

Article

Overexpression of MnERF/ABR1 from Mulberry Enhances Resistance to *Botrytis cinerea*

Hui An ^{1,2,†}, Hongshun Wu ^{3,†}, Lin Yu ³, Zichen Lu ³, Wenzhi Zhu ³, Youchao Xin ^{3,*}  and Xiaodong Li ^{1,2,*} ¹ Guangxi Key Laboratory of Sericulture Ecology and Applied Intelligent Technology, Hechi University, Hechi 546300, China² Guangxi Collaborative Innovation Center of Modern Sericulture Silk, School of Chemistry and Bioengineering, Hechi University, Hechi 546300, China³ College of Forestry, Shandong Agricultural University, Tai'an 271018, China

* Correspondence: ycxin@sdaa.edu.cn (Y.X.); lxdong_627@163.com (X.L.)

† These authors contributed equally to this work.

Abstract

Ethylene response factors (ERFs) are transcription factors specific to plants that serve critical functions in various aspects of plant growth, development, and responses to environmental stressors. Despite the significance of these factors, the specific mechanisms by which mulberry ERFs interact with and respond to the pathogenic fungus *Botrytis cinerea* have not yet been fully elucidated. This study focuses on the isolation of a particular ERF transcription factor, known as MnERF/ABR1, which is localized in the cell nucleus and is derived from mulberry. Overexpression of *MnERF/ABR1* in *Arabidopsis* or transient overexpression of *MnERF/ABR1* in mulberry leaves can significantly enhance its resistance to *B. cinerea*. Our results suggest that empty vector control (CK) has higher levels of malondialdehyde (MDA), a marker of oxidative stress, compared to overexpression lines. In contrast, the catalase (CAT) activity of overexpression lines was higher than that of CK plants. Furthermore, staining with 3,3'-diaminobenzidine (DAB) and nitro blue tetrazolium (NBT) indicated that the resistance to *B. cinerea* was more pronounced in plants with overexpression than in those of the CK plants. These findings uncovered the molecular regulatory pathway involving MnERF/ABR1 in response to *B. cinerea* and established a basis for the development of disease-resistant mulberry varieties through genome editing.

Keywords: mulberry; MnERF/ABR1; *Botrytis cinerea*; resistance

1. Introduction

The mulberry tree (*Morus* spp.) consists of deciduous trees and shrubs of the Moraceae family. As the primary source of nutrition for *Bombyx mori*, mulberry has been cultivated in China for over 5000 years and has significantly influenced human civilization along the Silk Road. The medicinal value of mulberry fruit, leaves, and roots further increases its economic importance [1,2]. Mulberry is believed to have originated in the Himalayan foothills and has since spread across nearly all regions of the world, with the exception of Antarctica [3]. Its remarkable ability to adapt to various environmental conditions further enhances its significance in ecological conservation [4,5]. However, mulberry cultivation is frequently threatened by a variety of biotic stresses, particularly fungal, bacterial, and viral pathogens, which can severely reduce yield and quality [6]. Understanding the mechanisms underlying mulberry–pathogen interactions is therefore essential for improving disease resistance and sustaining production.



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To combat pathogen invasion, plants have evolved two major immune systems [7]. The first consists of transmembrane pattern recognition receptors (PRRs), which detect pathogen-associated molecular patterns (PAMPs). Recognition of microbial-associated molecular patterns (MAMPs) by PRRs activates a defense response known as PAMP-triggered immunity (PTI) [8]. The second system involves the activation of specific resistance genes that encode plant resistance proteins, which recognize pathogen effectors and trigger a stronger defense response known as effector-triggered immunity (ETI) [8]. In these immune processes, transcription factors play essential regulatory roles, with major families including bHLH, bZIP, MYB, NAC, WRKY, and AP2/ERF [9].

The apetala 2/ethylene response factor (AP2/ERF) transcription factors are one of the largest families of transcription factors involved in plant transcriptional regulation, with a highly conserved AP2 domain [10,11]. ERF proteins with ERF DNA-binding domains bind to conserved cis-elements to form GCC boxes or DRE motifs that mediate developmental changes or stress responses [12–15]. The ethylene signaling pathway plays an important role in plant response to biological stress, and many resistance genes are induced and regulated by this signaling pathway [16–20]. In Arabidopsis, fungal infection significantly induces the expression of AP2/ERF transcription factors such as AtERF1, AtERF6, AtERF104, and AtORA59, and overexpression of these genes enhances resistance to *B. cinerea* and *Alternaria alternata* [16,17]. The overexpression of *AtERF1* can promote the expression of *PDF1.2* in plants, thereby improving the resistance of overexpressed lines [21]. The overexpression of *GmERF5* enhanced the expression of the PR gene, which enhanced the resistance of soybean to *Phytophthora sojae* [22]. AtERF72 enhances plant resistance to *B. cinerea* by modulating the expression of the Camalexin biosynthesis gene [19].

In this study, the *ERF/ABR1* gene was identified and cloned from mulberry. Subsequently, through Arabidopsis overexpression and mulberry transient overexpression experiments, we elucidated the function of this gene, and its response to *B. cinerea* disease was mainly studied. This study has improved the understanding of the molecular mechanism of resistance to *B. cinerea* in mulberry and may help to discover new resistance genes in mulberry. In addition, this work identifies new genetic resources that can be used in mulberry-breeding programs to improve disease resistance.

