen interaction, MAPK signaling pathway-plant pathways respectively (Table S2). Among 40 families, MYB family had the largest gene number and was specifically expressed in every tissue (Table 2).

Table 1 Number of transcription factors in *C. brachiata*

Transcription factors family	Number	Transcription factors family	Number
Alfin-like	7	LFY	1
AP2/ERF-AP2	22	LIM	6
AP2/ERF-ERF	114	LOB	49
AP2/ERF-RAV	4	LUG	6
ARID	14	MADS-MIKC	26
AUX/IAA	37	MADS-M-type	26
B3	47	MBF1	3
B3-ARF	21	MED6	2
BBR-BPC	6	MED7	1
BES1	8	mTERF	44
bHLH	131	MYB	146
bZIP	80	MYB-related	97
C2C2-CO-like	13	NAC	109
C2C2-Dof	32	NF-X1	3
C2C2-GATA	34	NF-YA	8
C2C2-LSD	4	NF-YB	19
C2C2-YABBY	13	NF-YC	11
C2H2	135	ONP	22
C3H	71	Others	83
CAMTA	2	PHD	49
Coactivator p15	4	PLATZ	18
CPP	10	Pseudo ARR-B	2
CSD	7	RB	1
DBB	6	Rcd1-like	2
DBP	4	RWP-RK	9
DDT	7	S1Fa-like	1
E2F-DP	7	SAP	2
EIL	5	SBP	21
FAR1	12	SET	43
GARP-ARR-B	11	SNF2	37
GARP-G2-like	50	SOH1	2
GeBP	5	SRS	7
GNAT	29	SWI/SNF-BAF60b	19
GRAS	75	SWI/SNF-SWI3	6
GRF	15	TAZ	7
HB-BELL	12	TCP	25
HB-HD-ZIP	37	Tify	18
HB-KNOX	10	TRAF	19
HB-other	20	Trihelix	38
HB-PHD	2	TUB	21
HB-WOX	14	ULT	3
HMG	14	VOZ	1
HRT	3	Whirly	2
HSF	13	WRKY	88
IWS1	15	zf-HD	13
Jumonji	24		

Transcription Factors Expression Trends Analysis

We analyzed the expression trend of 630 genes that significantly enriched in plant hormone signal transduction, circadian rhythm-plant, plant-pathogen interaction and MAPK signaling pathway-plant. In 20 trend profiles, profile 0 and

profile 16 with the significant P value ($P < 0.05$) are assigned 257 and 116 genes respectively (Fig. 3). The remaining 18 profiles with the P value ≥ 0.5 and only a small number of genes were assigned to them (Fig. 3).

We screened 37 genes that significantly different expressed in certain tissue from profile0 and profile16 that significantly most highly expressed in each tissue and displayed them in heatmap (Fig. 4). These genes belong to 15 families. The top three families with largest gene number were AUX/IAA, bHLH and bZIP. The numbers were six, five and five. The genes number in root, stem, leaf, flower, ovule, fruit, seed and embryo were eight, one, ten, three, six, two, four and two respectively (Fig. 4). *IAA-2* and *NAC-1* were specifically expressed in leaf. *IAA-5* and *ARR-A* were specifically expressed in ovule, and *MYB-1* was specifically expressed fruit.

Gene Expression Validation by RT-qPCR

To validate the reliability of gene expression data obtained by transcriptome sequencing, six genes with differential expression in tissues were selected for RT-qPCR validation. These genes were divided into two groups, including tissue-specific genes (*IAA-2*, *IAA-5*, *MYB-1*) and highly expressed genes in certain tissues (*ARF18*, *ARR-B-3*, *ABI5*). The result of validation was consistent with the transcriptome data (Fig. 5).

Discussion

C. brachiata is very different from other species in the same family, for example, in terms of habitat and adaptive characteristics. *C. brachiata* is a typical terrestrial species, because of its beautiful tree shape, tolerance to barren and drought and other characteristics, in recent years become the new favorite of landscaping. In this study, from the perspective of transcription factors, we try to explore the molecular mechanism of the plant growth and development of *C. brachiata* to adapt to its environment.

Transcription factors can activate or inhibit the expression of regulatory genes by interacting with DNA or other proteins, and they play an important role in many physiological and biochemical metabolic processes of plants via participating in the hormones signal transduction (Jan et al. 2019; Li et al. 2022; Shahzad et al. 2020; Shen 2022). In our study, 2322 transcription factors were identified in *C. brachiata*. MYB family had 146 genes. In plants, the MYB is one of the largest families and involved in the regulation of numerous functions such as gene regulation in different metabolic pathways especially secondary metabolic pathways, regulation of different signaling pathways of plant hormones etc.

