Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Mechanism study of jasmonic acid and salicylic acid enhances the cabbage black rot resistance by improving oxidative clearance capacity and synthesis of secondary metabolites

Huiping Wang
Gansu Vocational College of Agriculture
Lina Zheng
Gansu Agricultural University
Hui Zhao
Gansu Vocational College of Agriculture
Bin Wang
Gansu Vocational College of Agriculture
Jue Wang
Gansu Agricultural University
Tingting Dou
Gansu Agricultural University
Xinyue Liu
Gansu Agricultural University
Zeci Liu
liuzc@gsau.edu.cn

Gansu Agricultural University

Research Article

Keywords: Cabbage, Black rot, Hormone, Oxidative damage, Secondary metabolism

Posted Date: June 26th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9852942/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Mechanism study of jasmonic acid and salicylic acid enhances the cabbage black rot resistance by improving oxidative clearance capacity and synthesis of secondary metabolites

Huiping Wang[1*], Lina Zheng[2], Hui Zhao[1], Bin Wang[1], Jue Wang[2], Tingting Dou[2], Xinyue Liu[2], Zeci Liu[2*]

1. College of Agriculture and Ecology, Gansu Vocational College of Agricultural, Lanzhou 730020, People's Republic of China

2. College of Horticulture, Gansu Agriculture University, Lanzhou 730070, People's Republic of China

Correspondence: liuzc@gsau.edu.cn

Abstract

Black rot caused by *Xanthomonas campestris* pv. *campestris* (*Xcc*) poses a serious threat to cabbage production. Jasmonic acid (JA) and salicylic acid (SA), as important plant defense hormones, are widely involved in the disease resistance process of plants. However, the mechanism of JA and SA enhance resistance to *Xcc* remains unclear. In this study, by physiological and biochemical analyses, we concluded that both exogenous SA and JA alone treatments could significantly alleviate the inhibitory effect of *Xcc* on cabbage seedlings by regulating endogenous hormones, reactive oxygen species scavenging capacity, cell membrane stability, and promoting the accumulation of secondary metabolites. Among them, the treatment effect of SA alone was the best, followed by JA. However, the combined treatment of JA and SA did not show a synergistic effect, suggesting that the application of SA or JA alone might be more effective in disease prevention and control strategies. Our research results provide theoretical basis and data support for the green prevention and control of black rot.

Key words: Cabbage; Black rot; Hormone; Oxidative damage; Secondary metabolism

1. Introduction

Cabbage (*Brassica oleracea* L. var. *capitata* L.) is an important leafy vegetable of Cruciferae. Due to its high yield, strong adaptability, good storage and transportation

properties, and rich nutrition, it is widely cultivated worldwide [40, 45]. With the introduction of varieties and changes in cultivation methods on a global scale, diseases have frequently occurred during the growth period of cabbage. Among them, black rot caused by *Xanthomonas campestris pv. campestris* (*Xcc*) is one of the most common and severe bacterial diseases [9, 17, 19, 45]. *Xcc* mainly invades plants through wounds or natural openings. After invasion, it can quickly colonize and spread in the vascular tissue, blocking the vascular system and causing obstruction in the transport of water and nutrients. The typical symptoms of black rot are "V"-shaped yellow spots on the leaf margins, which gradually expand towards the veins. The veins turn black, and in severe cases, the entire plant wilts or even dies [6, 9, 32, 41].

In the early stage of *Xcc* infection, it can disrupt the balance of reactive oxygen species (ROS) metabolism [8], induce the accumulation of free radicals and enhance membrane lipid peroxidation, leading to a decline in the stability of the cell membrane system and manifested as an increase in malondialdehyde (MDA) content [25, 27, 39]. As the disease worsens, this physiological and metabolic disorder will further inhibit the normal growth and development of the plant and have an adverse effect on the subsequent formation of leaf heads and the accumulation of yield [27, 50].

In terms of the prevention and control of *Xcc*, traditional agents such as copper-based preparations remain commonly used control measures in current production, while plant defense activators, antagonistic microorganisms and other biological control technologies also show good application potential [5, 15, 23, 26, 36]. In recent years, with the continuous deepening of research on plant disease resistance physiology, strategies based on exogenous regulatory substances to induce plant resistance have gradually attracted attention, especially jasmonic acid (JA) and salicylic acid (SA), which have shown significant roles in enhancing the disease resistance of plants [10, 22, 46]. JA can enhance the adaptability of plants to adverse stress by regulating stomatal movement, promoting the accumulation of osmotic regulatory substances and defense metabolites, strengthening the activity of the antioxidant system, and inducing secondary metabolic reprogramming [52, 58]. As an important signaling molecule

regulating secondary metabolism in Cruciferae, JA can also promote the accumulation of glucosinolates and their hydrolyzed products, phenols and antioxidant active substances in Cruciferae, and is closely related to the transformation from primary metabolism to defense metabolism [24, 55].

SA plays a significant role in maintaining REDOX homeostasis, enhancing antioxidant defense, alleviating membrane lipid peroxidation damage, and improving adaptability to adverse conditions [53, 57]. Exogenous SA can enhance the activities of antioxidant enzymes such as SOD, POD and CAT, reduce the accumulation of ROS and MDA, strengthen the stability of cell membranes, and improve photosynthetic performance and growth status [21]. In addition, SA is an important signaling molecule for the establishment of system-acquired resistance. It not only participates in local defense responses but also mediates immune warning and defense enhancement throughout the entire plant [16, 18].

Although JA and SA can enhance the plant's resistance to pathogen infection by increasing the activity of antioxidant enzymes, maintaining reactive oxygen homeostasis, and reducing membrane lipid peroxidation damage, etc [30, 51]. At present, there is still a lack of systematic research on the mechanism of action of JA and SA in the disease resistance response of cabbage black rot, especially in aspects such as endogenous hormones and secondary metabolic responses, which still need to be further clarified.

This study intends to systematically analyze the effects of exogenous JA and SA treatment on endogenous hormone levels, antioxidant defense and accumulation of secondary metabolites in cabbage, aiming to reveal the physiological regulatory mechanisms of the JA and SA in the defense process against black rot. The research results can provide a theoretical basis for clarifying the disease resistance response mechanism of cabbage black rot, optimizing the regulation strategy of exogenous hormones and establishing green prevention and control technologies.

2. Materials and methods

2.1 Experimental materials

The plant material used in this study was "Zhonggan 11" cabbage varieties, (susceptible to *Xanthomonas campestris* pv. *campestris*, *Xcc*). The inoculated pathogen was *Xcc* race 1 (one of the most pathogenic and common physiological strains in cabbage production) isolated from diseased leaves of cabbage in Yuzhong County, Lanzhou City, Gansu Province.

Jasmonic acid, JA (CAS No: 3572-66-5) was purchased from Shanghai Maclin Biochemical Technology Co., LTD. Salicylic acid, SA (CAS No: 69-72-7) was purchased from Shanghai Aladdin Biochemical Technology Co., LTD.

2.2 Growth conditions and treatments

Select plump and uniformly sized cabbage seeds and sow them in square pots (10 cm × 10 cm) with substrate. When the seedlings reached "three leaves and one heart" (about 45 days after germination), the plants with uniform growth and free from diseases and pests were selected for treatment. A total of four treatments were set in this experiment, namely CK (distilled water), 100 μM JA, 500 μM SA, and 100 μM JA + 500 μM SA. Spray the relevant agent evenly on both sides of the leaf surface by spraying until uniform droplets form on the leaf surface and start to flow down. After treatment, the *Xcc* solution was inoculated by spray inoculation method (with a concentration of 10^8CFU and OD_{600}=0.1) [54]. The inoculated plants are placed in a greenhouse for normal cultivation under the conditions of a temperature of 25-28℃ and a relative humidity of over 95%. The day of vaccination was recorded as Day 0. Samples were taken on 0, 1, 3 and 5 d respectively, the leaves were immediately frozen in liquid nitrogen after sampling and stored in a -80℃ refrigerator for the determination of relevant indicators.

