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Genome-Wide Characterization and Identification of the YABBY Gene Family in Mango (*Mangifera indica*)

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Abstract: YABBY is a specific transcription factor gene family in plants. It has the typical N-terminal C2C2-type zinc-finger domain and the C-terminal YABBY conservative structure domain, which play an important role in the development of the leaves and floral organs. The *YABBY* gene family directs leaf polarity in mango, playing an important role in maintaining species specificity. In this study, a total of seven *YABBY* genes were identified in the mango (*Mangifera indica*) genome. The seven YABBY family members possessed both typical C2C2 and YABBY domains. A phylogenetic tree was constructed based on the amino acid sequences of the 42 YABBY proteins of mango, *Arabidopsis*, apple, grape, and peach. The phylogenetic tree indicated that the members of the mango YABBY family could be divided into three subfamilies, including CRC, YAB5, and YAB3. Quantitative real-time PCR showed that the transcription levels of the *MiYABBYs* were significantly different under biotic and abiotic stresses. The transcription level of *MiYABBY7* was significantly down-regulated at 0–72 h after *Xanthomonas campestris* pv. *mangiferaeindicae* infection, methyl jasmonate and salicylic acid stresses. The *MiYABBY1* transcription level was significantly down-regulated at 0–72 h after *Colletotrichum gloeosporioides* infection. *MiYABBYs* were expressed specifically in different leaves and fruit, and *MiYABBY6* was significantly up-regulated during leaf and fruit development. However, *MiYABBY5* showed a contrary transcriptional pattern during leaf and fruit development. This is first report on the mango *YABBY* gene family at the genome-wide level. These results will be beneficial for understanding the biological functions and molecular mechanisms of *YABBY* genes.

Keywords: mango; transcription factor gene family; YABBY; bioinformatics; expression profile

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1. Introduction

Mango (*Mangifera indica* L.) is an evergreen fruit tree in the Anacardiaceae family that originated in South and Southeast Asia [1]. The fruit can be used as a traditional medicinal resource in addition to being enjoyed as a food and fresh fruit. Global mango production reached 51 million tons in 2019 [2]. In China, the extensive cultivation of mango has great economic and ecological benefits.

In the production of mango, leaf and fruit growth is impacted by pathogen infection. The leaves are the primary organs of photosynthesis, which directly or indirectly affects the yield of plants. Leaf development is determined by both environmental and genetic factors. The leaves of most higher plants exhibit flattening perpendicular to the meristem,

with obvious adaxial–abaxial characteristics. Leaf development is an important component of plant morphogenesis. Therefore, exploring the leaf flattening mechanism may help us to clarify the process of leaf morphogenesis, thereby helping plants better adapt to production requirements. In 2019, Li and colleagues sequenced the variety of mango, and generated a 371.6-Mb mango genome assembly with 34,529 predicted protein-coding genes; this work provides the genetic and molecular and biological basis [3].

YABBY is a specific transcription factor gene family in plants that possesses the typical N-terminal C2C2-type zinc-finger domain and the C-terminal YABBY conservative structure domain, which play an important role in the establishment of the adaxial and abaxial polarity of the leaves and floral organs [4–6]. There are six *YABBY* gene family members in *Arabidopsis* that are specifically expressed in the dorsal area of the nectar gland and carpel (AtCRC), lateral primordium of the aboveground part (AtFIL, AtYAB2, and AtYAB3), the ovule (AtINO), and vegetative organs (AtYAB5) [4]. YABBY transcription factors experienced functional differentiation in the process of evolution of monocotyledonous and dicotyledonous plants. There are five subfamilies of the YABBY family (FIL/YAB3, YAB2, YAB5, CRC, and INO) in *Arabidopsis* [6], but only four subfamilies of the YABBY family (FIL/YAB3, YAB2, CRC, and INO) in rice [7]. At present, many YABBY family members have been identified and studied in a variety of plant species, such as pak-choi (*Brassica rap*a) [8], grapevine (*Vitis vinifera*) [9], moso bamboo (*Phyllostachys edulis*) [10], cotton (*Gossypium* spp.) [11], pineapple (*Ananas comosus*) [12], tomato (*Solanum lycopersicum*) [13], walnut (*Juglans regia* L.) [14], cucumber(*Cucumis sativus* L.) [15], *Brassicaceae* [16], rapeseed (*Brassica napus* L.) [17], and soybean (*Glycine max*) [18]. Researchers have generally focused on the role of YABBY transcription factors in vegetative and reproductive processes [18]; however, their functions in stress responses and phytohormones in plants are also integral [12,19].