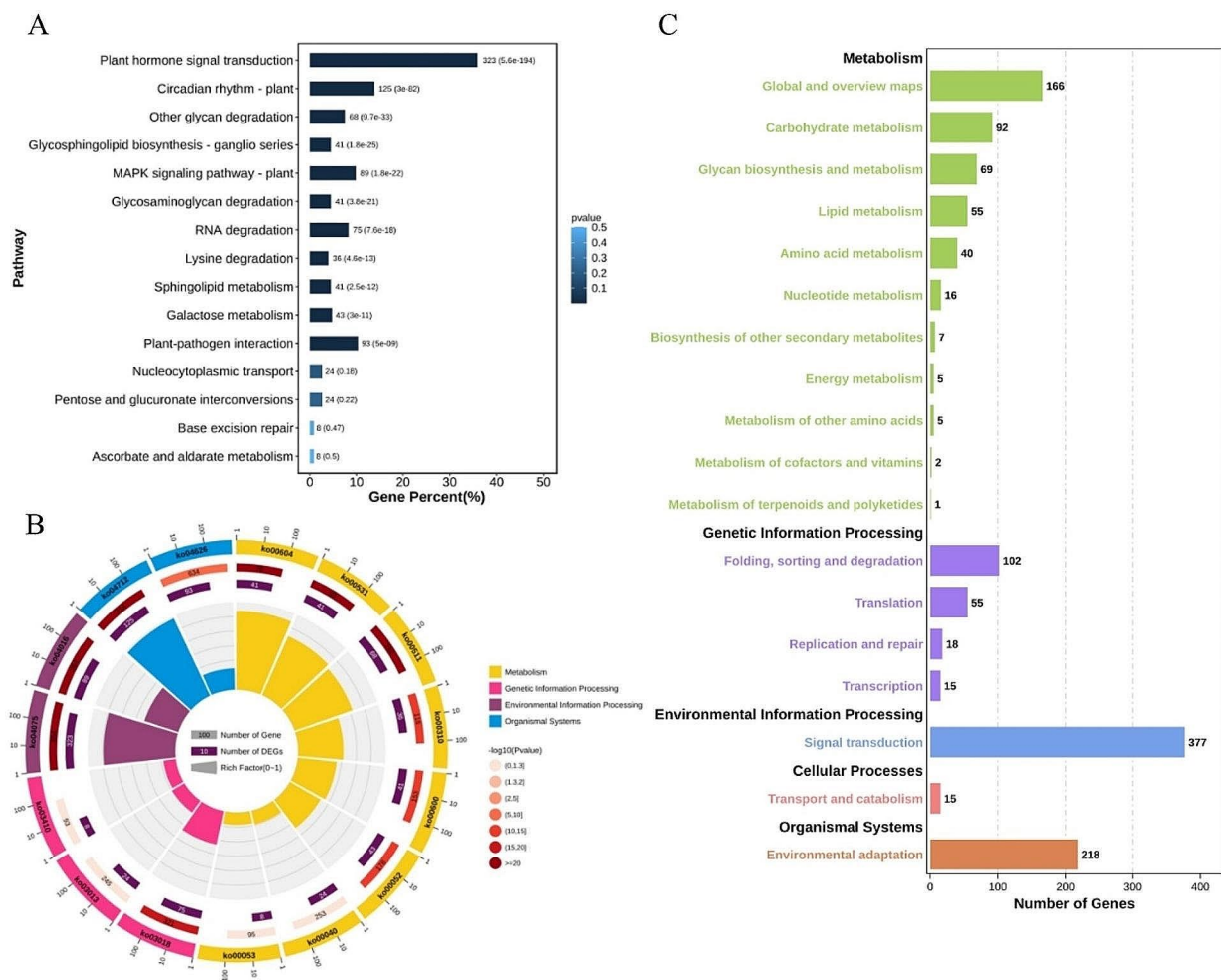


Fig. 1 KEGG pathways enriched by transcription factors expressed in *C. brachiata*. **A**, Bar diagram of enrichment KEGG pathways. The darker the color, the more significant the enrichment; **B**, KEGG enrichment loop diagram. The first circle: enrich the top 15 pathways, outside the circle is the coordinate ruler of the number of differential genes. Different colors indicate different A classes. The second circle: the number and Q value of the pathway in the differential gene back-

ground. The more the number of differential genes background, the longer the bar, the smaller the Q value, the redder the color. The third circle: total number of foreground genes. The fourth circle: the Rich-Factor value of each pathway (the number of differential genes in the pathway divided by all the numbers in the Pathway), background grid lines, each grid indicates 0.1; **C**, Statistical charts of Grade B classification of each pathway, the number represents the number of genes.

Fig. 2 GO enrichment of transcription factors expressed in *C. brachiata*. **A**, GO terms loop diagram; **B**, Description of each GO term. The illustration of the Fig. 2a is the same as that of Fig. 1b.