2. Materials and Methods

2.1. Plant Material, Fungus and Gene Selection

Mulberry seedlings were cultured in a growth chamber with a light/dark cycle of 27 °C (daytime)/23 °C (nighttime). Wild-type *Arabidopsis thaliana* (COL-0) was cultured at 22 °C with a light/dark cycle of 16/8 h. *B. cinerea* (MM1) was cultured on potato dextrose agar (PDA) plates under standard laboratory conditions (22–25 °C in the dark) [23]. Based on previously available RNA-Seq data [24], *MnERF/ABR1* was selected for subsequent experiments due to its high expression of *B. cinerea* infection. Plant inoculation treatments were divided into two groups and carried out for three days: one group was inoculated with agar blocks free of *B. cinerea* (Mock group), and the other group was inoculated with agar blocks containing *Botrytis cinerea* (Inoculated group).

2.2. Phylogenetic Analysis

MnERF/ABR1 protein sequence was retrieved from mulberry database (<https://morus.swu.edu.cn>, accessed on 7 July 2026) [25]. ERF/ABR1 protein sequences of different species were extracted from National Center for Biotechnology Information database (<https://www.ncbi.nlm.nih.gov/>, accessed on 25 October 2025). Then, MUSCLE v5 [26] was used to align the conserved domains of ERF/ABR1 in mulberry and other species, and

phylogenetic trees of ERF/ABR1 members were constructed using maximum likelihood method with 1000 bootstrap replicates.

2.3. RNA Extraction and Quantitative PCR

Total RNA was isolated from 1 g samples using the RNeasy Pure Plant Kit (Qiagen, Beijing, China) according to the manufacturer's instructions. The first strand cDNA was generated using the PrimeScript™ RT Kit (Takara, Kusatsu, Japan) according to the manufacturer's instructions. On the QuantStudio® 3 real-time fluorescent quantitative PCR instrument (Thermo, Waltham, MA, USA), we used SYBR® Premix Ex Taq™ (Takara, Kusatsu, Japan) with *MnActin* as the reference gene, and followed the manufacturer's recommendation for all reagents. Three days after *B. cinerea* inoculation, qRT-PCR experiments were performed with three biological replicates and three technical replicates. Relative gene expression was calculated by $2^{-\Delta\Delta CT}$ [27]. qRT-PCR primers were shown in Table S1.

2.4. Generation of Transgenic Arabidopsis

The *MnERF/ABR1* gene was linked to the *KpnI* and *EcoRI* restriction sites. This resulted in the development of an expression vector known as pLGNL-*MnERF/ABR1*. This vector was used to transform *Agrobacterium* strain GV3101. Transgenic Arabidopsis plants were produced using a flower-soaking dip [28]. T3 transgenic lines were selected on half-strength Murashige and Skoog medium that was supplemented with kanamycin. The expression levels of the T3 transgenic lines were evaluated through qRT-PCR and were employed in further experiments.

2.5. GUS Staining Analysis

The 7-day-old Arabidopsis seedlings and mulberry leaves were treated with histochemical GUS staining. After soaking in vacuum for 15 min, the samples were incubated in the dyeing solution at 37 °C overnight. The tissue was decolorized with 70% ethanol to completely remove the chlorophyll and photographed with a stereo microscope.

2.6. Transient Overexpression of *MnERF/ABR1*

Agrobacterium strain GV3101 harboring either the pLGNL-*MnERF/ABR1* or pLGNL constructs was prepared using a conversion solution consisting of 1/2 MS, 5% sucrose, 200 µM acetosyringone, 0.05% Tween-20, and adjusted to a pH of 5.6, achieving a final optical density (OD₆₀₀) of 0.5. Mulberry seedlings, 15 days old, were immersed in the GV3101 infiltration solution containing either pLGNL-*MnERF/ABR1* or pLGNL and then subjected to vacuum at room temperature for a duration of 20 min.

2.7. Biochemical Analysis

The concentrations of malondialdehyde (MDA) and catalase (CAT) were measured using a kit from Solarbio (Beijing, China), following the guidelines provided by the manufacturer. Each treatment was conducted in triplicate. The levels of superoxide radical (O_2^-) and hydrogen peroxide (H_2O_2) present in the leaves were assessed using nitro blue tetrazolium (NBT) and 3,3'-diaminobenzidine (DAB) staining techniques.

2.8. Transactivation Assay

The coding sequence (CDS) of *MnERF/ABR1* was inserted into pGBKT7 vector and introduced into yeast strain AH109 according to our previous protocol [29]. The empty vector was used as control. The growth was detected on SD/-Trp/-His/-Ade and SD/-Trp/-His/-Ade/X-α-Gal medium, respectively.

2.9. Subcellular Localization

The *MnERF/ABR1*-GFP overexpression vector was constructed by integrating the full-length encoding sequence of *MnERF/ABR1* with the termination codon removed into pCambia3300 vector containing GFP tags. GFP- and mCherry-tagged proteins were expressed in *N. benthamiana* leaves through *Agrobacterium*-mediated gene expression. Subsequently, a solution comprising *MnERF/ABR1*-GFP along with a suitable buffer was injected into the leaves of 4-week-old tobacco plants using a syringe. The injection buffer consisted of 10 mM MES, 10 mM MgCl₂, and 200 µM acetosyringone (AS), with the pH precisely adjusted to 5.7. After the injection, the treated tobacco plants were initially kept in the dark for a duration of 24 h to facilitate the process. Following this dark phase, the plants were moved to normal light conditions for the following 72 h. The emission of fluorescence from the leaves was then examined using confocal laser microscopy, allowing for detailed observation of the introduced fluorescence marker.