The available evidence has confirmed that a number of YABBYs are induced by abiotic stresses and phytohormones. One study found that *BcYABBY* genes play a role in the response to various abiotic stresses and phytohormone treatments in pak-choi [8], such as salicylic acid (SA), abscisic acid (ABA), polyethylene glycol (PEG), and cold-stress. Furthermore, *AcYABBY* genes were found to be responsive to NaCl treatment and low temperature stress in pineapple [12]. It has also been reported that some *GmYABBY* genes are involved in the resistance of soybean to drought, salt-stress, and ABA stress [18]. To date, no information is available on the *YABBY* gene family in the economically important crop mango. In this study, we used bioinformatic methods to identify the *YABBY* gene family in the mango genome and analyze the sequence features, phylogenetic relationships, and specific expression in the leaves and fruit. In addition, we studied the expression patterns of the mango *YABBY* genes under different biotic and abiotic stresses by quantitative real-time PCR (qRT-PCR). These results improve our understanding of the biological functions and molecular mechanisms of *YABBY* genes.

2. Materials and Methods

2.1. Plant Materials and Treatments

The Mango Planting Resource Nursery, Danzhou City, Ministry of Agriculture and Rural Affairs provided the Guifei Mango variety for the experiment. We selected seven-day-old leaves from one-year-old seedlings of the same height for grafting in the greenhouse. The culture conditions were 25 °C, a relative humidity of 70–90%, and a photoperiod of 16:8 h (L:D). The leaves at 3 d, 21 d, and 35 d and the fruits at 3 d, 7 d, 10 d, 21 d, and 35 d were snap-frozen in liquid nitrogen and placed at −80 °C. The leaves were infected with *Colletotrichum gloeosporioides* and *Xanthomonas campestris* pv. *mangiferaeindicae* at 2×10^6 mL^{-1} and sprayed with polyethylene glycol (PEG) and methyl jasmonate (MeJA) and salicylic acid (SA) at 5 mM. The processed leaves were sampled at 0 h, 3 h, 6 h, 12 h, 24 h, 48 h, and 72 h, snap-frozen in liquid nitrogen, and stored at −80 °C. The experiments were repeated three times.

2.2. Genome-Wide Identification of the MiYABBY Gene Family in Mango

The whole-genome data of mango from NCBI (Taxonomy ID 29780), the genome data of *Arabidopsis thaliana* from TAIR (https://www.arabidopsis.org/, accessed on 3 April 2022), apple (*Malus pumila*), peach (*Prunus persica*), and grape (*Vitis vinifera*) genome data from NCBI (https://www.ncbi.nlm.nih.gov/, accessed on 3 April 2022), and YABBY transcription factor sequences data from PlantTFDB (http://planttfdb.gao-lab.org/, accessed on 3 April 2022) were used. The *YABBY* gene sequences of *A. thaliana* were blasted against the mango genome database to screen YABBY family members of mango with an E-value setting of 10^{-5} [20]. The physicochemical properties, including the number of amino acids, protein molecular weight, isoelectric point, stability index, and hydrophilic of mango YABBY proteins, were predicted with ProtParam (http//web.Expasy.org/protparam/, accessed on 3 April 2022). The conservative motifs of the mango YABBY protein were detected with DNAMAN9 software, MEME (http://meme-suite.org/tools/meme, accessed on 3 April 2022), and NCBI (https://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.Cgi, accessed on 3 April 2022) [21], this method referred to Asma [22] and Muhammad [23] article. The protein secondary and tertiary structure of mango YABBYs were predicted with SOPMA SECONDARY STRUCTURE PREDICTION METHOD (https://www.expasy.org/, accessed on 3 April 2022) [24] and SWISS-MODEL (https://swissmodel.expasy.org/, accessed on 3 April 2022). Multiple sequence alignment of mango with four other dicotyledons was achieved with MUSCLE software, and a phylogenetic tree with 1000 bootstrap replicates was constructed using MEGA7.0 software [25].

