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Research Article

Exogenous methyl jasmonate promotes susceptibility of strawberry crown rot caused by *Colletotrichum siamense* through down-regulating defense gene and flavonoids biosynthesis

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Abstract

Colletotrichum siamense, a hemibiotrophic pathogen which caused serious strawberry crown rot. Jasmonic acid (JA) is shown to reduce or promote pathogen infection, but the effect of JA on strawberry crown rot is still unknown. Identified the effect and mechanism of JA on strawberry crown rot is the base of resistance induction and genetic improvement for strawberry crown rot. Exogenous methyl jasmonate (MeJA) was tested for its effect for *C. siamense* causing strawberry crown rot in this study. MeJA significantly increased lesion width and hypha density caused by *C. siamense* infection in crown. MeJA reprogrammed crown transcriptome, and it induced 1642 significantly differentially expressed genes. In addition, most differentially expressed genes were most enriched in 'metabolite biosynthetic processes' and 'response to stimulus' by COG enrichment and KOG function classification. Further, KEGG function enrichment showed 'flavonoid biosynthesis' vested in 'metabolite biosynthetic processes', 'plant-pathogen interaction' vested in 'response to stimulus' were suppressed by MeJA. qRT-PCR showed expressions of defense genes like heat shock protein, MYB and cellulose synthase A catalytic subunit 8 and structural genes in 'flavonoid biosynthesis' were all suppressed. Confirmed with gene expressions, MeJA decreased total flavonoid and down-regulated activities of chalcone synthase and chalcone isomerase. Thus, exogenous MeJA enhanced *C. siamense* causing crown rot in strawberry by down-regulating defense genes and flavonoids biosynthesis.

Keywords: 'Benihoppe' strawberry; enzyme activity; metabolite; resistance; transcriptome

Introduction

Strawberry (*Fragaria* × *ananassa*) is a popular berry worldwide, and crown rot caused by *Colletotrichum* (*C. gloeosporioides*, *C. siamense*, *C. fragariae* or *C. acutatum*) exhibits a sudden wilt of the entire strawberry plant, threaten its production in nearly all main production area (Anciro *et al*., 2018). To date, there is no

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cultivar that exhibits complete resistance to crown rot caused by *Colletotrichum* (Anciro *et al*., 2018; Miller-Butler, 2019). Understanding the physiological process associated with resistance induction for cultivated strawberry responding to *C. siamense* infection is the foundation of disease management.

Jasmonic acid (JA) is involved in the defense against necrotrophic pathogens, preventing plant cell death and inducing defense responses to restrict further pathogen infection, normally (Ghorbel *et al*., 2021). The exogenous application of methyl jasmonate (MeJA) or other JA functional analogues is shown to reduce the severity of infection by necrotrophic fungi. Previous study showed MeJA caused efficient reduction of disease development by necrotrophic *Alternaria brassicicola* (agent of black spot disease in rape, cabbage and other plants) and *Botrytis cinerea* (agent of gray mold in strawberry, tomato and other plants) infection (Thomma *et al*., 2000). Besides protecting plant from necrotrophic pathogens, JA signaling also plays an important role in mediating plant defense against some biotrophic or hemibiotrophic pathogens (Yan and Xie, 2015; Zalewski *et al*., 2019). Several researches showed exogenous application of MeJA up-regulated some defense genes and results in efficient reduction of disease development (Desmond *et al*., 2005; Wasternack, 2007). However, contradictory evidences have been published regarding the role of JA in powdery mildew (*Bgt*) resistance in wheat. Duan *et al*. (2014) reported that exogenous MeJA significantly enhanced *Bgt* resistance in susceptible wheat varieties, while Xiang *et al*. (2011) found that MeJA application did not induce resistance to *Bgt* in wheat. Recently, study showed application of JA biosynthesis inhibitor diethyldithiocarbamate could induce high resistance to *Bgt* in wheat (Xiang *et al*. 2020).

Strawberry crown rot caused by *C. siamense* is a serious disease of strawberry in China (Han *et al*., 2014). It contains both biotrophic and necrotrophic processes in pathogenesis of *C. siamense*. Although transcriptional characterizations of genes related to JA biosynthesis and signal transduction were found to regulate the resistance of strawberry to anthracnose caused by *C. gloeosporioides* (He *et al*., 2019; Fang *et al*., 2021), the effect and related genes involved for exogenous JA on strawberry responding for *C. siamense* crown infection are largely unknown. The aims of this work were to investigate exogenous MeJA on strawberry resistance to *C. siamense* using lesion size and pathological analysis. In addition, the gene expression profiles were studied by transcriptome to identify molecular response induced by exogenous MeJA.

Materials and Methods

Materials and experiment design

The aseptic strawberry seedlings (*F.* × *ananassa* Duch 'Benihoppe') were transplanted to the pots with seedling substrates (Pindstrup, 5-20 mm) in a growth chamber (25 °C/15 °C, 16 h light/8 h dark). Seedlings were watered three times a week and fertilized weekly with 30 mL of Hoagland's nutrient solution according to the description of Li *et al*. (2023). The seedlings were prepared for evaluating MeJA effects on strawberry crown rot after three months growth.