2.10. Statistical Analysis

Data were analyzed using GraphPad Prism 8 (version 8.4.3). The differences were assessed by a two-tailed *t*-test. Data are expressed as mean ± standard deviation (SD).

3. Results

3.1. Phylogenetic Analysis of *MnERF/ABR1*

Multiple alignments were performed with other plant ERF/ABR1 protein sequences retrieved from the NCBI database. Phylogenetic and molecular evolutionary analyses of ERF/ABR1 proteins between different species were performed using MEGA 7 (Figure 1). As shown in the figure, ERF/ABR1 in mulberry trees is more closely related to ERF/ABR1 in the *Humulus lupulus* and *Cannabis sativa*, but is less related to ERF/ABR1 in *Morella rubra*.

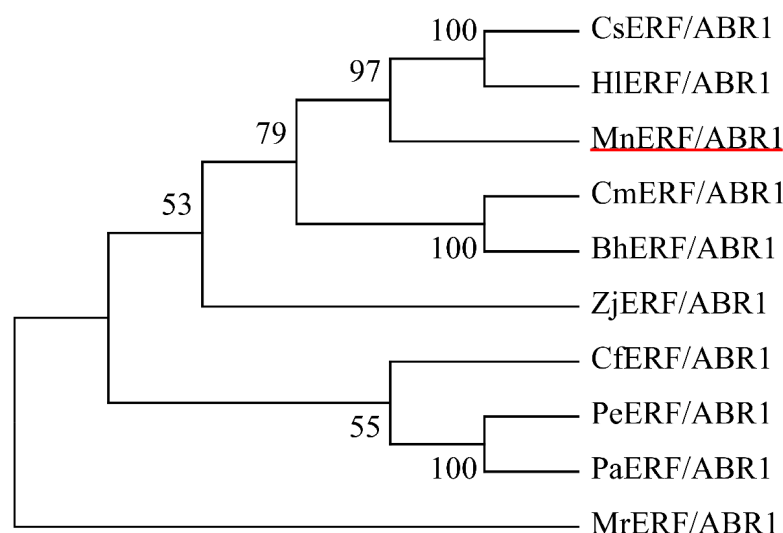


Figure 1. A phylogenetic tree illustrating the ERF/ABR1 from mulberry and other plant species. The numbers indicate the confidence percentages for the relationships depicted. The accession numbers for these sequences, which were sourced from GenBank, are as follows: CsERF/ABR1 (*C. sativa*, XP_030496366.2); HIERF/ABR1 (*H. lupulus*, XP_062097225.1); MnERF/ABR1 (*Morus notabilis*, XP_024021449.1); CmERF/ABR1 (*Cucurbita moschata*, XP_022950524.1); BhERF/ABR1 (*Benincasa hispida*, XP_038883082.1); ZjERF/ABR1 (*Ziziphus jujuba*, XP_015890996.3); CfERF/ABR1 (*Cornus florida*, XP_059624789.1); PeERF/ABR1 (*Populus euphratica*, XP_011021969.1); PaERF/ABR1 (*Populus alba*, XP_034901430.1); and MrERF/ABR1 (*M. rubra*, KAB1210350.1). Red underlines indicate the mulberry *MnERF/ABR1*.

3.2. *B. cinerea* Induced the Expression of *MnERF/ABR1*

qRT-PCR was used to analyze the expression of *MnERF/ABR1* in the infected *B. cinerea* of mulberry seedlings (Figure 2). Compared with the simulated treatment for 3 days, the expression level of *MnERF/ABR1* after inoculation for 3 days was significantly increased, which was consistent with our previous transcriptomic data. This indicates that the *MnERF/ABR1* gene could be significant in mulberry's resistance to *B. cinerea*.

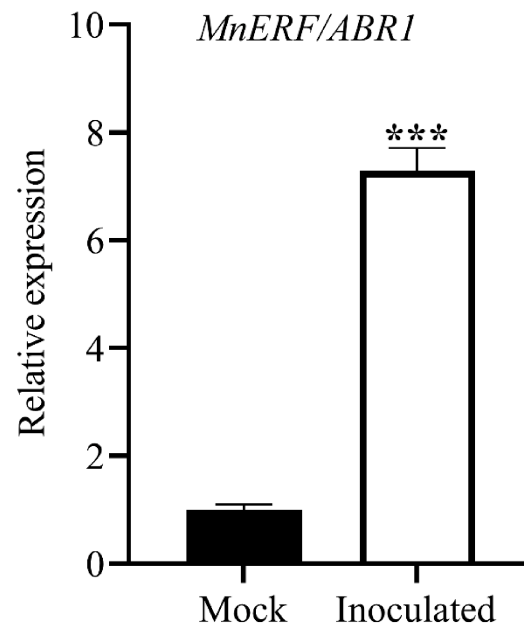


Figure 2. The expression levels of *MnERF/ABR1* in mulberry leaves were compared between the mock treatment (Mock) and after inoculation with *B. cinerea* (Inoculated). The values shown represent averages, with the standard error (SE) indicated as error bars. This data is based on three independent biological samples, each consisting of three technical replicates (** $p < 0.001$; two-tailed t -test). Mock refers to agar blocks free of *B. cinerea*; Inoculated denotes agar blocks that were inoculated with *B. cinerea*.