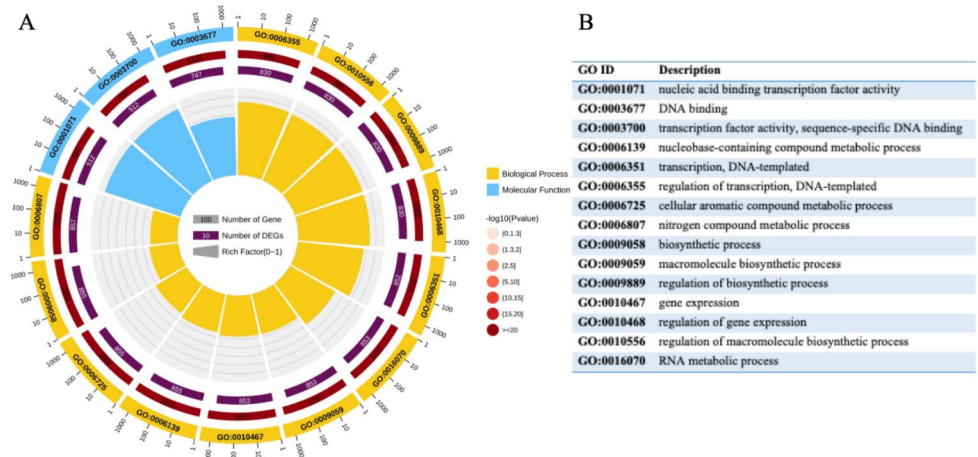


Table 2 Number of tissue specific expression TFs (TSEs) in tissues of *C. brachiata*.

Num. TSEs	Root	Stem	Leaf	Flower	Ovule	Fruit	Seed	Embryo
AP2/ERF-AP2		1						
AP2/ERF-ERF	2			2		3		3
AP2/ERF-RAV					2			
ARID			1	1				
AUX/IAA			1	1	1			
B3				2				1
bHLH	3		1	6	2	3	1	
bZIP				1	2			
C2C2-CO-like			1					1
C2C2-GATA			2		1			
C2C2-YABBY			1	4	1	1		
C2H2	4		3	5	1	3		
C3H							2	
GARP-ARR-B					1			
GARP-G2-like			1	1				
GeBP						1		
GNAT			1				1	
GRAS	1		1	2	2	2		
HB-BELL			1					
HB-HD-ZIP					1			
HB-other			1	1	3			
HB-WOX			1	2				2
IWS1				1				
LOB	1			5	2	1	1	
MADS-MIKC	1			4	3			
MADS-M-type					4			
mTERF					1		2	
MYB	14	2	1	5	5	4	2	1
MYB-related	1			1	1	2	2	
NAC				2	1	4		1
NF-YB	3				1			1
Others			1	1	3	3		1
PHD				1		1		
PLATZ							1	
SRS	1							
TCP		1			1			
Trihelix						1		
ULT					1			
WRKY	2		2			3	1	
zf-HD	1				2			
SUM	34	4	20	48	42	32	13	11