2.3. Quantitative RT-PCR Data Analysis

The total RNA from the mango leaves was extracted with an RNA prep Pure Plant Plus Kit. The cDNA was reverse transcribed with a Revert Aid First Strand cDNA Synthesis Kit. The RNA and cDNA of mango were rapidly frozen at −80 °C. The cDNA of the treated leaves was used as the template and primers of MiYABBYs were designed with Primer 3 plus (http://www.primer3plus.com/cgibin/dev/primer3plus.cgi, accessed on 3 April 2022) for qRT-PCR amplification. The experiments used SYBR Mixture Kit and a 20 μL PCR system to determine whether *MiYABBY* genes expression differed at different times and in different organs. *Miactin* was used as the reference gene, and the gene expression in the no treatment mango leaves (0 h) were normalized to 1.0. The $2^{-\Delta\Delta Ct}$ method was used to process the CT value data, and values greater than 1.5 were considered up-regulated and values less than 0.5 were considered down-regulated.

3. Results

3.1. Identification and Characterization of MiYABBY

Local BLAST and conserved domains searches were performed, and those without a complete YABBY domain were removed. Finally, seven remaining putative functional *YABBY* genes with high confidence were identified in mango, named *MiYABBY1* to *MiYABBY7* (Table S1). The number of amino acids ranged between 176 and 239, the protein molecular weight ranged from 19.54 kDa to 26.52 kDa, and the isoelectric point ranged between 8.24 and 9.24 as a basic protein. The grand average of hydropathy (GRAVY) score was used to evaluate the protein hydrophobicity, with an aliphatic index from 67.61 to 75.82 and an instability index from 40.35 to 49.41. While MiYABBY2 had eight exons, the rest of the MiYABBY had seven exons.

The phylogenetic tree of the YABBY transcription factors of mango showed that the MiYABBYs were divided into three groups, including CRC, YAB5, and YAB3 (Figure 1A). The motif of the MiYABBYs was predicted with MEME software (Figure 1B), and the multiple sequence alignment results of the MiYABBYs showed that all members possessed the C2C2 domain in the N-terminal and the YABBY domain in the C-terminal, which con-

firmed that the seven MiYABBYs were YABBY transcription factors (Figure 1C). The superfamily domains of the MiYABBYs were analyzed using NCBI CD-Search, and the results showed that all members had the YABBY domain (Figure 1D). Based on the homology modeling method, the 6zme.80 model was used to predict the protein tertiary structure of MiYABBYs with SWISS-MODEL software, and the results showed all members had a similar structure (Figure 1E).