2.3 Measurement indexes and methods

2.3.1 Determination of disease index

In order to understand the incidence of black rot disease in the seedling stage, 20 plants were randomly investigated for each repetition. The disease classification standards are as follows: Grade 0: No symptoms on the leaves; Grade 1: The diameter of the lesion is less than 3 mm, with dark brown lesions that have spread locally,

covering less than 15% of the leaf area. Grade 3: The diameter of the lesion is less than 6mm, no characteristic lesions appear, and it accounts for 15-30% of the leaf area. Grade 5: The diameter of the lesion is less than 10 mm, with "V" -shaped lesions appearing, covering 30-55% of the leaf area. Grade 7: The diameter of the lesion is less than 15 mm, the diseased leaves have not withered, and they account for 55-75% of the leaf area. Grade 9: The diameter of the lesion is greater than 15 mm, covering more than 75% of the leaf area, and some diseased leaves wither and die. Disease index = ∑ at all levels (level value × number of) at all levels/series × highest (total number) by 100.

2.3.2 Determination of endogenous hormone content

Endogenous hormone content was determinate using high performance liquid chromatography (HPLC) (Agilent1290-6400) [33]

2.3.3 Determination of antioxidant enzyme activity

Activities of superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) were determined in accordance with the method according to the manufacturer's instructions.

2.3.4 Determination of reactive oxygen species

Contents of superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2) were determined using the Solarbio kit. The qualitative analysis of O_2^- and H_2O_2 was carried out in accordance with the method of Sun et al [43], using nitrocyanidazole (NBT) and 3, 3-diaminobenzidine (DAB), respectively. Finally, the stained leaves were scanned and photographed for observation using the EPSON expression 11000XL color image scanner (WinRHIZO Pro LA2400, Canada).

2.3.5 Determination of osmotic regulating substances

The determination of soluble sugar, soluble protein and proline (Pro) contents was carried out in accordance with the method proposed by previous report [3, 28, 37].

2.3.6 Determination of membrane permeability

Relative conductivity (REC) was determined using a conductivity meter (Shanghai Jingke, DDSJ-308F), content of malondialdehyde (MDA) was determined by the

thiobarbituric acid [25].

2.3.7 Determination of the glucosinolate content

The glucosinolates in cabbage were extracted and determined by referring to the method of previous report [48].

2.3.8 Determination of phenolic acid compounds

Phenolic compound components were determined by Waters high performance liquid chromatography according to the method described by Wang et al [49]. The sample pretreatment steps are as follows: Take 0.1 g of freeze-dried powder, add 2 mL of methanol, shake thoroughly, and then extract in a 4℃ refrigerator for 60 min. After the extraction is completed, centrifuge at 4℃ and 10,000*g* for 15 min. Carefully draw the supernatant, filter it through a 0.22 μm microporous filter membrane into the injection bottle, and the test solution is obtained for HPLC machine detection.

2.3.9 Observation of leaf structure and determination of lignin content

Fresh leaves were placed into the fixative solution for electron microscopy at room temperature for 2 h and then transfer them to a refrigerator at 4℃. The fixed samples were sent to Baisiwei Biotechnology Co., Ltd (Xi'an, China) for toluidine blue staining sections and transmission electron microscope image acquisition. Content of endogenous lignin was determined using kits (Suzhou Keming Biotechnology Co., LTD., Suzhou, the product ID: MZS-2-G) according to the manufacturer’s instructions.

2.4 Data statistics and analysis

Data collation and statistics were conducted using Microsoft Excel 2019. Statistical analyses were based on three independent biological replicates (n = 3). Analysis of variance was performed using SPSS 27.0 software, and multiple comparisons of significance were conducted using Duncan's test ($p<0.05$). Figures were plotted using Origin 2025 (OriginLab Corporation, Northampton, MA, USA). The Mantel correlation heatmap analysis was conducted using Chiplot (https://www.chiplot.online/).

3. Results

3.1 Effects of exogenous JA and SA on the disease index

Different exogenous hormone treatments all reduced the occurrence of black rot to a certain extent, and there were significant differences in the disease prevention effects (Table 1). Among the four treatments, the SA treatment had the best disease prevention effect. Its incidence rate was 64.00% and the disease index (DI) was 29.78, both of which were the lowest values. The DI of JA treatment is the second, with an incidence rate and DI of 72.00 and 31.56 respectively. The incidence rate of JA+SA combined treatment was 76.00%, and the DI was 37.78. Although it was still lower than CK, it was significantly higher than that of the treatment of JA and SA alone. Compared with CK, the DI of SA, JA and JA+SA treatments decreased by 32.32%, 28.27% and 14.14% respectively. Compared with the SA treatment, the DI of the JA+SA treatment increased by 26.86%. Overall, the pattern of the DI is CK>JA+SA >JA>SA. This indicates that both exogenous SA and JA alone treatments reduced the occurrence of diseases to a certain extent, among which the effect of SA treatment was slightly better than that of JA treatment (Figure 1). However, the combined use of the SA and JA may not show a significant synergistic effect, and its disease prevention effect lies between that of JA alone treatment and the CK.

Table 1. Effects of exogenous JA and SA on the disease index of black rot in cabbage.

Statistical data	CK	JA	SA	JA+SA
Number of leaves at grade 0	10	14	18	12
Number of leaves at grade 1	5	9	12	7
Number of leaves at grade 3	12	13	12	14
Number of leaves at grade 5	10	7	5	8
Number of leaves at grade 7	5	2	1	3
Number of leaves at grade 9	8	5	2	6
Number of leaves	50	50	50	50
Number of diseased leaves	40	36	32	38
Incidence rate	80.00%	72.00%	64.00%	76.00%
Disease index	44.00	31.56	29.78	37.78



Figure 1. Phenotypes of black rot in cabbage seedlings after 14 d of exogenous JA and SA treatment.

3.2 Effects of exogenous JA and SA on the endogenous hormone levels

Endogenous hormone content under black rot stress showed significant differences among different treatments (Figure 2). With the extension of treatment time, the content of ABA generally showed an increasing trend, the contents of GA and IAA generally showed a decreasing trend, while the contents of JA and SA significantly increased. The content of BR also showed a certain upward range in the middle and later stages of treatment. The regulatory directions and intensifications of various hormones vary among different treatments. Among them, SA treatment is more conducive to increasing the contents of SA, BR and GA, JA treatment is more beneficial to promoting the accumulation of JA, while the levels of ABA and IAA are relatively higher under CK. Although the combined treatment of JA and SA is superior to CK in most endogenous hormone, its overall regulatory effect is generally weaker than that of the corresponding individual treatments.

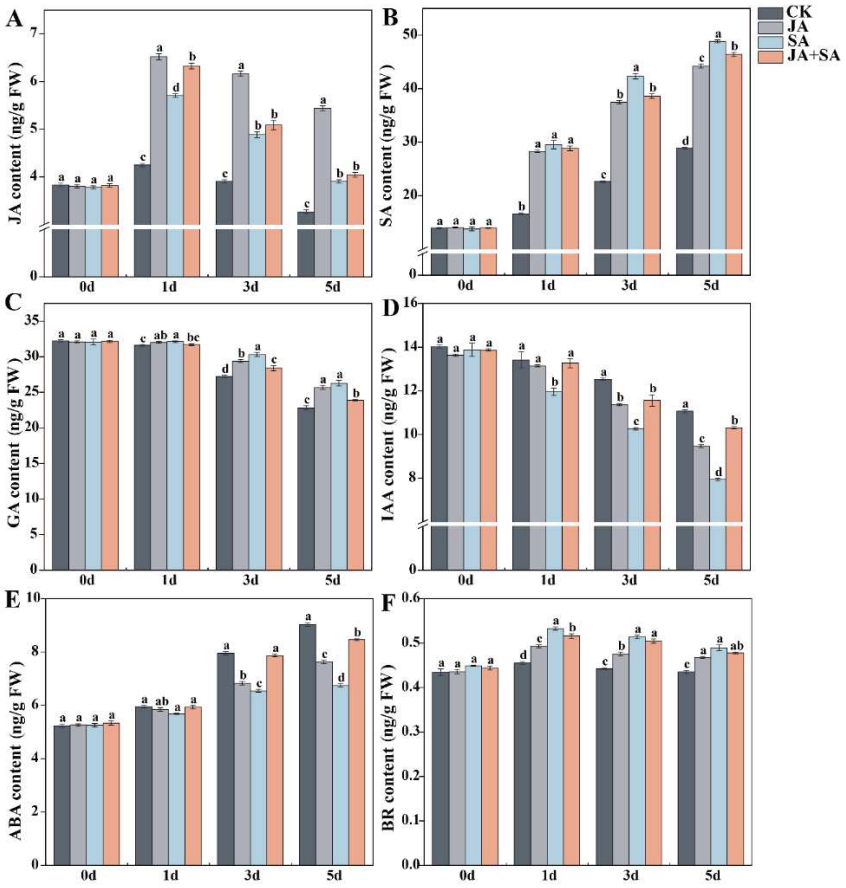


Figure 2. Effects of exogenous JA and SA on JA (A), SA (B), GA (C), IAA (D), ABA (E) and BR (F) content in cabbage seedlings after *Xcc* infection.