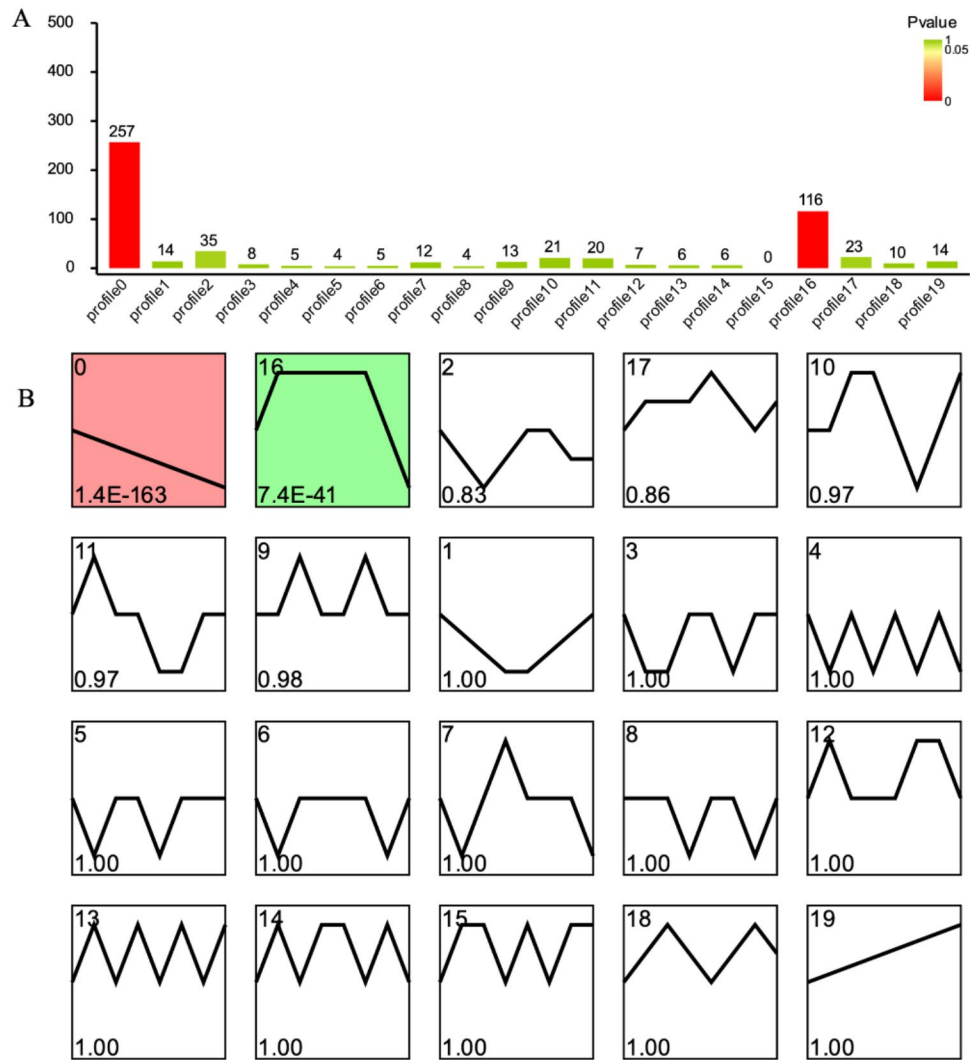
(Thakur and Vasudev 2022). Among 2322 transcription factors, 204 were tissue specifically expressed. MYB family had the largest number and specifically expressed in every tissue (Table 2). This result also illustrated the broad role of this family.

2322 transcription factors significantly enriched in 12 pathways. Four of them were divided into environmental adaptation and 698 genes were enriched in. They are hormone signal transduction, circadian rhythm-plant, plant-pathogen interaction and MAPK signaling pathway-plant. 204 tissue-specific genes were also significantly enriched in these four pathways, which demonstrated the importance

of them. These pathways have been repeatedly reported to be involved in plant response to environmental signaling. The fruit of *C. brachiata* is often infested by pests. Genes enriched in plant-pathogen interaction and MAPK signaling pathway-plant response to this signal (Yin et al. 2021). Understanding the interaction between plant and pathogen is of great significance for studying the mechanism of plant response to disease.

Most of the tissue-specific genes and differently expressed genes are involved in plant hormone signal transduction such as *IAA-2*, *IAA-5*, *MYB-1*, *ARF18*, *ARR-B-3*, *ABI5*, *DELTA*, *PIF3/4*, *MYC2*, *NPRI*, *TGA* and so on.

Fig. 3 Trend analysis of transcription factors expressed in *C. brachiata*. A, Statistical map of the number of genes in different trend sets, red to green indicates *P* values from small to large; B, Profiles ordered based on the *P* value significance of number of genes assigned versus expected.



These genes are responsible for the signal transduction of cytokinin, auxin, gibberellin, jasmonic acid, salicylic acid, ethylene and abscisic acid (Fig. 6). Transcription factors in MYB, NAC and bHLH families have been reported that they play roles in response to drought, UV, high temperature etc. via regulating the hormones signal transduction (Blázquez et al. 2020; Li et al. 2020; Liu et al. 2007; Papon and Courdavault 2022; Wang et al. 2018, 2023; Xiang et al. 2023). *C. brachiata* grows in inland area in tropical regions with climatic characteristics of drought, UV radiation and high temperature and so on. These transcription factors make *C. brachiata* better respond to its environment by involving in hormone signal transduction. Jasmonic acid and salicylic acid are two important hormones for stress response and disease resistance of plants (Hu et al. 2022; Lee et al. 2010). *MYC2*, *NPR1* and *TGA* were key factors in jasmonic acid and salicylic acid signal transduction respectively. Ethylene and abscisic acid are also two

hormones that plants sometimes rely on to survive adversity (Blázquez et al. 2020). ERFs respond to the ethylene and abscisic acid to help activate ABA dependent and independent stress-responsive genes (Matilla 2020). For example, *ABI5* regulating seed dormancy is an important factor in response to ABA hormones, and ERF is also involved in this process. The high expression of these genes in the reproductive organs is consistent with their role in the relative process. We know that the role of hormones is often multiple, involved in the various processes of plant growth and development (Xie et al. 2019; Varshney et al. 2023; Zhang et al. 2023). Cytokinin, auxin and gibberellin were three main positive hormones in plant growth process such as promoting cell differentiation and lead to tillering of new branches, inducing seed germination and stem growth (Blázquez et al. 2020; Papon and Courdavault 2022). ARR, DELLAs and PIFs are key factors in cytokinin and gibberellin signal transduction. IAAs and ARFs are transcription factors that

Fig. 4 Expression of key transcription factors that significantly enriched in plant hormone signal transduction pathway in *C. brachiata*. Red means higher expression.