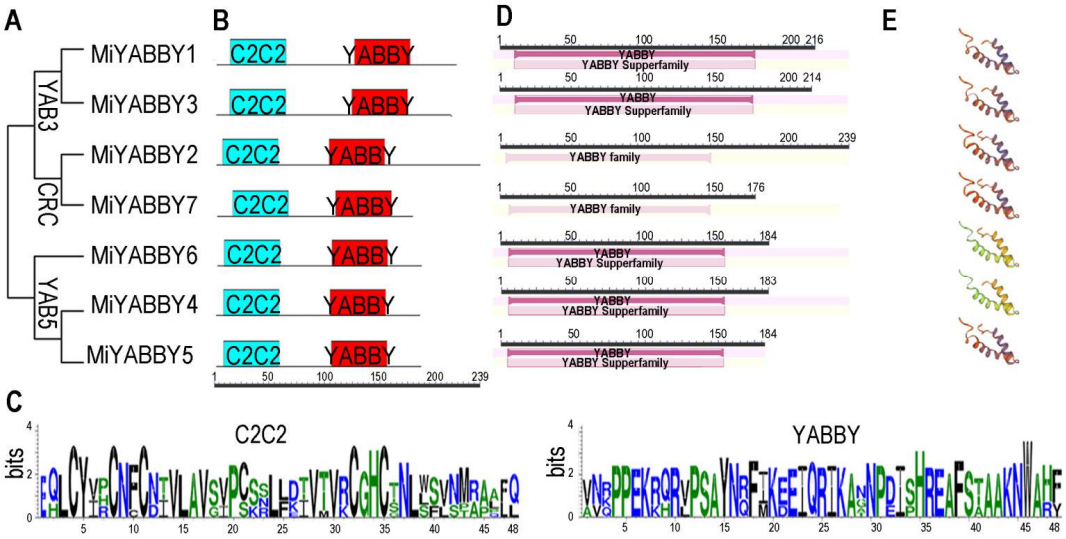

Figure 1. Phylogenetic analysis, conserved domain analysis, inherited superfamily domains, and tertiary structure of proteins in the MiYABBYs family. (**A**) is the phylogenetic tree of the MiYABBY family, and all members were classified into three groups, including YAB3, CRC, and YAB5. (**B**) are the two motifs of MiYABBYs: C2C2 (blue grid) in the N-terminal and YABBY (red grid) in the C-terminal. (**C**) are the sequences of these motifs. (**D**) is the forecast of the superfamily of MiYABBYs in NCBI Blast (CD-search). (**E**) is tertiary structure of the MiYABBYs in SWISS-MODEL software.

3.2. Phylogenetic Analysis and Classification of the MiYABBY Proteins

To analyze the evolutionary relationships of the MiYABBY proteins in mango, *Arabidopsis*, apple, peach, and grape, a phylogenetic tree was constructed using full-length amino acid sequences. A total of seven sequences from mango, eight sequences from *Arabidopsis*, eleven sequences from apple, five sequences from peach, and eleven sequences from grape were assessed in the phylogenetic tree (Figure 2). The results showed that the YABBY proteins were divided into five evolutionary groups, including thirteen FIL/YAB3, one YAB2, seven INO, eight YAB5, and ten CRC. The MiYABBYs were distributed into three groups, including FIL/YAB3 (MiYABBY1, MiYABBY3), YAB5 (MiYABBY4, MiYABBY5, MiYABBY6), and CRC (MiYABBY2, MiYABBY7).