Correlation analysis indicated that SA was significantly positively correlated with ABA, and GA was significantly negatively correlated with IAA. SA is negatively correlated with GA and IAA, GA is negatively correlated with ABA, and IAA is negatively correlated with ABA (Figure 3).

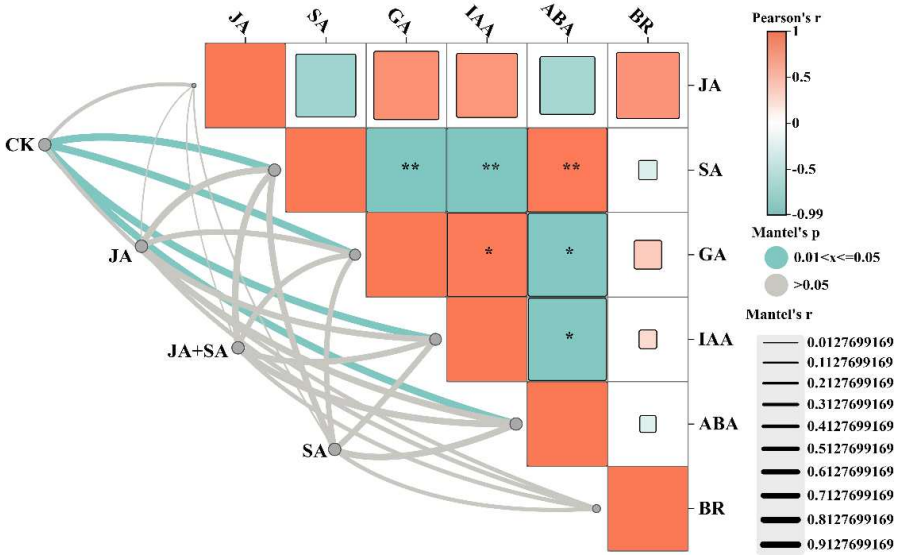


Figure 3. Correlation matrix among hormones (Pearson).

3.3 Effects of exogenous JA and SA on the antioxidant enzyme activities

From 0 to 5 d, the activities of the SOD, POD and CAT showed an overall upward trend, but the change patterns of different enzymes and the differences among treatments were different (Figure 4A~C). SOD activity continued to rise throughout the treatment period. On 1 d, each hormone treatment showed a promoting effect. Among them, the increase in SA treatment was the greatest. On 5 d, the SOD activities of SA, JA and JA+SA treatments reached 262.11, 248.65 and 200.84 U/g, respectively. Compared with the same period, CK increased by 63.49%, 55.09% and 25.27% respectively. JA+SA showed no significant difference from CK when treated after 1 d and 3 d. Although it was significantly higher than CK on 5 d, it was still lower than SA and JA treated alone. The changing trend of POD activity is characterized by an initial increase followed by a decrease, with the peak occurring in 3 d. There was no significant difference among the treatments at 0 d. After 1 d, the POD activities treated by SA and JA rapidly increased to 4796 U/g and 4691.33 U/g respectively, which were 16.80% and 14.25% higher than CK, respectively. The JA+SA treatment was 4390 U/g, which was 6.91% higher than CK and significantly lower than SA and JA. On 3 d, the activity of each treated POD reached its peak. The SA, JA and JA+SA were 5173.67, 4998 and 4915 U/g respectively, which increased by 12.33%, 8.52% and 6.72% respectively compared with CK in the same period. CAT activity continued to rise throughout the treatment period. On 1 d, the CAT activity of SA treatment rapidly increased to 387 U/g, which was 22.47% higher than that of CK. The treatments of JA and JA+SA were 358 U/g and 349.33 U/g respectively, which were 13.29% and 10.55% higher than CK respectively. On 5 d, the CAT activities in SA, JA and JA+SA treatments increased to 486.33, 464.33 and 449 U/g respectively, which were 12.49%, 7.40% and 3.86% higher than CK, respectively.

Under each treatment, the contents of H_2O_2 and O_2^- generally showed an upward trend, but there were significant differences in the accumulation rates among different treatments, and the contents in the JA, SA and JA+SA treatment groups were always

lower than those in the CK (Figure 4D, E). In terms of treatment effect, SA treatment performed most prominently in inhibiting the accumulation of ROS, with the contents of O_2^- and H_2O_2 remaining at the lowest level throughout the entire treatment period. The processing effect of JA is second, significantly better than CK but slightly inferior to SA. Although the combined treatment of JA and SA showed a certain inhibitory effect in the later stage, there was no significant difference from CK in the early stage of treatment, and the overall effect was significantly weaker than that of the single treatment. This indicates that both exogenous SA and JA can delay the accumulation of ROS in the leaves, and the effect of SA is more significant. However, the combined use of the two may weaken this protective effect due to antagonistic effects.

In NBT staining, the leaves of CK have the darkest blue color, followed by JA+SA treatment (Figure 4F). The blue color of JA treatment is relatively light, and that of SA treatment is the lightest. In DAB staining, the leaves of CK have the darkest brown color, followed by JA+SA treatment. The leaves of JA treatment have the lightest brown color, while those of SA treatment have the lightest brown color. This indicates that under *Xcc* infection, the contents of O_2^- and H_2O_2 in CK were the highest, followed by JA+SA treatment, with JA treatment being the lowest and SA treatment the lowest. Overall, both exogenous SA and JA alone can effectively reduce the accumulation of O_2^- and H_2O_2. Among them, the effect of SA treatment is the most significant, followed by JA. Although the combined treatment of JA and SA is superior to CK, its effect is significantly weaker than that of the single treatment.