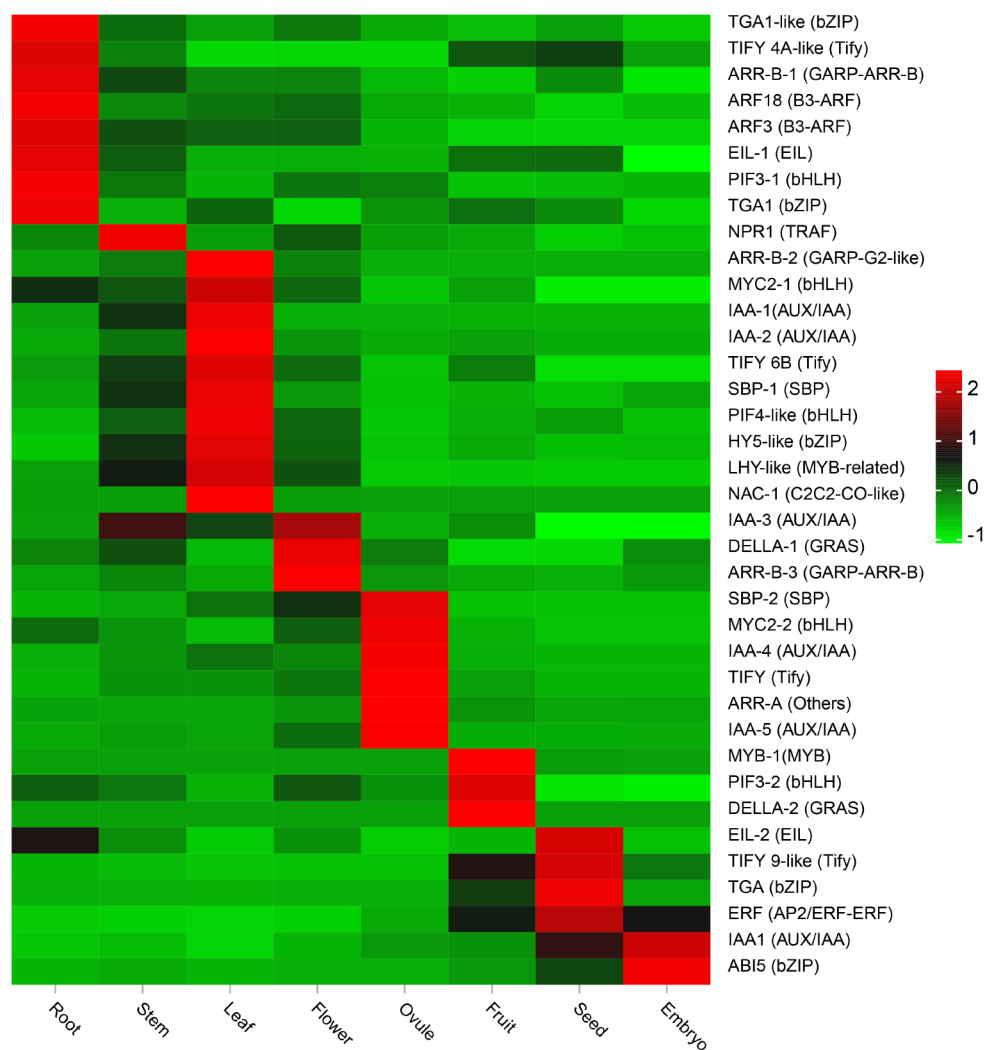


Fig. 5 RT-qPCR validations of key genes of *C. brachiata*. *IAA-2*, *IAA-5* and *MYB-1* are tissue-specific genes. *ARF18*, *ARR-B-3* and *ABI5* are highly expressed in certain tissues.