This experiment was designed as MeJA and mock pretreatment (distilled water). Seedlings were sprayed with an atomizer until thoroughly wetted with 1 mM MeJA, when are 8 days and 1 day before inoculation, respectively, as described by Desmedt *et al*. (2021). The 10 μL spore suspension of 10^4 conidia·mL^{-1} of *C. siamense* SCR-7 and mock (sterilized water) were squeezed to crowns after once sterilized toothpick stab respectively (Li *et al*., 2023). Samples were taken on 0 day and 2 days after inoculation, respectively. There was a total of four treatment groups, which were 0-day post inoculation with *C. siamense* SCR-7 of MeJA pretreatment (MeJA0DPI) and mock seedlings (Mock0DPI), and 2 days post inoculation with *C. siamense* SCR-7 of MeJA pretreatment (MeJA2DPI) and mock seedlings (Mock2DPI). Ten seedlings were mixed as one replicate and crowns of each replicate were achieved respectively. Each treatment contained six biological

replicates for infection observation, total flavonoids, and chalcone synthase and chalcone isomerase activities measurement. Three biological replicates were used for transcriptome and qRT-PCR analysis.

The infection observation of MeJA and mock pretreatment

The length and width of lesion were measured directly. The method of pathological analysis was according to the description of Shu *et al*. (2022). The 10 μL WGA storage solution and 20 μL PI stock solution were added to 970 μL 0.2% Tween-PBS and mixed thoroughly (Dye preparation). Carnot fixative was used to fix crown samples. The crowns were transferred into 10% KOH solution and the tube was sealed with a parafilm to prevent the tube from collapsing, and then incubated at 85 ℃ for 4 h (Fix). Crowns were washed 4 or 5 times with PBS (Staining pretreatment). Dye solution was added to the centrifuge tube containing blades and filtered 4 times with vacuum filter where each time lasted for 5 min, and each interval was 5 min under normal pressure (Staining). The crowns were washed 2 or 3 times with PBS and sealed with anti-fluorescence quenching to be stored at 4 °C in the dark, and then photographed with a fluorescence microscope (Photographing) (Nikon E400, Melville, NY).

Transcriptome analysis

Total RNA was extracted from the freeze-dried sample using Trizol reagent kit (Invitrogen, Carlsbad, CA, USA) according to the manufacturer's protocol. RNA quality was assessed on an Agilent 2100 Bioanalyzer (Agilent Technologies, Palo Alto, CA, USA) and checked using RNase free agarose gel electrophoresis. The fragments were purified by agarose gel electrophoresis, enriched by PCR amplification to create a cDNA library for each sample, and sequenced using Illumina HiSeq2500. To obtain high-quality clean reads, raw reads from the transcriptome sequencing were filtered by Fastp (Version 0.18.0) as described in Shu *et al*. (2016). The *F.* × *ananassa* 'Camarosa' genome v2.0 was taken as reference genome (Liu *et al*., 2020), and FPKM (fragment per kilobase of transcript per million mapped reads) value was calculated to quantify its expression abundance and variation using StringTie software. The FPKM data were directly used to estimate the differential expression of gene (DEG) between samples. FDR < 0.05 and |log2FC| > 1 were used as thresholds to identify significant DEG. Based on gene expression, pathways were identified by Kyoto Encyclopedia of Genes and Genomes (KEGG) annotations using the method of Shu *et al*. (2022).

qRT-PCR was performed according to the method of Luo *et al*. (2020) on three independent biological samples having two technical replications each. The relative gene expression was calculated using the $2^{-\triangle\triangle Ct}$ method, and *β-actin* was taken as the reference gene.

Measurement of total flavonoids and activities of chalcone synthase and chalcone isomerase

Total flavonoids and activities of chalcone synthase (CHS) and chalcone isomerase (CHI) were measured following the method of Li *et al*. (2023). Enzyme-linked immunosorbent assay kits (TongWei, Shanghai, China) were used for plant CHS and CHI according to the manuals. The flavonoids content was tested by using a flavonoid test kit according to the manual (Solarbio, Beijing, China).

Statistical analyses

Significant differences between treatments were determined by Duncan's Multiple Range Tests at $p = 0.05$ with SAS 8.1 (SAS Institute, Inc., Cary, NC, USA). Different letters indicate statistically significant differences.

Results

Effects of MeJA on C. siamense infection

Results of the lesion and pathological analysis showed *C. siam*ense infected the strawberry seedlings crown at two days post-inoculation with *C. siamense*. MeJA pretreatment showed larger size of lesion (Figure 1A), which significantly increased lesion width (Figure 1B). Consistent with the size of lesion, the density of hypha in MeJA treated crown was higher than that of mock (Figure 1C). The lesion size and pathological analysis suggested MeJA treatment promoted the infection of *C. siam*ense to strawberry crown.