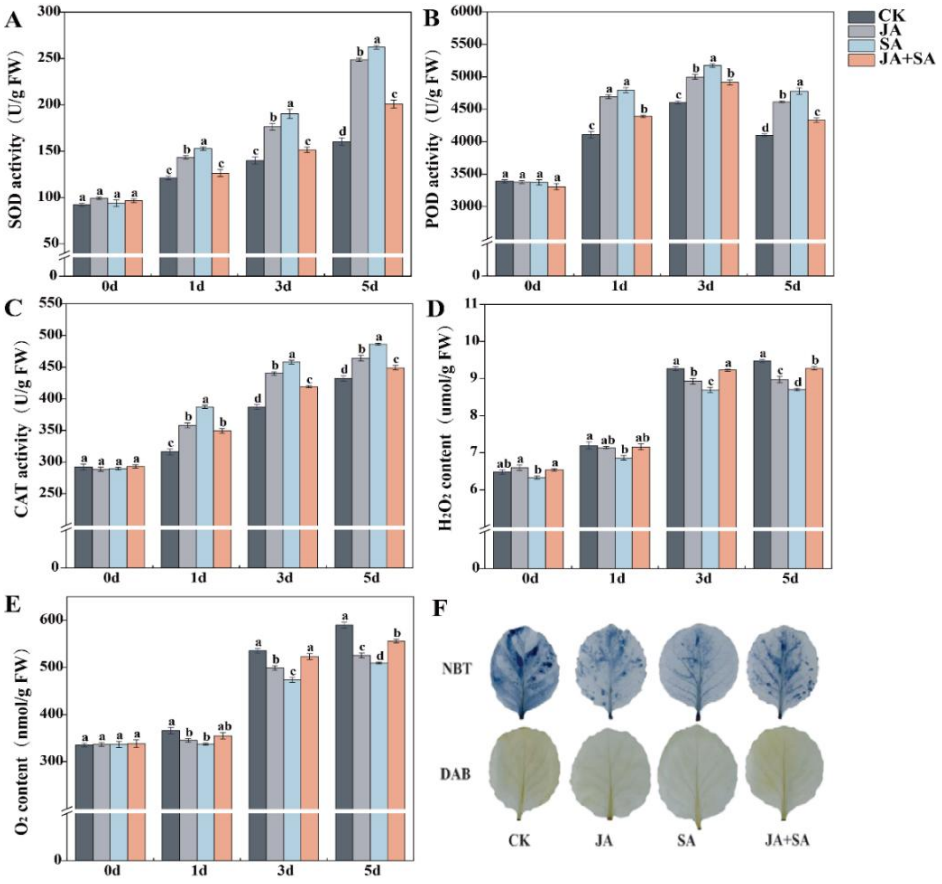


Figure 4. Effects of exogenous JA and SA on SOD (A), POD (B), and CAT (C) enzyme activities, H_2O_2 content (D), O_2 content (E), NBT and DAB staining cabbage seedlings after *Xcc* infection.

3.4 Effects of exogenous JA and SA on osmotic regulation

Compared with CK, SA treatment significantly increased the contents of soluble protein, soluble sugar and Pro, reaching 48.50 nmol/g, 22.79 nmol/g and 74.94 μg/g respectively on 5 d (Figure 5A~C). It increased by 16.84%, 21.90% and 13.68% respectively compared with CK. JA treatment also significantly increased the contents of the soluble protein, soluble sugar and Pro, reaching 45.67 nmol/g, 21.26 nmol/g and 72.15 μg/g respectively, which were 10.02%, 13.76% and 9.46% higher than CK respectively. However, the JA+SA treatment only significantly increased the content of Pro by 5.58% to 69.60 μg/g and had no significant effect on soluble proteins and soluble sugars. It indicates that both SA and JA alone can effectively promote the accumulation of osmotic regulatory substances, and the effect of SA is better than that of JA. However, the combined use of the two only has a weak inducing effect on free proline.

3.5 Effects of exogenous JA and SA on the cell membrane stability

Compared with CK, SA treatment significantly reduced the contents of REC and MDA, by 32.87% and 40.59%, respectively on 5 d (Figure 5D, E). JA treatment also significantly reduced the contents of REC and MDA, by 25.44% and 24.66% respectively. Although the JA+SA treatment reduced the contents of REC and MDA by 10.97% and 16.23% respectively, the reduction was significantly smaller than that of the treatment alone. Compared with SA treatment, the contents of REC and MDA in JA+SA treatment were significantly increased by 32.64% and 41.00%, respectively on 5 d. Compared with JA treatment, the content of REC and MDA in JA+SA treatment was significantly increased by 19.41% and 11.19% respectively. The results show that both JA and SA alone can effectively inhibit membrane lipid peroxidation and reduce cell membrane permeability, and the effect of SA is better than that of JA. However, the combined use of the JA and SA may produce antagonistic effects, and the protective effect is significantly weaker than that of the single treatment. Correlation analysis indicated that SOD was significantly positively correlated with CAT, MDA and REC, CAT was significantly positively correlated with MDA and O_2^-, and correlated with REC and H_2O_2. MDA was significantly positively correlated with REC and correlated with O_2^-, and H_2O_2 was correlated with O_2^- (Figure 5F).

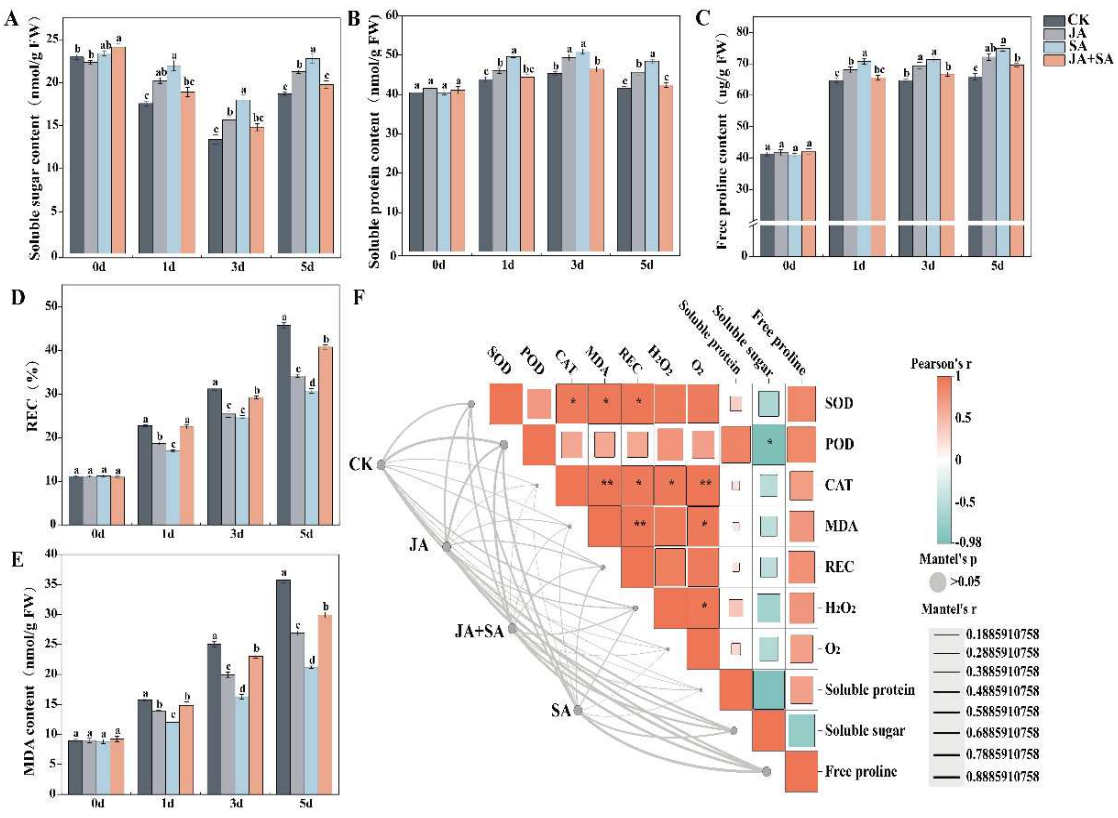


Figure 5. Effects of exogenous JA and SA on soluble sugar (A), soluble protein (B), free proline (C), REC (D), MDA (E) content in cabbage after *Xcc* infection, and correlation matrix among antioxidant and osmotic regulation indicators (Pearson).

3.6 Effects of exogenous JA and SA on the glucosinolate content

A total of 9 glucosinolate were monitored in each treatment (Figure 6A). The contents of IBE, PRO, SIN, RAA, NAP and 4ME showed an upward trend throughout the treatment period. However, the contents of 4OH, GBC and NEO showed a downward trend throughout the treatment period. Overall, the content of each glucosinolate component in the SA treatment was generally higher than that in the JA treatment, JA+SA treatment and CK, followed by the JA treatment. Although the JA+SA treatment was higher than the CK, it was generally lower than the individual treatment. Among them, the contents of GBC and IBE were the highest. In CK, GBC decreased from 6.05 μg·g^{-1} to 4.26 μg·g^{-1}. In the SA treatment, it decreased from 6.22 μmol·g^{-1} to 5.19 μmol·g^{-1}. In contrast, the content of IBE continued to increase with the extension of treatment time. In CK, it rose from 4.36 μmol·g^{-1} to 6.42 μmol·g^{-1}. In the SA treatment, it increased from 4.53 μmol·g^{-1} to 8.03 μmol·g^{-1}. The JA and JA+SA treatment increased by 68.30% and 59.01% respectively. GBC generally showed a downward

trend during the treatment process, while IBE not only had a relatively high content but also demonstrated significant accumulation in each treatment, with the SA treatment having the largest increase. In contrast, the contents of NAP, 4OH and NEO were relatively low. Although the content of NAP was low, it continued to increase overall during the treatment period, while the contents of 4OH and NEO continued to decline. Specifically, 4OH decreased from 0.20 μmol·g^{-1} to 0.09 μmol·g^{-1} in CK. In the SA treatment, it decreased from 0.22 μmol·g^{-1} to 0.15 μmol·g^{-1}. In CK, GBC decreased from 6.05 μmol·g^{-1} to 4.26 μmol·g^{-1}. In the SA treatment, it decreased from 6.22 μmol·g^{-1} to 5.19 μmol·g^{-1}. NEO decreased from 0.27 μmol·g^{-1} to 0.14 μmol·g^{-1} in CK. In the SA treatment, it decreased from 0.29 μmol·g^{-1} to 0.20 μmol·g^{-1}. These results indicated that although exogenous JA and SA did not change the downward trend of 4OH, GBC and NEO, they slowed down their degradation amplitude to a certain extent, especially the SA treatment was more obvious.