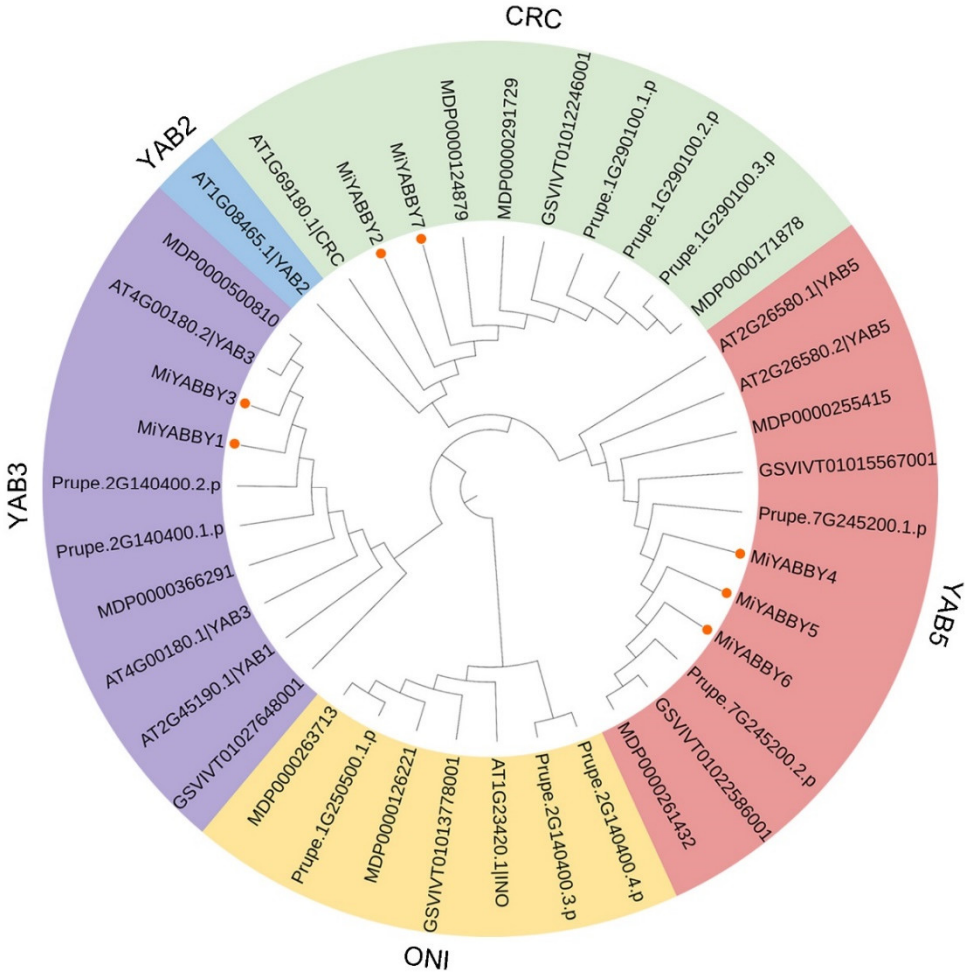

Figure 2. Phylogenetic analysis of the YABBY family in mango, *Arabidopsis*, apple, grape, and peach. MiYABBY represents mango (with orange dot mark), AT represents *Arabidopsis*, MDP represents apple, Prupe represents grape, and GSVIVT represents peach.

3.3. Expression Patterns of MiYABBY Genes in the Leaves and Fruits

The qRT-PCR primers of the *MiYABBY* genes were designed via Primer3Plus (https://www.bioinformatics.nl/cgi-bin/primer3plus/primer3plus.cgi, accessed on 3 April 2022) to determine the optimal primers (Table S2), and then the specificity of the melting curve was analyzed to determine the melting temperature (Figure S1A–H) and the parameters for the DNA agarose gel electrophoresis. For details, please see the melting curve and melting temperature (Figure S1A–H). The qRT-PCR-amplified product length of the amplified product was between 110 and 167 bp (Table S2).

To analyze the tissue-specific expression of *MiYABBY* genes in mango, we detected their expression in the leaves and fruits by qRT-PCR (Figure 3). The relative transcript levels of *MiYABBY* genes in the 3-day old leaves and fruits represented the control. In the 3–35 d leaves of mango, *MiYABBY4*, *MiYABBY5*, and *MiYABBY6* were persistently significantly up-regulated. *MiYABBY1* was significantly up-regulated in different fruit development stages. *MiYABBY7* exhibited low expression levels at 7–21 d and high expression levels at 35 d. In the 3 d, 21 d, and 35 d fruits of mango, *MiYABBY1*, *MiYABBY2*, *MiYABBY3*, *MiYABBY6*, and *MiYABBY7* exhibited high expression levels at 21 d and 35 d.

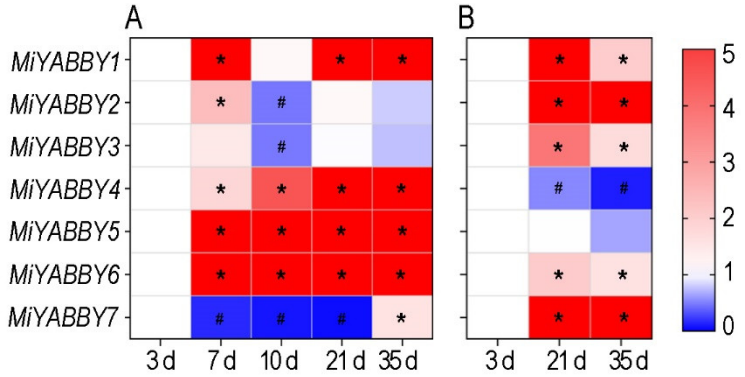

Figure 3. Relative expression analysis of the *MiYABBY* gene family in different mango organs. (**A**) shows the results from different leaves, and (**B**) shows the results of different fruits. The calculation method was $2^{-\Delta\Delta CT}$, and '*' means the value exceeds 1.5, whereas '#' means the value is below 0.5.