3.3. *MnERF/ABR1* Acts as an Activating Transcription Factor

To investigate whether *MnERF/ABR1* is a typical transcription factor, its transcriptional activity was measured. After fusing *MnERF/ABR1* with the GAL4 DNA-binding domain in the yeast expression vector pGBKT7, it was found that the yeast grew vigorously, whereas yeast transformed with the empty pGBKT7 vector showed inhibited growth (Figure 3A). These results indicate that *MnERF/ABR1* has transcriptional activation activity. At the same time, a fusion protein of *MnERF/ABR1* and green fluorescent protein (GFP) was constructed and expressed, and the subcellular localization of *MnERF/ABR1* was explored (Figure 3B). The fluorescence signal showed that *MnERF/ABR1* is a nuclear-localized protein.

3.4. Heterologous Expression of *MnERF/ABR1*

In order to further explore the function of the *MnERF/ABR1* gene in plant disease resistance, we overexpressed the *MnERF/ABR1* gene in Arabidopsis. Under the control of the 35S promoter of *Cauliflower mosaic virus*, the cDNA of *MnERF/ABR1* was transferred into Arabidopsis and T3 transgenic Arabidopsis lines were screened. Then, the positive transgenic plants were identified by GUS staining. After GUS staining, positive plants appeared blue (Figure 4A). Meanwhile, the gene expression of *MnERF/ABR1* was detected by qRT-PCR (Figure 4B), and the gene expression of *MnERF/ABR1* in positive plants was

significantly enhanced. These results indicated that the *MnERF/ABR1* gene was successfully overexpressed in Arabidopsis.

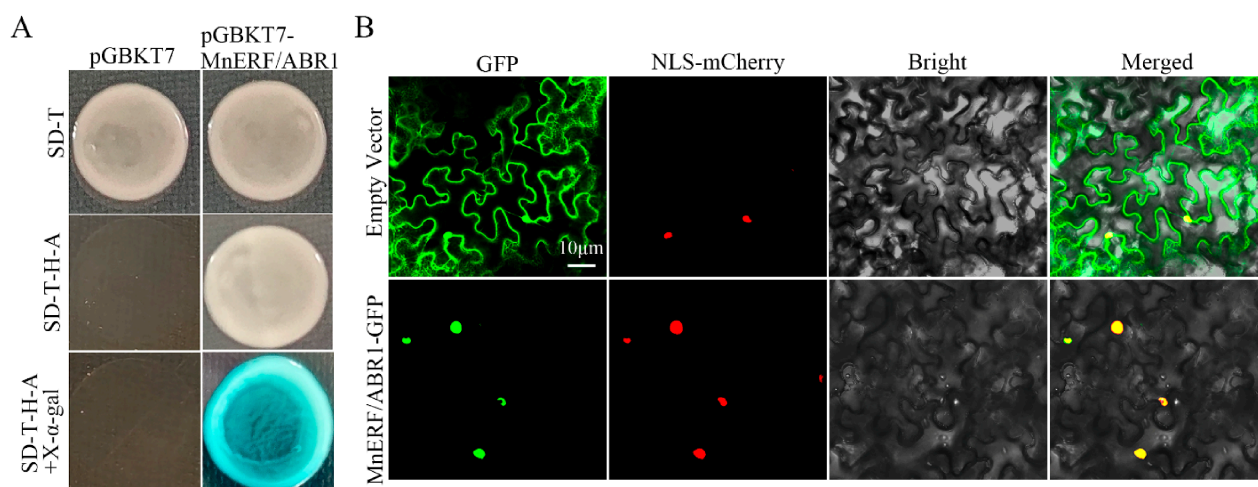


Figure 3. Transcriptional activation assay and subcellular localization of MnERF/ABR1. **(A)** Assessment of the transcriptional activity of MnERF/ABR1. The negative control employed an empty vector, pGBKT7. Growth conditions for yeast transformed with the empty vector and those expressing MnERF/ABR1 were evaluated across different media. **(B)** The constructs 35S::GFP and MnERF/ABR1-GFP were co-transformed into tobacco leaves. The fluorescence of GFP was observed using a laser confocal scanning microscope. NLS-mCherry: a nuclear marker.