Except for the glucosinolate component, the contents of total aliphatic, indole and total glucosinolate in the four treatments all showed an upward trend 0 to 5 d after inoculation with *Xcc* (Figure 6B~D). Among them, SA treatment had the most significant effect on enhancing glucosinolates, followed by JA. Although the combined treatment of JA and SA is superior to CK, its effect is weaker than that of the individual treatment.

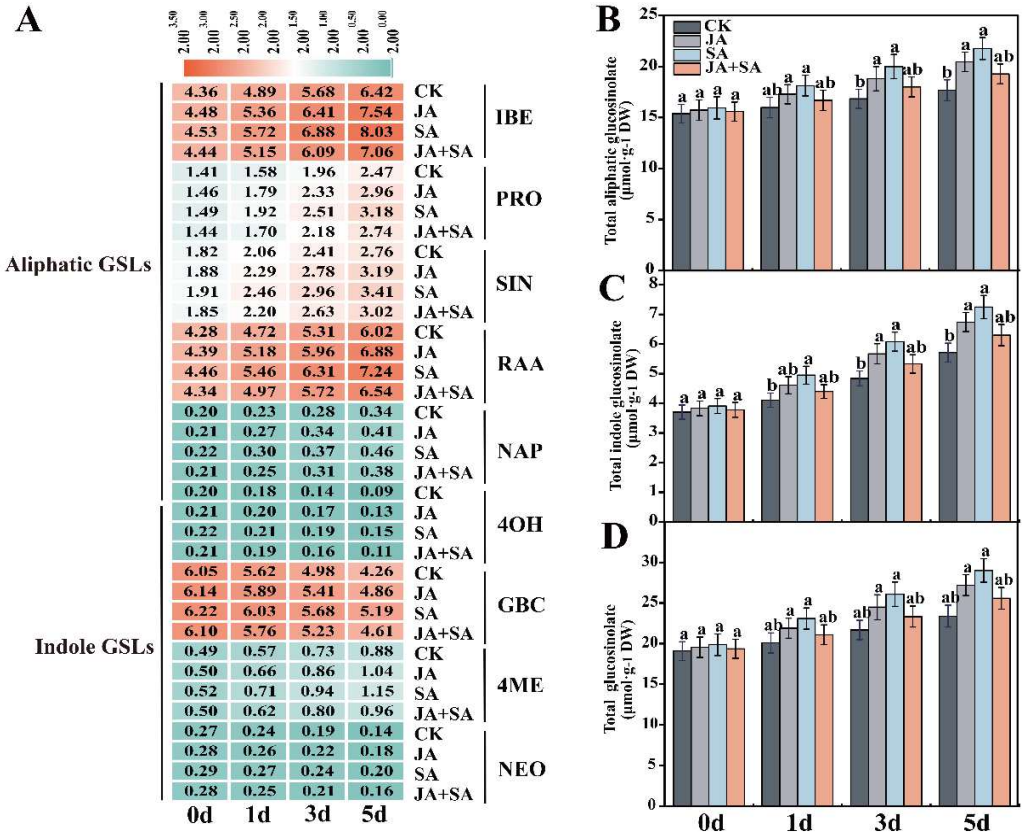


Figure 6. Effects of exogenous JA and SA on glucosinolate component content (A), total aliphatic glucosinolate content (B), total indole glucosinolate content (C), total glucosinolate content (D) in cabbage after *Xcc* infection.

By analyzing the correlations of each glucosinolate component before and after *Xcc* inoculation, it was found that there was a positive or negative correlation between almost every glucosinolate component (Figure 7). This might be related to the activation of the glucosinolate synthesis pathway by hormones, which enhanced the synthesis of each glucosinolate component.

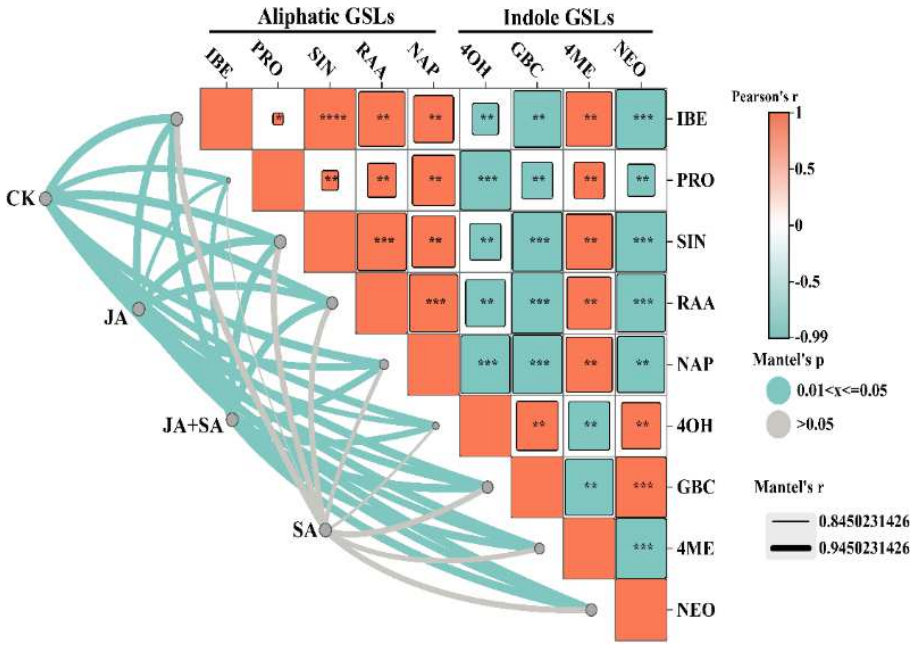


Figure 7. Correlation matrix among glucosinolate (Pearson).

3.7 Effects of exogenous JA and SA on phenolic acids, lignin and leaf structure

Under *Xcc* infection, the content of most phenolic acids shows a continuous upward trend with the extension of time, and different exogenous hormone treatments have a significant regulatory effect on their accumulation. Among them, the SA treatment had the most significant promoting effect on most phenolic acids such as ferulic acid, chlorogenic acid, gallic acid, coumaric acid, naringin, and protocatechuic acid. The contents of each substance reached the highest at 5 d. For example, ferulic acid increased by 29.5% compared with CK, chlorogenic acid increased by 40.3%, and gallic acid increased by 19.8%, all of which were significantly better than other treatments. JA treatment came second and could also effectively increase the accumulation of phenolic acid substances, but the increase was generally lower than that of SA. For example, ferulic acid increased by 17.0% compared with CK, chlorogenic acid increased by 30.0%, and gallic acid increased by 11.3%. Although the combined treatment of JA and SA was superior to CK in most indicators, its effect was significantly weaker than that of SA and JA alone. For instance, ferulic acid only increased by 9.8% compared to CK, and chlorogenic acid increased by 9.9%. Some substances, such as p-hydroxybenzoic acid and rutin, even showed no significant difference from CK. It is worth noting that the content of gentian acid reached its peak

on 3 d and then decreased, but the SA treatment still maintained the highest level. Rutin continued to rise in CK, while it was higher in the early stage of hormone treatment and slightly decreased in the later stage. On 5 d, all treatments tended to be consistent. Overall, it shows the pattern of SA > JA > JA+SA > CK, indicating that exogenous SA and JA can enhance the defense ability of cabbage by promoting the synthesis and accumulation of phenolic acids. Among them, the inducing effect of SA is stronger, while the combined use of the two has a significant antagonistic effect.