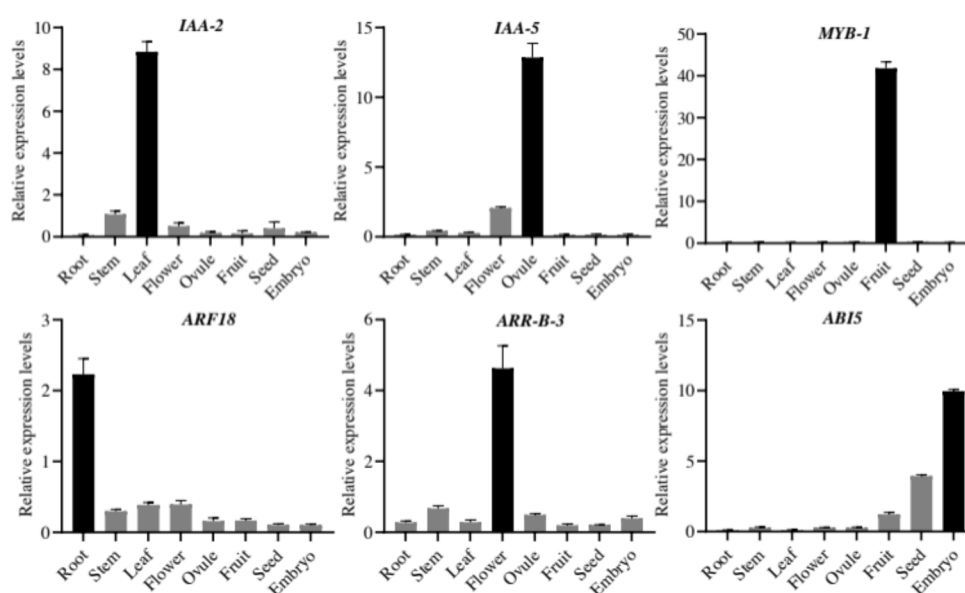
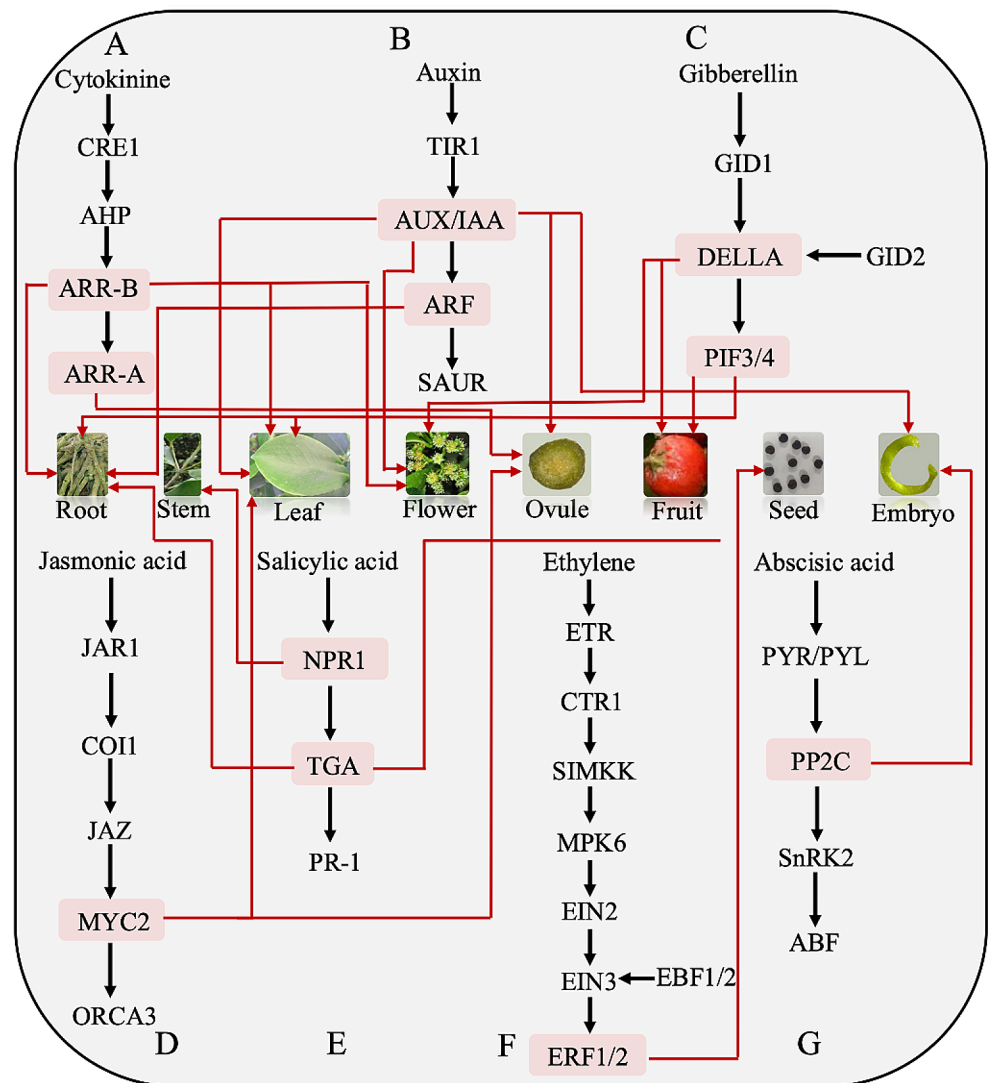


Fig. 6 Regulation of key transcription factors in *C. brachiata* adaptation. A, B, C, D, E, F, G, are signal response pathways of cytokinin, auxin, gibberellin, jasmonic acid, salicylic acid, ethylene and abscisic acid.



regulate the transcription of auxin-responsive genes during plant growth and development (Blázquez et al. 2020; Li et al. 2020). These factors with positive roles in plant growth and development were mainly working in vegetative organs (root, stem, leaf), while the ethylene and abscisic acid were specially working in reproductive organs. The transcription factors regulated the different tissues completing the process of plant growth and development of *C. brachiata* in its environment via hormones signal transduction.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12042-024-09358-0>.