3.4. MiYABBY Genes Expression Profiles in Response to C. gloeosporioides and X. campestris pv. Mangiferaeindicae Infection

To investigate the possible role of *MiYABBY* genes in plant-pathogen interactions, qRT-PCR was used to analyze the response of mango leaves that were infected with *C. gloeosporioides* and *X. campestris* pv. *mangiferaeindicae* in comparison to a control. During infection of the mango leaves by *C. gloeosporioides* (Figure 4A), *MiYABBY2* and *MiYABBY3* exhibited high expression levels at 3 h after infection, whereas *MiYABBY4*, *MiYABBY5*, and *MiYABBY6* exhibited high expression levels at 48–72 h after infection (Figure 4B). During infection of the leaves by *X. campestris* pv. *mangiferaeindicae*, *MiYABBY4*, *MiYABBY5*, and *MiYABBY6* exhibited high expression levels at 48 h.

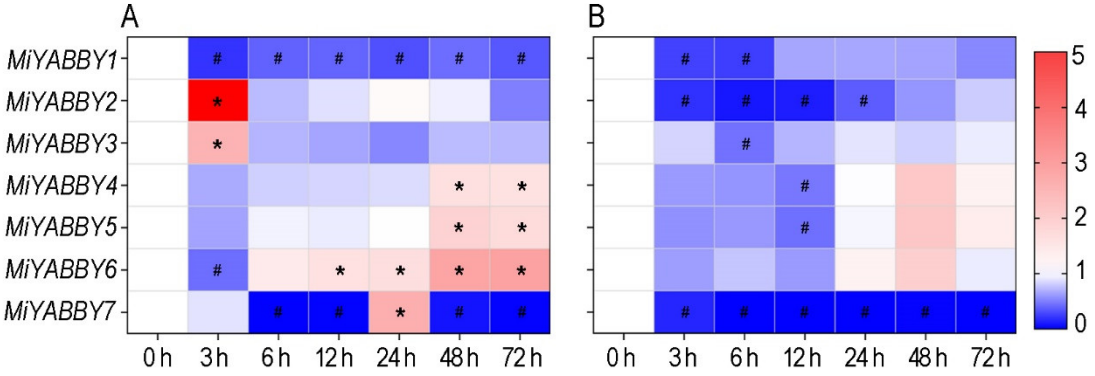

Figure 4. Relative expression analysis of the *MiYABBY* gene family that were infected with different pathogens in mango. (**A**) shows the results of *Cg* infection, and (**B**) shows the results of *Xcm* infection. The calculation method was $2^{-\Delta\Delta CT}$, and '*' means the value exceeds 1.5, whereas '#' means that the value is below 0.5.

3.5. MiYABBY Genes Expression Profiles upon Exposure to Drought- and Salt-Stresses

Quantitative RT-PCR was used to investigate the response of *MiYABBY* genes to drought- and salt-stresses. During drought-stress (Figure 5A), all *MiYABBY* genes were up-regulated at 6 h in the leaves. *MiYABBY2*, *MiYABBY4*, *MiYABBY5*, and *MiYABBY6* were significantly up-regulated at 3–24 h after drought-stress. Notably, *MiYABBY2* had the highest transcription level at 3 h, 6 h, and 72 h. During salt-stress, *MiYABBY1*, *MiYABBY4*, *MiYABBY5*, and *MiYABBY6* were significantly down-regulated at four consecutive treatment time points in the leaves. However, *MiYABBY2* and *MiYABBY3* were significantly up-regulated at 48 h after salt-stress.