Except for the phenolic acid component, the contents of total polyphenols, total flavonoids and total phenolic acids in the four treatments all showed an upward trend 0 to 5 d after *Xcc* infection (Figure 8B~D). Among them, SA treatment had the most significant effect on enhancing glucosinolates, followed by JA. Although the combined treatment of JA and SA is superior to CK, its effect is weaker than that of the individual treatment.

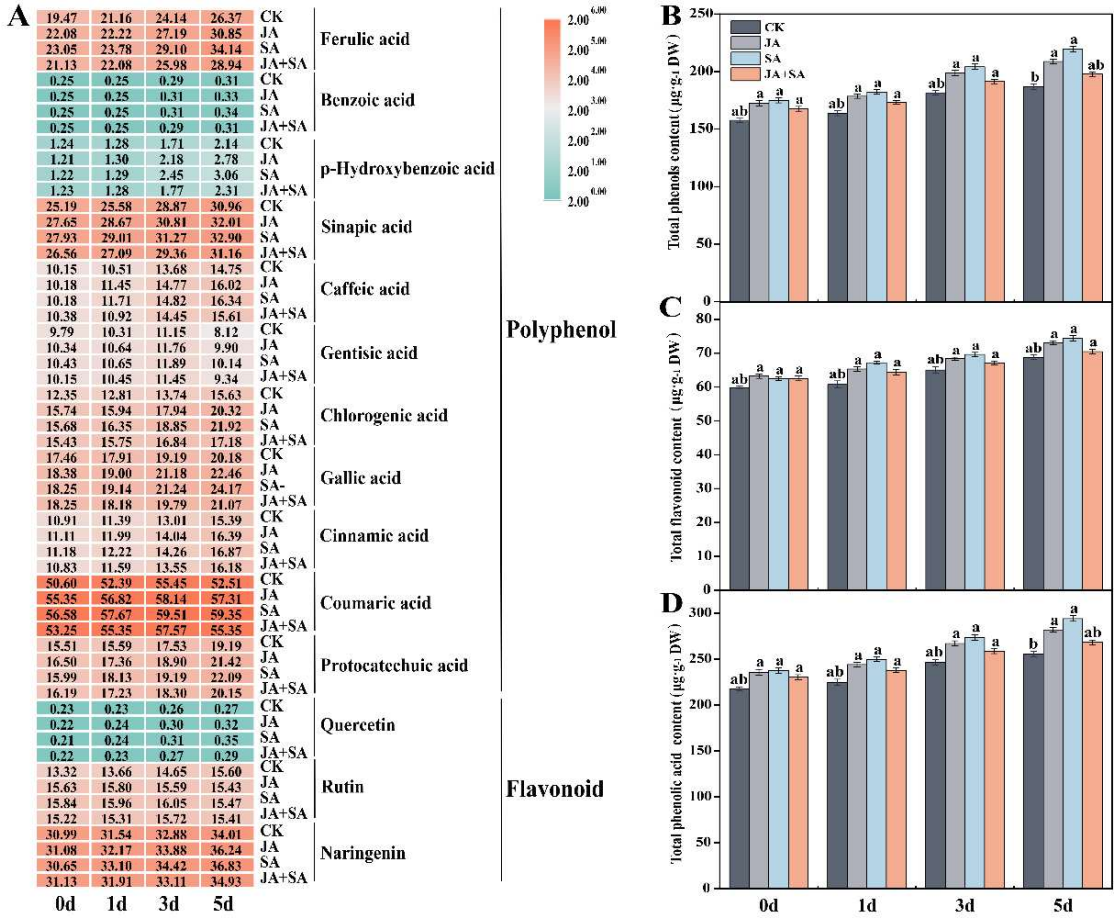


Figure 8. Effects of exogenous JA and SA on phenolic acids content after *Xcc* infection.

Results of histochemical staining of paraffin sections on 5 d showed that the depth of lignin staining in the xylem of the veins in the SA treatment was significantly enhanced, there was no obvious abnormal staining in the parenchyma tissue, and the basic anatomical structures such as the upper and lower epidermis of the leaves, palisal tissue, and spongy tissue were intact. In the JA treatment, the staining depth of the xylem in the veins only slightly increased, and there was no obvious lignin deposition in the mesophyll tissue. Although the staining intensity of the xylem in the veins of the JA+SA treatment was higher than CK, it was significantly lower than that of the SA treatment. There was no additional accumulation of lignin in the mesophyll tissue, and the leaf structure remained intact. The dynamic determination results of lignin content indicated that there was no significant difference in lignin content among the treatments from the 0 d to the 3 d. On 5 d, the contents of the JA, SA and JA+SA treatments were all significantly higher than those of CK.

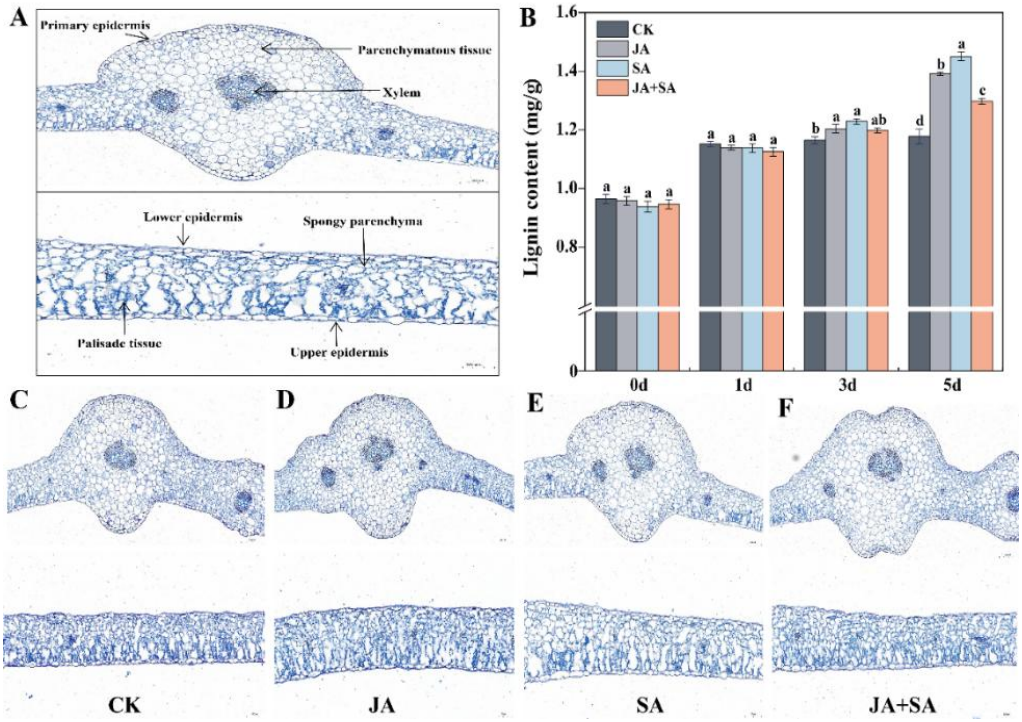


Figure 9. Effects of exogenous JA and SA on lignin and leaf structure after *Xcc* infection.

Through the correlation analysis of phenolic acids and lignin before and after *Xcc* inoculation, it was found that there was a positive correlation among most phenolic acid components (Figure 10). This might be related to the hormone-activated phenylpropane synthesis pathway.