Author Contributions H.Q. conceived and designed the project. H.Q. did data analyses. H.Q. wrote the manuscript.

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Data Availability The datasets used in this study are available in the NCBI sequence archive, the accession number is PRJNA632974 (*C. brachiata*) which was published [15].

Declarations

Competing Interests The authors declare no competing interests.

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References

- Anders S, Pyl PT, Huber W (2015) HTSeq—a Python framework to work with high-throughput sequencing data. *Bioinformatics* 31(2):166–169. <https://doi.org/10.1093/bioinformatics/btu638>
- Benjamini Y, Hochberg Y (2000) On the adaptive control of the false discovery rate in multiple testing with independent statistics. *J Educational Behav Stat* 25(1):60–83. <https://doi.org/10.3102/10769986025001060>
- Blázquez MA, Nelson DC, Weijers D (2020) Evolution of lant hormone response pathways. *Annu Rev Plant Biol* 71. <https://doi.org/10.1146/annurev-arplant-050718-100309>
- Brooks MJ, Rajasimha HK, Roger JE et al (2011) Next-generation sequencing facilitates quantitative analysis of wild-type and Nrl-/- retinal transcriptomes. *Mol Vis* 17:3034–3054 (327–30)
- Finn RD, Clements J, Eddy SR (2011) HMMER web server: interactive sequence similarity searching. *Nucleic Acids Res* 39:29–37 (Web Server issue)
- Hu YL, Zhi LL, Li P et al (2022) The role of salicylic acid signal in plant growth, development and abiotic stress. *Phyton-International J Experimental Bot* 91(12):2591–2605. <https://doi.org/10.32604/phyton.2022.023733>
- Jan S, Abbas N, Ashraf M et al (2019) Roles of potential plant hormones and transcription factors in controlling leaf senescence and drought tolerance. *Protoplasma* 256(2):313–329. <https://doi.org/10.1007/s00709-018-1310-5>
- Junejo JA, Rudrapal M, Zaman K (2020) Antidiabetic activity of *Carallia Brachiata* Lour. Leaves hydro-alcoholic extract (HAE) with antioxidant potential in diabetic rats. *Indian J Nat Prod Resour* 11(1):18–29
- Kim D, Landmead B, Salzberg SL (2015) HISAT: a fast spliced aligner with low memory requirements. *Nat Methods* 12(4):357–U121. <https://doi.org/10.1038/nmeth.3317>
- Kucera B, Cohn MA, Leubner-Metzger G (2005) Plant hormone interactions during seed dormancy release and germination. *Seed Sci Res* 15(4):281–307. <https://doi.org/10.1079/ssr2005218>
- Lee S, Kim SG, Park CM (2010) Salicylic acid promotes seed germination under high salinity by modulating antioxidant activity in *Arabidopsis*. *New Phytol* 188(2):626–637. <https://doi.org/10.1111/j.1469-8137.2010.03378.x>
- Li SB, Xie ZZ, Hu CG et al (2016) A review of auxin response factors (ARFs) in plants. *Front Plant Sci* 7. <https://doi.org/10.3389/fpls.2016.00047>
- Li QF, Zhou Y, Xiong M et al (2020) Gibberellin recovers seed germination in rice with impaired brassinosteroid signalling. *Plant Sci* 293. <https://doi.org/10.1016/j.plantsci.2020.110435>
- Li H, Duan SY, Sun WL et al (2022) Identification, through transcriptome analysis, of transcription factors that regulate anthocyanin biosynthesis in different parts of red-fleshed apple ‘May’ fruit. *Hortic Plant J* 8(1):11–21. <https://doi.org/10.1016/j.hpj.2021.07.001>
- Liu PP, Montgomery TA, Fahlgren N et al (2007) Repression of auxin response factor10 by microRNA160 is critical for seed germination and post-germination stages. *Plant J* 52(1):133–146. <https://doi.org/10.1111/j.1365-3113X.2007.03218.x>
- Liu YT, Guo P, Wang J et al (2023) Growth-regulating factors: conserved and divergent roles in plant growth and development and potential value for crop improvement. *Plant J* 113(6):1122–1145
- Matilla AJ (2020) Auxin: hormonal signal required for seed development and dormancy. *Plants-Basel* 9(6). <https://doi.org/10.3390/plants9060705>