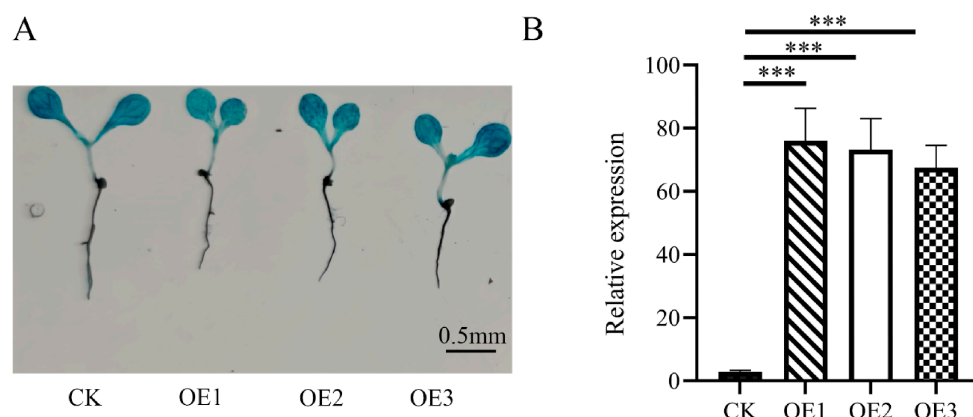


Figure 4. Identification of transgenic Arabidopsis. **(A)** GUS staining results for transgenic Arabidopsis. **(B)** Relative expression levels of *MnERF/ABR1* in transgenic Arabidopsis were assessed. CK refers to empty vector control Arabidopsis, and OE indicates Arabidopsis containing the *MnERF/ABR1* transgene. The values represent averages, with standard error (SE) shown as error bars. This data is derived from three independent biological samples, each with three technical replicates (** $p < 0.001$; two-tailed t -test).

3.5. Overexpression of MnERF/ABR1 Enhances Resistance to *B. cinerea*

To test the resistance of *MnERF/ABR1* overexpressed lines to *B. cinerea*, we inoculated Arabidopsis leaves with agar blocks containing the mycelia of *B. cinerea* (Figure 5A). After treatment for 36 h, the leaves of control plants showed large areas of disease spots, while the leaves of *MnERF/ABR1* overexpression plants only showed small areas of disease spots. Measurement analysis showed that overexpression of *MnERF/ABR1* significantly inhibited the infection of *B. cinerea* (Figure 5B). Simultaneously, the accumulation of reactive oxygen species (ROS) reflects the plant's stress response. To explore this further, staining with DAB and NBT was employed to quantify the levels of hydrogen peroxide (H_2O_2) and superoxide (O_2^-) in the leaves of Arabidopsis, respectively (Figure 5C,D). The results

showed that the leaves of *Arabidopsis* overexpressing *MnERF/ABR1* had only a small area of dark brown patches after DAB staining, indicating less H_2O_2 accumulation. In contrast, CK *Arabidopsis* leaves showed large areas of dark brown patches, indicating higher H_2O_2 accumulation. Similarly, NBT staining showed a small area of dark blue patches in the leaves of *Arabidopsis* overexpressing *MnERF/ABR1*, indicating less O_2^- content, while a large area of dark blue patches in the leaves of CK *Arabidopsis* indicated more O_2^- content.

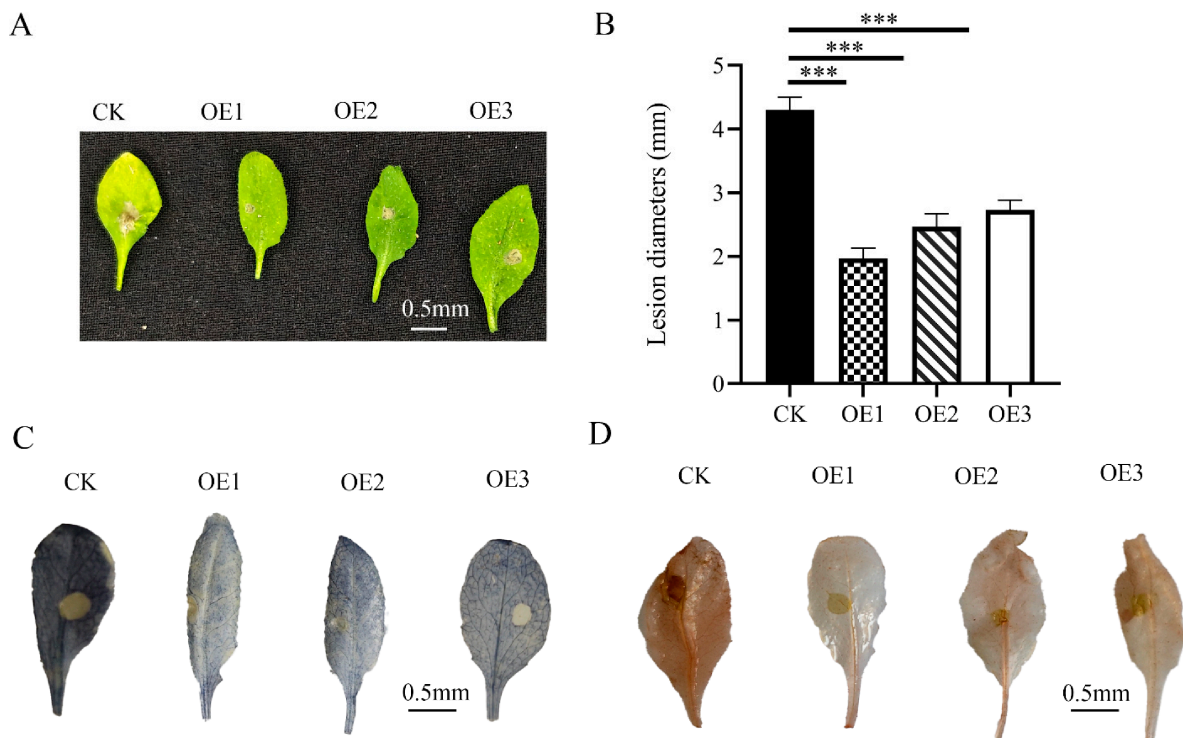


Figure 5. Assessment of transgenic *Arabidopsis* resistance to *B. cinerea*. **(A)** Leaf morphology of *Arabidopsis* observed 36 h post-infection with *B. cinerea*. **(B)** Quantitative evaluation of resistance in transgenic *Arabidopsis*. **(C)** NBT staining was employed to illustrate O_2^- levels. **(D)** DAB staining was used to visualize H_2O_2 levels. Values represent averages, with standard error (SE) indicated as error bars. This data is based on three independent biological samples, each comprising three technical replicates (** $p < 0.001$; two-tailed t -test).