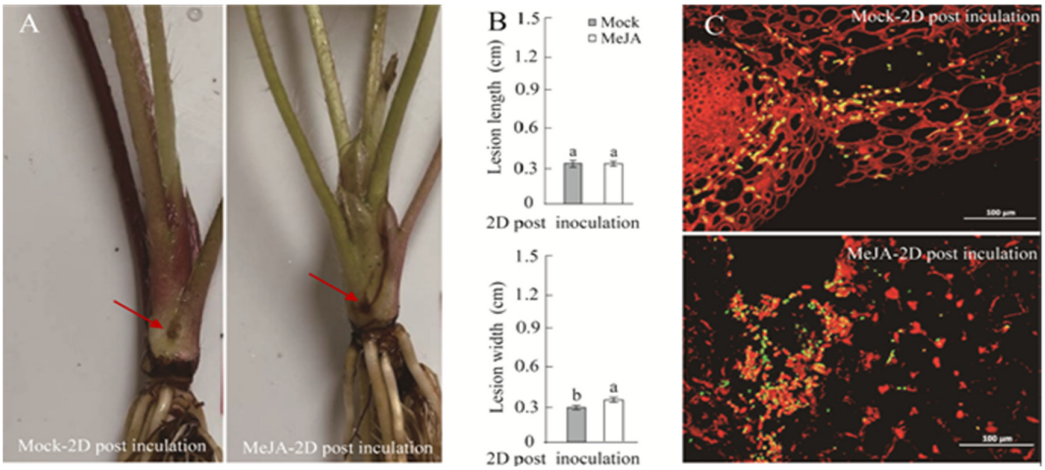

Figure 1. Effect of MeJA on *Colletotrichum siamense* infection in strawberry crown

A was the lesion post 2 days of *C. siamense* SCR-7 inoculation on strawberry crown of MeJA and mock treatments. B was the lesion length and width post 2 days of SCR-7 inoculation on strawberry crown of MeJA and mock treatments; C was the hypha post 2 days of SCR-7 inoculation in strawberry crown (green) of MeJA and mock treatment, respectively. Data (Means ± SE, n = 6) followed by different letters above the bars among treatments indicate significant differences at the 5% level.

Effecting of MeJA on physiological responding to C. siamense infection

Transcriptomic data showed the total reads of each sample were nearly 50 million, the ratio of Q30 of each sample was above 95%, and the ratio of N bases ratio was under 0.04%. The GC content of each sample was about 48% (Table S1). All clean reads were compared to the reference genome and most of the proportion of reads mapped reference genome ranged 92.51%-94.29%, the ratio of mapped reads to sense strand and anti-sense chain both was nearly 38% to 40% (Table S2). These results ensured the reliability of our data, and transcriptomic data has been deposited at NCBI Sequence Read Archive under the accession number PRJNA1021745 and PRJNA1021273.

MeJA treatment reprogramed transcripts in strawberry crown, the MeJA0DPI vs Mock0DPI comparison group showed 343 (171 transcripts down-regulated and 172 up-regulated) significant differential expression genes (DEG), while the MeJA2DPI vs Mock2DPI comparison group showed 1299 (1016 transcripts down-regulated and 283 up-regulated) DEGs (Figure 2).

GO enrichment showed 'biological process' enriched most DEGs. The 'metabolic process', 'response to stimulus' and 'celluar process' clustering into 'biological process', 'organelle', 'cell' and 'cell part' clustering into 'cellular component', and 'transporter activity', 'catalytic activity' and 'binding' clustering into 'molecular function' contained the most DEGs both in MeJA0DPI vs Mock0DPI and MeJA2DPI vs Mock2DPI comparison groups (Figure 3). Enrichment map of GO showed metabolic process such as 'positive regulation of secondary metabolite biosynthetic process', 'regulation of secondary metabolite biosynthetic process', and response to stimulus such as 'response to external stimulus' and 'response to external biotic stimulus' enriched

most DEGs in MeJA0DPI vs Mock0DP comparison group (Figure 4A). Different from MeJA0DPI vs Mock0DP comparison group, 'cell wall biogenesis', 'cell wall organization or biogenesis' and 'xylan biosynthetic process' were enriched most DEGs in MeJA2DPI vs Mock2DPI comparison group (Figure 4B).

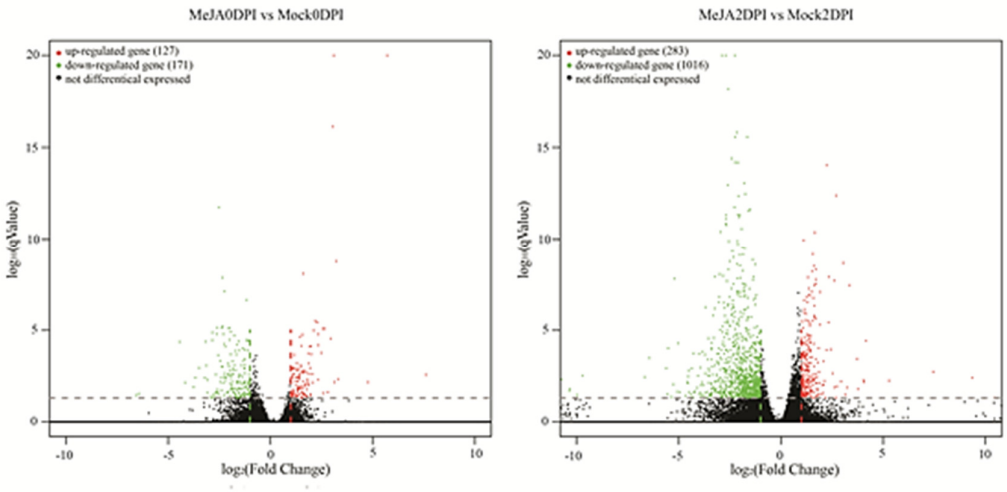

Figure 2. Effect of MeJA on differentially expressed genes number in *Colletotrichum siamense* infected strawberry crown