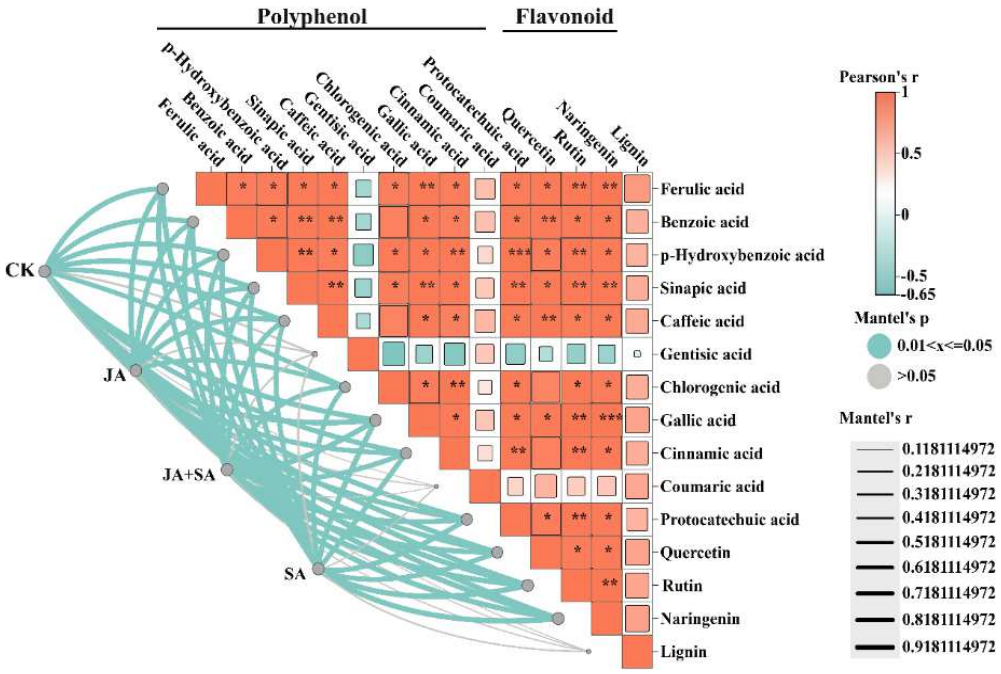


Figure 10. Correlation matrix among phenolic acids and lignin (Pearson).

4. Discussion

Black rot caused by *Xanthomonas campestris* pv. *campestris* (*Xcc*) is a serious bacterial disease in the production of cabbage. Chemical control has many drawbacks, and it is crucial to explore green induction and resistance technology [26]. Jasmonic acid (JA) and salicylic acid (SA) are core defense signal molecules in plants and can induce disease resistance in plants [12, 56]. In this study, disease index analysis showed that exogenous SA treatment had the best control effect on black rot, followed by JA, while the reduction in JA + SA was the smallest, indicating that both SA and JA alone can induce resistance to black rot, and the induction effect of SA is better than that of JA. After *Xcc* infection, the endogenous hormones changed significantly. In the CK, ABA continued to increase, and GA and BR decreased more significantly, reflecting the disruption of normal growth regulation by pathogen stress. Under SA treatment, the endogenous SA content was always the highest, while ABA decreased and GA and BR maintained a relatively high level, indicating that SA treatment not only enhanced defense signals but also may help maintain a better growth-defense balance. Previous Brassica-related studies have pointed out that SA and JA are core defense hormones in response to biotic stress, and the hormone balance state, especially the enhancement of SA-related metabolism, is often associated with stronger resistance [2].

Antioxidant enzyme system is an important protective mechanism for plants to eliminate ROS and maintain REDOX balance [7, 42]. In this study, both SA and JA treatments alone significantly increased the activities of SOD, POD and CAT. This is consistent with the results of previous studies that exogenous SA and JA can reduce the damage of oxidative stress to cells by enhancing the ability of plants to eliminate ROS. The research also found that the response patterns of the three antioxidant enzymes to hormone treatment were different. Among them, SOD activity increased the most, POD showed a trend of first rising and then falling, and CAT continued to rise slowly. This might be related to the different functional divisions of the three in the ROS clearance system [29, 42]. It is generally believed that SOD is the first line of defense for eliminating O_2^-, while POD and CAT mainly participate in the decomposition of H_2O_2. Among them, POD is also related to processes such as lignification and cell wall reinforcement, so its change pattern is often more complex. In our study, the induction effect of the JA+SA against antioxidant enzymes was significantly weaker than that of the treatment alone, indicating that the antagonistic effect between the SA and JA signaling pathways might have interfered with the full activation of the antioxidant system.

Soluble proteins, soluble sugars and free proline are important osmotic regulatory substances, playing a significant role in maintaining cellular turgor pressure, stabilizing protein structure and eliminating ROS [38, 44]. Under stress conditions, plants often maintain osmotic balance, protect cell structure and enhance their adaptability to adverse conditions by accumulating soluble sugars, soluble proteins and proline [4]. In this study, both SA and JA treatments alone significantly increased the contents of osmoregulatory substances such as soluble protein, soluble sugar and free proline in cabbage leaves, indicating that exogenous hormone treatment helps enhance the osmoregulatory ability. This is basically consistent with the existing research results that SA and JA can promote the accumulation of osmoregulatory substances under adverse conditions and improve the stress resistance. The mixed treatment of JA+SA only slightly increased the content of free proline, but had no significant effect on

soluble proteins and soluble sugars, indicating that the promoting effect of the combined treatment in osmotic regulation was significantly weaker than that of the individual treatment. This suggests that the antagonistic effect between JA and SA may also exist at the osmotic regulation level. The combined treatment almost loses the ability to promote the accumulation of soluble proteins and soluble sugars, but still retains a certain influence on proline metabolism, which may be related to the relative independence of proline synthesis regulation. In addition, both SA and JA alone significantly reduced the MDA content and electrical conductivity, which is basically consistent with the reports that exogenous SA or JA can alleviate membrane lipid peroxidation, reduce membrane permeability and improve membrane stability. The protective effect of the JA+SA mixed treatment on membrane damage is significantly weaker than that of the individual treatment, indicating that the combined treatment may weaken the antioxidant defense and membrane protection effect due to the SA-JA signal interaction, thereby leading to stronger membrane lipid peroxidation and increased membrane permeability.

In terms of glucosinolate metabolism, there are significant differences in the response patterns of different glucosinolate components to black rot [1, 35]. Among them, IBE, PRO, SIN, RAA, NAP and 4ME generally showed an upward trend, while 4OH, GBC and NEO showed a downward trend. Similar studies have also shown that during the defense against Brassica disease, different glucosinolate components exhibit differentiated accumulation and metabolic dynamics. Some components accumulate rapidly in the early stage, while others remain stable or decline in the later stage. Overall, the content of most glucosinolate components was the highest under SA treatment, followed by JA treatment. Although the combined JA and SA treatment was higher than CK, it was significantly lower than the treatment alone. Previous studies have pointed out that exogenous hormones can significantly affect the rate of glucosinolates biosynthesis by regulating endogenous hormone balance [47]. This indicates that hormone treatment does not change the metabolic direction of each glucosinolate

component, but it can significantly affect their accumulation degree and degradation rate, thereby regulating the intensity of the defense response.

After *Xcc* infection, most phenolic acids generally show an accumulation trend, and SA treatment has the strongest promoting effect on ferulic acid, chlorogenic acid, gallic acid, coumaric acid, naringin and protocatechin, etc. The results of lignin histochemical staining and quantitative determination both indicated that SA treatment was more conducive to lignin deposition in the xylem. This indicates that exogenous SA can significantly enhance the phenylpropane metabolism and cell wall reinforcement. Previous studies have shown that the phenylpropane pathway is an important metabolic basis for disease defense [1, 54]. Its products not only include various phenolic acids and flavonoids, but also lignin precursors and lignin polymers [13, 20]. These substances can jointly participate in the disease resistance response through antibacterial, antioxidant and cell wall reinforcement [11]. Therefore, in this study, SA treatment significantly promoted the accumulation of phenolic acids and enhanced lignin deposition, indicating that it may more effectively inhibit the spread of black rot by activating phenylpropane metabolism, increasing the level of antibacterial metabolites and strengthening the mechanical barrier [1, 31]. This might be related to the fact that SA is the core molecule for the system to acquire the resistance (SAR) signaling pathway, which can activate the expression of disease-related protein (PR protein) genes, enabling plants to develop broad-spectrum resistance to a variety of pathogenic bacteria. JA mainly mediates induced systemic resistance (ISR), which is related to enhancing disease resistance by activating defense genes [14, 34].