- Mostafa MG, Rahman MM, Ghosh TK et al (2022) Potassium in plant physiological adaptation to abiotic stresses. *Plant Physiol Biochem* 186:279–289. <https://doi.org/10.1016/j.plaphy.2022.07.011>
- Nalinratana N, Suriya U, Laprasert C et al (2023) In vitro and in silico studies of 7”, 8”-buddlenol D anti-inflammatory lignans from *Carallia brachiata* as p38 MAP kinase inhibitors. *Sci Rep* 13(1). <https://doi.org/10.1038/s41598-023-30475-5>
- Papon N, Courdavault V (2022) ARResting cytokinin signaling for salt-stress tolerance. *Plant Sci* 314. <https://doi.org/10.1016/j.plantsci.2021.111116>
- Patil PD, Chavan NS (2015) A comparative study of nutrients and mineral composition of *Carallia brachiata* (Lour.) Merrill. *Int J Adv Sci Res* 1(2):90
- Punta M, Coggill PC, Eberhardt RY et al (2012) The pfam protein families database. *Nucleic Acids Res* 40(D1):D290–D301. <https://doi.org/10.1093/nar/gkr1065>
- Qiao HM, Zhou XX, Su WY et al (2020) The genomic and transcriptomic foundations of viviparous seed development in mangroves. *bioRxiv*. <https://doi.org/10.1101/2020.10.19.346163>
- Robinson MD, McCarthy DJ, Smyth GK (2010) edgeR: a Bioconductor package for differential expression analysis of digital gene expression data. *Bioinformatics* 26(1):139–140. <https://doi.org/10.1093/bioinformatics/btp616>
- Shahzad R, Jamil S, Ahmad S et al (2020) Harnessing the potential of plant transcription factors in developing climate-smart crops: future prospects, challenges, and opportunities. *Preprints*. <https://doi.org/10.20944/PREPRINTS202010.0532.V1>
- Shen CX (2022) Regulatory network established by transcription factors transmits drought stress signals in plant. *Stress Biology* 2(1):322–343
- Thakur S, Vasudev PG (2022) MYB transcription factors and their role in medicinal plants. *Mol Biol Rep* 49(11):10995–11008. <https://doi.org/10.1007/s11033-022-07825-z>
- Varshney V, Hazra A, Majee M (2023) Phy meets ERFs to regulate seed germination. *Trends Plant Sci* 28(1):7–9. <https://doi.org/10.1016/j.tplants.2022.10.003>
- Wang LK, Feng ZX, Wang X et al (2010) DEGseq: an R package for identifying differentially expressed genes from RNA-seq data. *Bioinformatics* 26(1):136–138. <https://doi.org/10.1093/bioinformatics/btp612>
- Wang L, Sun Y, Yao LI (2018) Research advances of AP2/ERF transcription factors. In: *International Conference on Biological Sciences and Technology*
- Wang Y, Li Y, He SP et al (2023) The transcription factor ERF108 interacts with auxin response factors to mediate cotton fiber secondary cell wall biosynthesis. *Plant Cell*. <https://doi.org/10.1093/plcell/koad214>
- Xiang C, Jia-De T, Yue-Lian D et al (2016) Effects of drought stress on growth of *Carallia brachiata* seedling. *Journal of Fujian Forestry Science and Technology*
- Xiang ZX, Li W, Lu YT et al (2023) Hydrogen sulfide alleviates osmotic stress-induced root growth inhibition by promoting auxin homeostasis. *Plant J* 114(6):1369–1384. <https://doi.org/10.1111/tbj.16198>
- Xie ZL, Nolan TM, Jiang H et al (2019) AP2/ERF transcription factor regulatory networks in hormone and abiotic stress responses in *Arabidopsis*. *Front Plant Sci* 10. <https://doi.org/10.3389/fpls.2019.00228>
- Yin ZJ, Zhu WD, Zhang XP et al (2021) Molecular characterization, expression and interaction of MAPK, MAPKK and MAPKKK genes in upland cotton. *Genomics* 113(1):1071–1086. <https://doi.org/10.1016/j.ygeno.2020.11.004>
- Zhang J, Zhao PX, Chen SY et al (2023) The ABI3-ERF1 module mediates ABA-auxin crosstalk to regulate lateral root emergence. *Cell Rep* 42(7). <https://doi.org/10.1016/j.celrep.2023.112809>
- Zhou TT, Xu JX, Xue L et al (2015) Physiological changes of *Carallia brachiata*, *Ficus Microcarpa* and *Phoebe Zhennan* seedlings under low temperature stress. In: *2nd International Conference on*

Material Engineering and Application (ICMEA), Wuhan, PEOPLES R CHINA, Oct 17–18 2015. pp 466–473

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