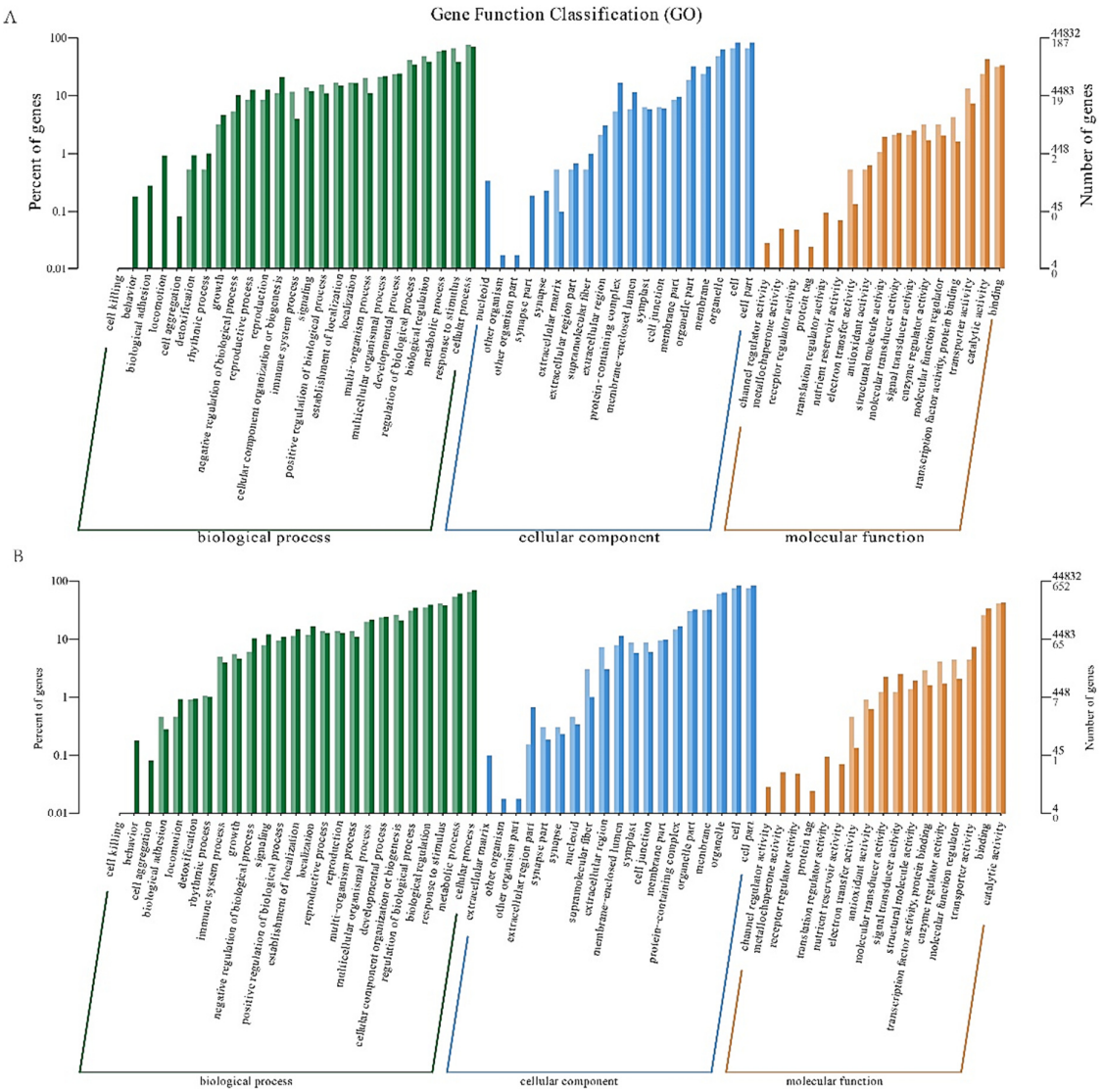

Figure 3. The gene function classification (GO) of differentially expressed genes in strawberry crown caused by MeJA

A and B was analyzed based on the differentially expressed genes of MeJA vs mock treatment post 0 and 2 days of *Colletotrichum siamense* SCR-7 inoculation, respectively.