3.6. Biochemical Index Determination

The physiological changes of overexpressed *MnERF/ABR1* *Arabidopsis* and CK *Arabidopsis* were analyzed by detecting MDA content and CAT activity (Figure 6). Under normal conditions, there was no significant difference in MDA content and CAT activity between *Arabidopsis* overexpressing *MnERF/ABR1* and CK *Arabidopsis*. Following infection with *B. cinerea*, the activity of CAT in *Arabidopsis* plants overexpressing *MnERF/ABR1* was found to be markedly elevated compared to that of the CK *Arabidopsis* (Figure 6A). In contrast, the MDA levels in the CK *Arabidopsis* were significantly greater than those in the *Arabidopsis* lines overexpressing *MnERF/ABR1* (Figure 6B). These results confirmed that CK *Arabidopsis* showed more serious plasma membrane damage after *B. cinerea* infection than *Arabidopsis* overexpressing *MnERF/ABR1*. Overexpression of the *MnERF/ABR1* gene significantly enhanced the ability of plants to resist oxidative damage.

3.7. Transient Overexpression of *MnERF/ABR1* Increased Resistance of Mulberry

In order to further understand the role of *MnERF/ABR1* in mulberry disease resistance, transient overexpression of *MnERF/ABR1* was performed in mulberry (Figure 7). Histochemical staining showed that transient overexpression plants in mulberry leaves

showed strong GUS staining (Figure 7A). Meanwhile, the gene expression of *MnERF/ABR1* was detected by qRT-PCR, and the gene expression of *MnERF/ABR1* in positive plants was significantly enhanced (Figure 7B). These results indicated that *MnERF/ABR1* demonstrated successful transient overexpression in mulberry leaves. Compared with the control plants, the transient overexpression of *MnERF/ABR1* significantly increased the resistance to *B. cinerea* (Figure 7C). After infection with *B. cinerea*, in plants with transient overexpression of the *MnERF/ABR1* gene, the activity of CAT significantly increased (Figure 7D), while the content of MDA significantly decreased (Figure 7E). These results are consistent with those previously observed in *Arabidopsis* with overexpression of *MnERF/ABR1*.

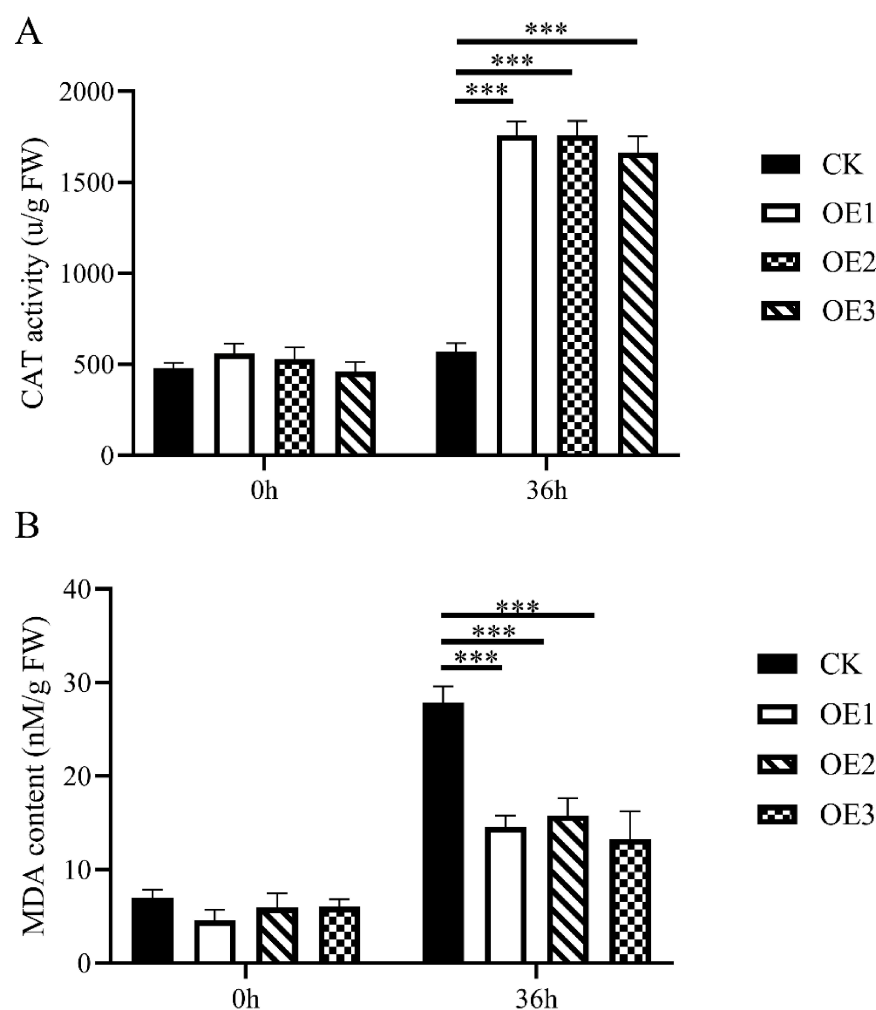


Figure 6. Physicochemical indexes before and after *B. cinerea* inoculation. (A) CAT activity, and (B) MDA content. The values represent averages, with standard error (SE) shown as error bars. This data is derived from three independent biological samples, each consisting of three technical replicates (***) $p < 0.001$; two-tailed t -test).