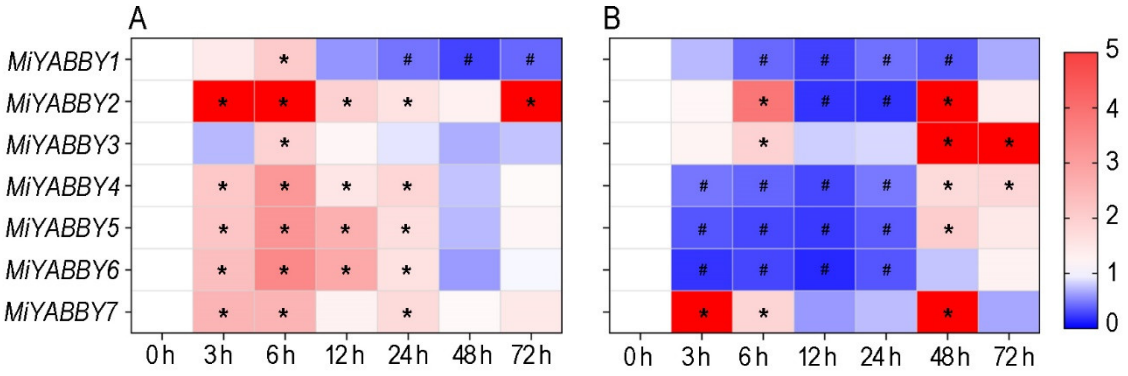

Figure 5. Relative expression analysis of the *MiYABBY* gene family under different stress treatments in mango. (**A**) shows the results of the PEG treatment, and (**B**) shows the results of the NaCl treatment. The calculation method was $2^{-\Delta\Delta CT}$, and '*' means the value exceeds 1.5, while '#' means the value is below 0.5.

3.6. MiYABBY Genes Expression Profiles upon Exposure to MeJA and SA Stresses

MiYABBY genes expression was detected under MeJA and SA treatment using qRT-PCR, and the results showed that the *MiYABBY* genes responded positively to MeJA treatment (Figure 6A) but negatively to SA (Figure 6B). During MeJA stress in the leaves, the expression of all *MiYABBY* genes was down-regulated at 3 h–24 h and subsequently increased at 48–72 h, except for *MiYABBY7*. During SA stress in the leaves, *MiYABBY2* had the highest transcription level at 3 h, while *MiYABBY6* had the higher transcription level at 24 h.

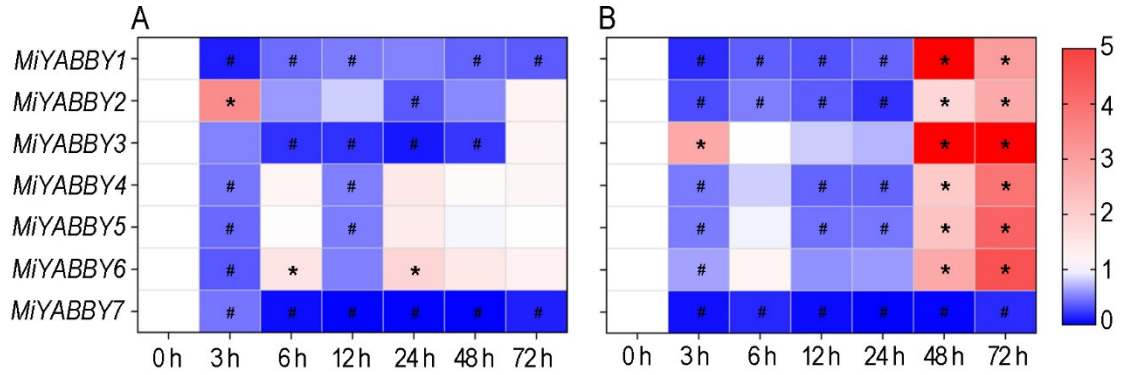

Figure 6. Relative expression analysis of the *MiYABBY* gene family under phytohormone treatments in mango. (**A**) shows the results of the MeJA treatment, and (**B**) shows the results of the SA treatment. The calculation method was $2^{-\Delta\Delta CT}$, and '*' means the value exceeds 1.5, while '#' means the value is below 0.5.

4. Discussion

YABBY is a specific transcription factor in seed plants that has been widely studied in *A. thaliana*. It plays an important role in the development of the leaves and floral organs. Through bioinformatic analysis of MiYABBYs, we found that mango possesses more YABBY members than *Arabidopsis* and can be divided into just three groups (YAB5, YAB3, and CRC), whereas *Averrhoa carambola* has five groups and eight members [26]. In mango, most members possess seven exons, except for MiYABBY2, which has eight exons. The physicochemical properties prediction results of the MiYABBYs indicated that all members are alkaline hydrophobic proteins, as also reported for *Punica granatum* [27]. The prediction of the motifs, conserved domains, and tertiary structures of the MiYABBYs showed that all members had typical C2C2 and YABBY motifs, and the tertiary structures

were also similar. The C2C2 and YABBY motifs of YABBY transcription factor are conserved in dicotyledonous plants [28].