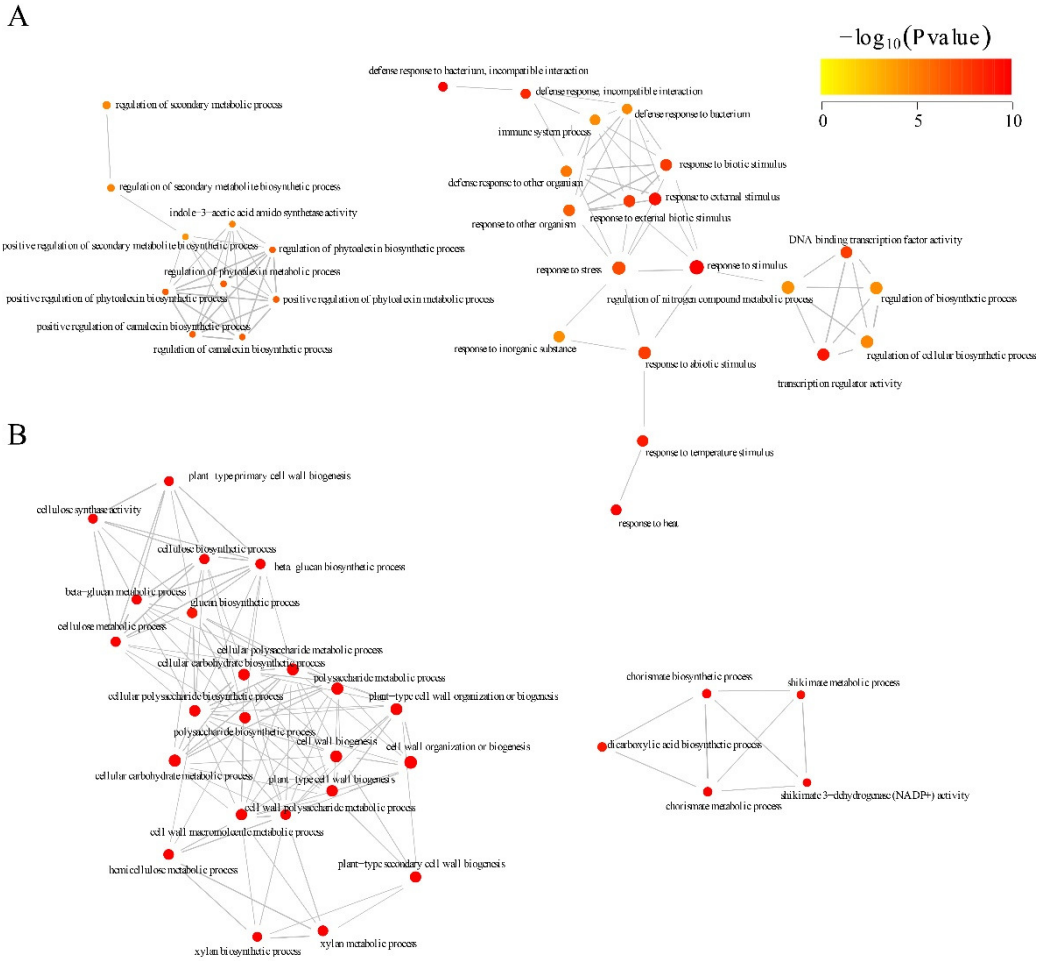

Figure 4. The GO enrichment map of differentially expressed genes in strawberry crown caused by MeJA
A and B was analyzed based on the differentially expressed genes of MeJA vs mock treatment post 0 and 2 days of *Colletotrichum siamense* SCR-7 inoculation, respectively.

KOG function classification showed 'posttranslational modification, protein turnover, chaperones' and 'signal transduction mechanisms' were mapped most DEGs both in MeJA0DPI vs Mock0DPI and MeJA2DPI vs Mock2DPI comparison groups (Figure 5). Enrichment map supplied KOG function classification which showed FxaC_10g18060, FxaC_11g15640, FxaC_12g19430 and other genes in 'secondary metabolites biosynthesis, transport and catabolism', FxaC_24g46920, FxaC_15g15070, FxaC_14g14270 and other genes in 'cell cycle control, cell division, chromosome partitioning' were enriched in MeJA0DPI vs Mock0DPI and MeJA2DPI vs Mock2DPI comparison groups, respectively (Figure 6).

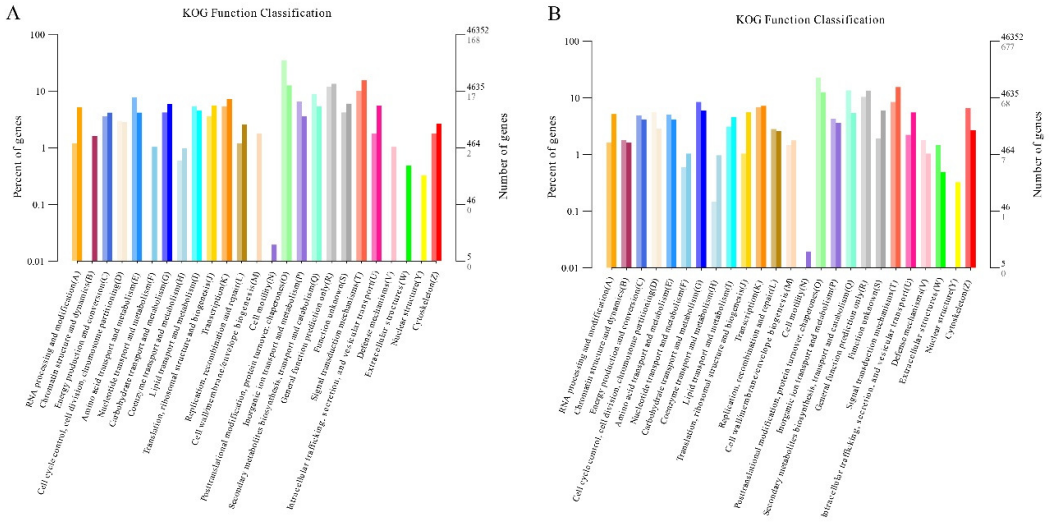

Figure 5. The KOG function classification of differentially expressed genes in strawberry crown caused by MeJA

A and B was analyzed based on the differentially expressed genes of MeJA vs mock treatment post 0 and 2 days of *Colletotrichum siamense* SCR-7 inoculation, respectively.