3.8. Overexpression of *MnERF/ABR1* Enhanced the Expression of *AtPR1* in Transgenic Plants

The *PR1* gene is a defense-related marker gene in plants. After infection by *B. cinerea*, the expression level of *AtPR1* in *Arabidopsis* plants overexpressing *MnERF/ABR1* was significantly increased compared with that of CK *Arabidopsis* (Figure 8). There was no difference in *PR1* gene expression between *Arabidopsis* overexpressing *MnERF/ABR1* gene and CK *Arabidopsis* before infection by *B. cinerea*. These results suggest that overexpression of the *MnERF/ABR1* gene may protect against *B. cinerea* infection by enhancing the expression of the resistance-related gene *AtPR1*.

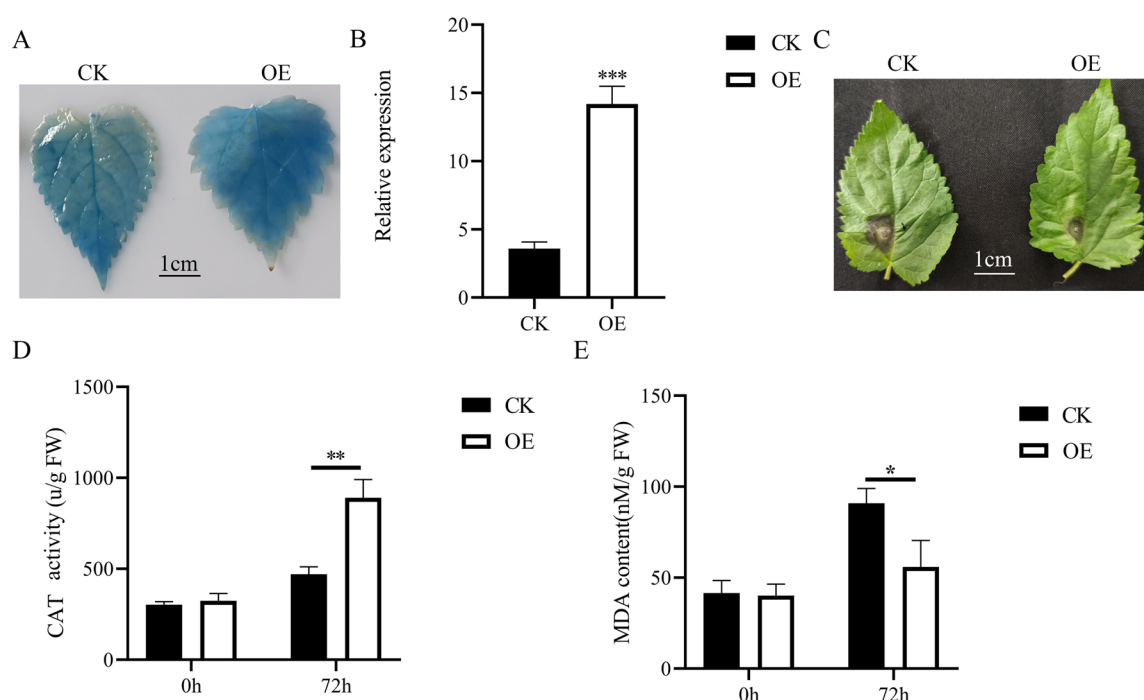


Figure 7. Analysis of *MnERF/ABR1* resistance to *B. cinerea* through transient expression in mulberry. (A) GUS staining results for CK plants and those with transient overexpression after 72 h in mulberry leaves. CK refers to the empty vector. (B) Relative expression levels of *MnERF/ABR1* in transgenic mulberry were assessed. (C) Photographs of mulberry leaves taken 72 h post-infection with *B. cinerea*. (D) CAT activity, and (E) MDA content measurements are presented. The values shown represent averages, with standard error (SE) indicated by error bars. Data are based on three independent biological samples, each consisting of three technical replicates (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$; two-tailed t -test).