The evolutionary analysis of mango and *Arabidopsis* divided the MiYABBYs into three groups, namely CRC (MiYABBY2, MiYABBY7), YAB3 (MiYABBY1, MiYABBY3), and YAB5 (MiYABBY4, MiYABBY5, MiYABBY6). According to the current research, CRC and INO are specifically expressed in the nectary, abaxial side of the carpel, and during the process of integument development [29,30], and therefore, these are referred to as reproductive growth *YABBY* genes. YAB2, YAB3, and YAB5 are specifically expressed in the cotyledon leaves and flowers, and these are called vegetative growth *YABBY* genes [31,32]. The expression pattern of the mango *YABBY* genes herein was similar to that of *Arabidopsis YABBY* genes [4,33]. The expression level of MiYABBY1 in the YAB3 group and MiYABBY (MiYABBY4, MiYABBY5, MiYABBY6) in the YAB5 group, which are related to vegetative growth, were up-regulated in the mango leaves. However, MiYABBY2 and MiYABBY7 of the ORC group, which are related to reproductive growth, were down-regulated in the mango leaves.

In mango, *C. gloeosporioides* and *X. campestris* pv. *mangiferaeindicae* are significant pathogens. We analyzed the *MiYABBY* genes expression levels during infection of the leaves with *C. gloeosporioides* and *X. campestris* pv. *mangiferaeindicae* at 0–72 h. The *MiYABBY* genes responded negatively to *X. campestris* pv. *mangiferaeindicae* infection, especially *MiYABBY7*. Meanwhile, *MiYABBY7* was significantly down-regulated under MeJA and SA treatment at 0–72 h. Salicylic acid and MeJA play important roles in plant stress and disease resistance, and SA in particular minimizes heat and photooxidative stress in leaves [34]. Moreover, JA inhibits fungal infection during storage [14,19,35,36]. This implies that MiYABBY7 negatively regulates disease resistance through the modulation of the immune response by MeJA and SA in mango. *YABBY* genes have been demonstrated to be related to drought- and salt-stress [12,18]. In this study, the responses of MiYABBY to drought- and salt-stress differed. This is first report on the mango *YABBY* gene family at the genome-wide level. These results improve our understanding of the biological functions and molecular mechanisms of *YABBY* genes.

5. Conclusions

In this study, a total of seven YABBY transcription factor family genes were identified in mango, which were divided into three groups of CRC, YAB5, and YAB3. The seven YABBY family members possessed both typical C2C2 and YABBY domains. Quantitative real-time PCR showed that the transcription levels of the *MiYABBYs* were significantly different under biotic and abiotic stresses. The transcription level of *MiYABBY7* was significantly down-regulated at 0–72 h after *Xanthomonas campestris* pv. *mangiferaeindicae* infection and methyl jasmonate and salicylic acid stresses. The *MiYABBY1* transcription level was significantly down-regulated at 0–72 h after *Colletotrichum gloeosporioides* infection. *MiYABBYs* were expressed specifically in different leaves and fruit, and MiYABBY6 was significantly up-regulated during leaf and fruit development. This is first report on the mango *YABBY* gene family at the genome-wide level. These results will be beneficial for understanding the biological functions and molecular mechanisms of *YABBY* genes, to further explore the function of MiYABBY6 as a gene for resistance to pathogens and response to abiotic stresses.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14100861/s1, Figure S1: The melting curve plot of the *MiYABBY* gene family; Table S1: Prediction of physicochemical properties of YABBYs family in mango; Table S2 qRT-PCR primer sequences.

Author Contributions: H.Z. and A.G. conceived the study and participated in its design and coordination; Y.X. and R.L. did most experimental work and wrote the manuscript; R.S., N.Y., and J.P. did experimental work and database analysis; H.Z. supervised this project. All authors have read and agreed to the published version of the manuscript.

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