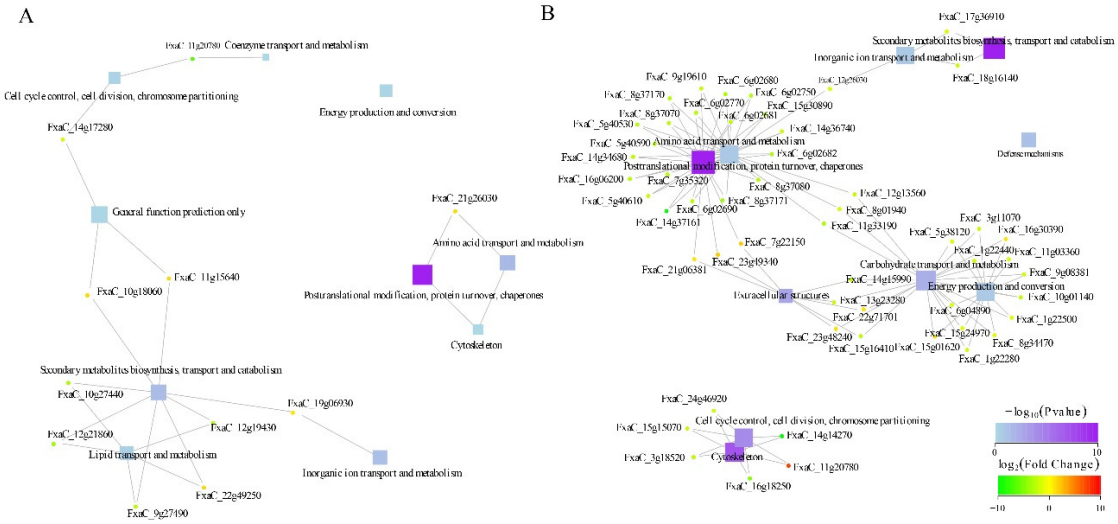

Figure 6. The KOG enrichment network of differentially expressed genes in strawberry crown caused by MeJA

A and B was analyzed based on the differentially expressed genes of MeJA vs mock treatment post 0 and 2 days of *Colletotrichum siamense* SCR-7 inoculation, respectively.

Gene expression involved in 'Plant–pathogen interaction', 'plant hormone signal transduction', 'diterpenoid biosynthesis' and 'carotenoid biosynthesis' were suppressed by MeJA based on KEGG enrichment in MeJA0DPI vs Mock0DPI comparison group (Figure 7A). Similar as MeJA0DPI vs Mock0DPI comparison group, pathways such as 'plant-pathogen interaction', 'phenylpropanoid biosynthesis' and 'flavonoid biosynthesis' pathways were all inhibited in MeJA2DPI vs Mock2DPI comparison group (Figure 7B). Enrichment map showed the expression of genes encoding CHS, CHI, anthocyanidin synthase and anthocyanidin reductase involved in 'flavonoid biosynthesis' KEGG pathways were all suppressed by MeJA (Figure 8A). The result of qRT-PCR was in accordance with the transcriptome analysis, and the expression of structural genes in 'flavonoid biosynthesis' were all down-regulated. In addition, the defense genes such as *MYB46*, *Cellulose synthase A catalytic subunit 8*, *Heat shock protein 90* were also down-regulated (Figure 8B).

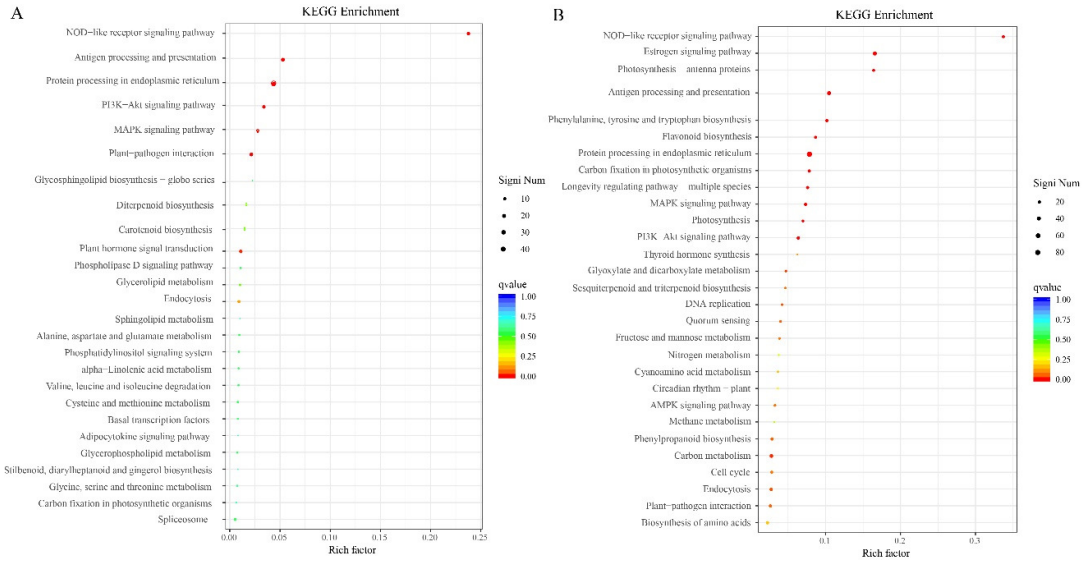

Figure 7. The KEGG enrichment map of differentially expressed genes in strawberry crown caused by MeJA

A and B was analyzed based on the differentially expressed genes of MeJA vs mock treatment post 0 and 2 days of *Colletotrichum siamense* SCR-7 inoculation, respectively