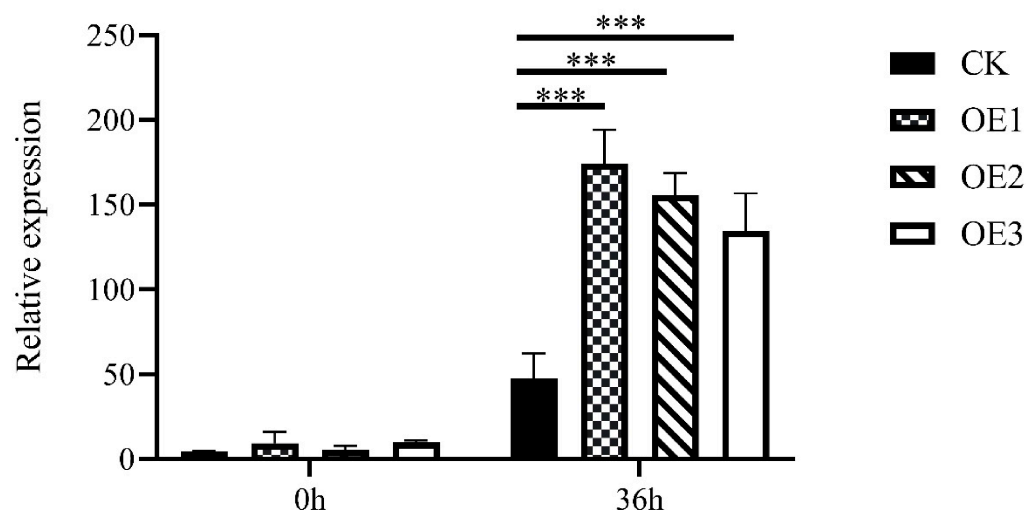


Figure 8. Relative expression of *AtPR1* in leaves of Arabidopsis CK and *MnERF/ABR1* transgenic (OE) plants before and after inoculation with *B. cinerea*. The values represent averages, with standard error (SE) indicated by error bars. This data is based on three independent biological samples, each comprising three technical replicates (***) $p < 0.001$; two-tailed t -test).

4. Discussion

The AP2/ERF transcription factor family plays essential roles in plant growth, development, and stress responses, particularly in regulating resistance to both biotic and abiotic stresses [30]. However, functional characterization of ERF genes in mulberry remains lim-

ited compared with model plants. In this study, we identified and characterized a mulberry *ERF* gene, *MnERF/ABR1*, and demonstrated its positive role in resistance to *B. cinerea*.

Phylogenetic analysis indicated that *MnERF/ABR1* is closely related to *ABR1*-like proteins from other plant species, suggesting evolutionary conservation of its function (Figure 1). Consistently, *MnERF/ABR1* was significantly induced after *B. cinerea* infection (Figure 2), indicating its involvement in pathogen-responsive signaling pathways. Similar induction patterns have been reported for other *ERF* genes associated with fungal resistance [16,19], supporting the idea that *ERF* family members are key components of plant defense against necrotrophic pathogens.

Functional analysis in both *Arabidopsis* and mulberry showed that *MnERF/ABR1* overexpression significantly enhanced resistance to *B. cinerea*. Overexpression lines exhibited reduced disease symptoms compared with control plants, indicating a conserved positive regulatory role. These findings are consistent with previous reports showing that *ERF* transcription factors such as *AtERF1* and *GmERF5* improve resistance to *B. cinerea* and other necrotrophic fungi [17,22].

Physiological analyses further revealed that *MnERF/ABR1* improves resistance by enhancing antioxidant capacity. Overexpression lines showed decreased MDA content and reduced accumulation of reactive oxygen species (H_2O_2 and O_2^-), as well as increased CAT activity. These results suggest that *MnERF/ABR1* helps maintain redox homeostasis and reduces oxidative damage during pathogen infection, which is consistent with previous studies highlighting the importance of antioxidant systems in plant defense [31,32].

In addition, *MnERF/ABR1* overexpression led to increased expression of the defense-related gene *AtPR1*, a marker of the salicylic acid signaling pathway. This suggests that *MnERF/ABR1* may participate in the regulation of immune-related gene expression through SA-associated defense responses. Similar regulatory effects of *ERF* proteins on *PR* gene expression have been reported in other plant systems [33–35].

Taking these findings together, *MnERF/ABR1* functions as a positive regulator of resistance to *B. cinerea* by modulating antioxidant defenses and activating defense-related gene expression. This study provides new evidence for the role of *ERF* transcription factors in mulberry immunity and identifies *MnERF/ABR1* as a potential candidate gene for improving disease resistance through molecular breeding.

5. Conclusions

B. cinerea poses a significant threat to mulberry, leading to increasing yield losses each year. As a result, the development of disease-resistant mulberry varieties has become an urgent need. Identifying candidate genes that are responsible for disease resistance, particularly against the pathogenic fungus *B. cinerea*, is crucial for the breeding of resistant plant varieties. This study focused on selecting and screening the *MnERF/ABR1* gene derived from mulberry trees to investigate its potential role in providing protection against *B. cinerea* in both mulberry and *Arabidopsis* species. The results showed that overexpressing the *MnERF/ABR1* gene in both *Arabidopsis* and mulberry plants serves as a positive regulator of disease resistance, indicating its significant impact on the plant's ability to fend off this specific pathogen. To validate the findings, we employed qRT-PCR and DAB staining techniques, which collectively confirmed that the *MnERF/ABR1* gene is instrumental in boosting plant resistance to *B. cinerea*. The data strongly support the conclusion that *MnERF/ABR1* enhances the defensive mechanisms of the plants against this disease-causing agent. Consequently, these findings provide a solid foundation for utilizing *MnERF/ABR1* in future breeding programs aimed at developing mulberry varieties that exhibit improved resistance to diseases, thus advancing agricultural practices and enhancing crop resilience.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12070844/s1>, Table S1. Primers used in this study.

Author Contributions: Conceptualization, X.L.; methodology, Z.L. and X.L.; formal analysis, W.Z.; writing—original draft preparation, H.A.; validation, H.W.; investigation, L.Y.; data curation, Z.L. and W.Z.; writing—review and editing, Y.X.; visualization, H.A. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The original contributions presented in this study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Conflicts of Interest: The authors declare no conflicts of interest.

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