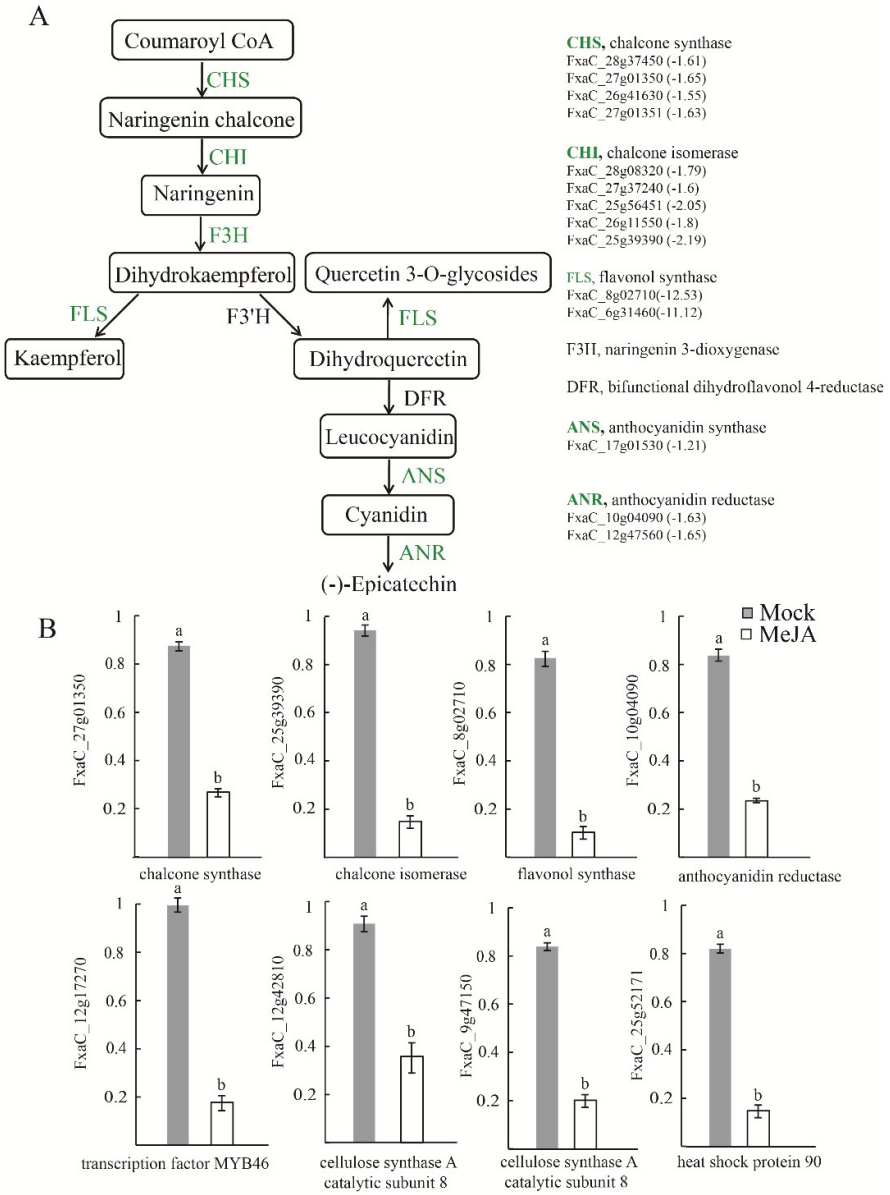

Figure 8. Effect of MeJA on potential genes involved in resistance to crown rot caused by *Colletotrichum siamense* SCR-7

A was variation of structural genes expressions of 'flavonoid biosynthesis' in MeJA vs mock treatment post 2 days of *C. siamense* SCR-7 inoculation. B was qRT-PCR results of structural genes expressions of 'flavonoid biosynthesis' and defense genes post 2 days of *C. siamense* SCR-7 inoculation. Data (Means ± SE, n = 6) followed by different letters above the bars among treatments indicate significant differences at the 5% level.

Effecting of MeJA on flavonoid biosynthesis responding to C. siamense infection

The CHS activities varied from 40.00 to 100.00 U g^{-1} FW, and the CHI activities ranged from 900.00 to 1500.00 U g^{-1} FW in strawberry crown, respectively. Compared with 0 day, *C. siamense* down-regulated the activity of both CHS and CHI after two days of *C. siamense* inoculation, and MeJA pretreatment significantly suppressed the activity of both CHS and CHI only after two days of *C. siamense* inoculation. The flavonoid

contents varied from 6.00 to 10.00 mg g^{-1} FW in strawberry crown. MeJA pretreatment decreased the flavonoid contents after two days of *C. siamense* inoculation (Figure 9).

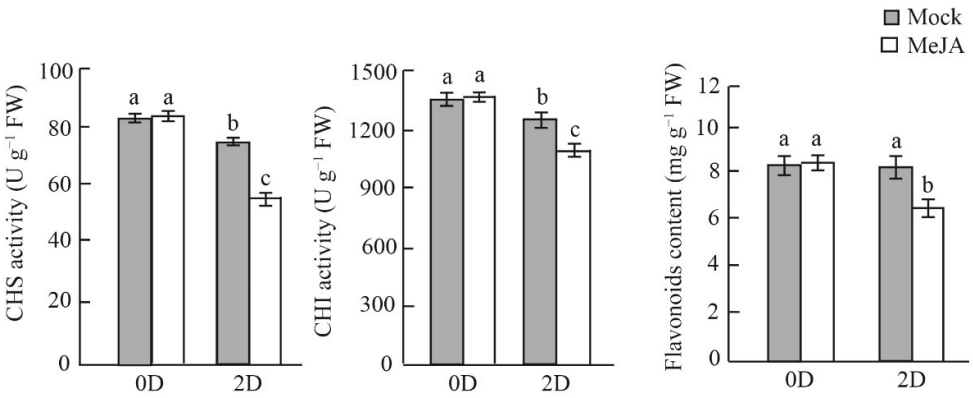

Figure 9. Effect of MeJA on total flavonoids and the activities of chalcone synthase and chalcone isomerase
Data (Means ± SE, n = 6) followed by different letters above the bars among treatments indicate significant differences at the 5% level.

Discussion

JA is involved in the defense against necrotrophic pathogens through preventing plant cell death and inducing defense responses to restrict further pathogen infection (Singh *et al*., 2019). However, contradictory evidences have been published regarding the role of JA in powdery mildew resistance in wheat. Duan *et al*. (2014) found that exogenous MeJA significantly enhanced *Bgt* resistance in susceptible wheat varieties, while Xiang *et al*. (2011) and Li *et al*. (2020) showed that MeJA application did not induce resistance and JA biosynthesis inhibitor diethyldithiocarbamate could induce high resistance to *Bgt* in wheat. The lesion size and pathological analysis in this study suggested MeJA treatment promoted the infection of *C. siam*ense to strawberry crown (Figure 1), which was similar as that MeJA application did not induce resistance to *Bgt* in wheat. This might due to MeJA down-regulated *MYB46*, *Cellulose synthase A catalytic subunit 8*, *Heat shock protein 90* and other defense genes in strawberry crown (Figure 7; Figure 8), which was different from exogenous application of MeJA up-regulated some defense genes and resulted in efficient reduction of disease development in previous reports (Wasternack, 2007; Ali *et al*., 2018; Wang *et al*., 2018). Thus, MeJA showed diverse and complex effects on pathogen infection as different types of diseases.

Besides defense gene, secondary metabolites, including major groups such as phenolics, terpenes, and nitrogen-containing compounds, are often lineage specific and aid plants to interact with the biotic environment (Erb and Kliebenstein, 2020; Dong and Lin, 2021). MeJA pretreatment reprogrammed transcriptome in strawberry crown, and 1642 genes significantly differentially expressed in two groups (Figure 2). This is consistent with that MeJA pretreatment regulated 1108 unigenes in *Panax notoginseng* (Burk) roots with *Fusarium solani* infection (Liu *et al*., 2018). Our DEGs were enriched in 'secondary metabolite biosynthetic' (Figure 3; Figure 4; Figure 5; Figure 6; Figure 7). Enrichment map and qRT-PCR showed the expression of genes encoding chalcone synthase, chalcone isomerase, flavonol synthase, anthocyanidin synthase and anthocyanidin reductase involved in 'flavonoid biosynthesis' of 'secondary metabolite biosynthetic' were all suppressed by MeJA (Figure 8). Confirmed with gene expressions, exogenous MeJA decreased total flavonoid contents and down-regulated CHS and CHI activities (Figure 9). All those evidences suggested the regulation of MeJA to strawberry crown rot was related with flavonoids biosynthesis. To date, some reports showed flavonoids enhanced pathogen resistance (Wang *et al*., 2022; Ramaroson *et al*., 2022), i.e., *PalbHLH1*

and *PalMYB90* overexpression lines of *Populus alba* upregulation of flavonoid structural genes was found to promote the accumulation of quercetin, kaempferol, and anthocyanins, and enhance resistance to *Dothiorella gregaria* infection (Bai *et al*., 2020). Overexpression of *F3H* resulted in higher levels of flavanols such as kaempferol, isorhamnetin, and syringetin, reducing the oxidative damage and susceptibility to *C. sublineola* (*Sorghum bicolor*) (Wang *et al*., 2020). In view of that flavonoids enhanced pathogen resistance and exogenous MeJA decreased its biosynthesis under *C. siamense* infection, we suggested exogenous MeJA enhanced crown rot caused by *C. siamense* in octoploid strawberry by down-regulating flavonoids metabolism.

Conclusions

Exogenous MeJA was tested for its effects on strawberry crown rot resistance to *C. siamense* in this experiment. The lesion size and pathological analysis showed MeJA pretreatment significantly increased lesion width and hypha density in crown tissue, which promoted the infection of *C. siamense* to strawberry crown. MeJA pretreatment reprogrammed crown transcriptome, structural involved in 'flavonoid biosynthesis' and defense genes were all suppressed during *C. siamense* infection. Confirmed with gene expressions, exogenous MeJA decreased content of total flavonoid and down-regulated activities of CHS and CHI significantly. Thus, exogenous MeJA enhanced crown rot caused by *C. siamense* in octoploid strawberry by down-regulation defense genes expression and flavonoids biosynthesis.

Authors' Contributions

BS and CL: conceived the experiments and wrote the manuscript. BS, AP and LL: carried out the experiments and analyzed the data. CL: critically reviewed the manuscript.

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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