5. Conclusion

Under the stress of black rot, significant changes occurred in the endogenous hormone levels, phenolic acid/lignin metabolism and glucosinolate components of cabbage. Exogenous SA and JA can enhance the adaptability of cabbage to black rot by regulating these defensive-related processes. Among them, SA treatment demonstrated the strongest promoting effect in hormone balance remodeling, phenylpropane metabolism activation, lignin deposition and glucosinolates accumulation, followed by

JA. However, the combined treatment of JA and SA did not show a significant synergistic effect and was weaker than the single treatment in most indicators. This indicates that under the conditions of this experiment, SA played a more crucial role in regulating the chemical and structural defenses of cabbage against black rot.

Acknowledgements

We are grateful for the support of the Gansu Province Youth Talent Individual Project (2025QNGR10), Gansu Province University Teachers' Innovation Fund Project (2025A-371), Key Project of Gansu Provincial Natural Science Foundation (25JRRA351) and Youth Mentor Support Fund of Gansu Agricultural University (GAU-QDFC-2024-16).

Author contributions

Huiping Wang, Lina Zheng and Zeci Liu designed the manuscript, Huiping Wang, Lina Zheng, Jue Wang, Tingting Dou, Jue Wang, and Xinyue Liu completed the measurement and data analysis of relevant indexes, Huiping Wang, Lina Zheng and Zeci Liu completed the manuscript. All the authors have reviewed and approved the final version of the submitted manuscript.

Declarations

The authors declare no competing interests.

References

1. Aires A, Dias CS, Carvalho R, Oliveira MH, Monteiro AA, Simões MV, Rosa EA, Bennett RN, Saavedra MJJSH. 2011. Correlations between disease severity, glucosinolate profiles and total phenolics and *Xanthomonas campestris* pv. *campestris* inoculation of different Brassicaceae. *Scientia Horticulturae*. 129: 503-510.
2. Al Mamun M, Lee BR, Park SH, Muchlas M, Bae DW, Kim TH. 2024. Interactive regulation of immune-related resistance genes with salicylic acid and jasmonic acid signaling in systemic acquired resistance in the *Xanthomonas*–Brassica pathosystem. *Frontiers in Plant Science*. 302: 154323.
3. Chi FW, Ai WD, Guo ZL, Shu L, Yong L. 2005. Determination of total sugar and reducing sugar in viola philippicassp Munda W. Becker by Anthrone Colorimetry. *Guangzhou Food Science Technology*.
4. Das K, Roychoudhury AJ. 2014. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Frontiers in Environmental Science*. 2: 53.
5. Dillard HR, Bellinder RR, Shah D. 2004. Integrated management of weeds and diseases in a cabbage cropping system. *Crop Protection*. 23: 163-168.

6. Eichmeier A, Peňázová E, Pokluda R, Vicente JG. 2019. Detection of *Xanthomonas campestris* pv. *campestris* through a real-time PCR assay targeting the Zur gene and comparison with detection targeting the hrpF gene. *European Journal of Plant Pathology*. 155: 891-902.
7. Fathi A, Shiade SR, Saleem A, Shohani F, Fazeli A, Riaz A, Zulfiqar U, Shabaan M, Ahmed I, Rahimi M. 2025. Reactive oxygen species (ROS) and antioxidant systems in enhancing plant resilience against abiotic stress. *International Journal of Agronomy*. 2025: 8834883.
8. Ferreres F, Sousa C, Vrchovská V, Valentão P, Pereira JA, Seabra RM, Andrade PB. 2006. Chemical composition and antioxidant activity of tronchuda cabbage internal leaves. *European Food Research and Technology*. 222: 88-98.
9. Holtappels D, Fortuna KJ, Moons L, Broeckaert N, Bäcker LE, Venneman S, Rombouts S, Lippens L, Baeyen S, Pollet S. 2022. The potential of bacteriophages to control *Xanthomonas campestris* pv. *campestris* at different stages of disease development. *Microbial Biotechnology*. 15: 1762-1782.
10. Islam MT, Al Mamun M, Lee BR, La VH, Jung WJ, Bae DW, Kim TH. 2021. Role of salicylic acid signaling in the biotrophy-necrotrophy transition of *Xanthomonas campestris* pv. *campestris* infection in *Brassica napus*. *Physiological and Molecular Plant Pathology.* 113: 101578.
11. Islam MT, Lee BR, Das PR, La VH, Jung HI, Kim T. 2018. Characterization of p-Coumaric acid-induced soluble and cell wall-bound phenolic metabolites in relation to disease resistance to *Xanthomonas campestris* pv. *campestris* in Chinese cabbage. *Plant Physiology and Biochemistry*. 125: 172-177.
12. Islam MT, Lee BR, Park SH, La VH, Bae DW, Kim TH. 2017. Cultivar variation in hormonal balance is a significant determinant of disease susceptibility to *Xanthomonas campestris* pv. *campestris* in *Brassica napus*. *Frontiers in Plant Science*. 8: 2121.
13. Islam MT, Lee BR, Park SH, La VH, Jung WJ, Bae DW, Kim TH. 2019. Hormonal regulations in soluble and cell-wall bound phenolic accumulation in two cultivars of *Brassica napus* contrasting susceptibility to *Xanthomonas campestris* pv. *campestris*. *Plant Science*. 285: 132-140.
14. Jamiołkowska A. 2020. Natural compounds as elicitors of plant resistance against diseases and new biocontrol strategies. *Agronomy*. 10: 173.
15. Jensen BD, Massomo SM, Swai IS, Hockenhull J, Andersen SB. 2005. Field evaluation for resistance to the black rot pathogen *Xanthomonas campestris* pv. *campestris* in cabbage (*Brassica oleracea*). *European Journal of Plant Pathology*. 113: 297-308.
16. Klessig DF, Choi HW, Dempsey DM. 2018. Systemic acquired resistance and salicylic acid: past, present, and future. *Molecular plant-microbe interactions*. 31: 871-888.
17. Kong C, Chen G, Yang L, Zhuang M, Zhang Y, Wang Y, Ji J, Fang Z, Lv HH. 2021. Germplasm screening and inheritance analysis of resistance to cabbage black rot in a worldwide collection of cabbage (*Brassica oleracea* var. *capitata*) resources. *Scientia Horticulturae*. 288: 110234.
18. Kumar D. 2014. Salicylic acid signaling in disease resistance. *Plant Science*. 228: 127-134.
19. Lange HW, Tancos MA, Smart CD. 2022. Cruciferous weeds do not act as major reservoirs of inoculum for black rot outbreaks in New York state. *Plant disease*. 106: 174-181.
20. Lee MH, Jeon HS, Kim SH, Chung JH, Roppolo D, Lee HJ, Cho HJ, Tobimatsu Y, Ralph J, Park OK. 2019. Lignin-based barrier restricts pathogens to the infection site and confers resistance in plants. The EMBO Journal. 38(23).

21. Li T, Huang Y, Xu ZS, Wang F, Xiong AS. 2019. Salicylic acid-induced differential resistance to the Tomato yellow leaf curl virus among resistant and susceptible tomato cultivars. *BMC Plant Biology*. 19: 173.
22. Li X, Niu G, Fan Y, Liu W, Wu Q, Yu C, Wang J, Xiao Y, Hou L, Jin D. 2023. Synthetic dual hormone-responsive promoters enable engineering of plants with broad-spectrum resistance. *Plant Communications*. 4.
23. Li AS, Lin YH, Huang TC, Sulistyowati L. 2017. Application of *Bacillus amyloliquefaciens* to control black rot disease on cabbage caused by *Xanthomonas campestris* pv. *campestris*. *Plant Med*. 59: 39-44.
24. Liu F, Li X, Wang M, Wen J, Yi B, Shen J, Ma C, Fu T, Tu J. 2018. Interactions of WRKY 15 and WRKY 33 transcription factors and their roles in the resistance of oilseed rape to Sclerotinia infection. *Plant Biotechnology Journal*. 16: 911-925.
25. Liu X, Wang H, Yue Z, Wang J, Wang J, Dou T, Zheng L, Liu X, Dai H, Yu J. 2026. Exogenous hydrogen sulfide enhances the resistance of cabbage seedlings to black rot by improving phenolic synthesis and reducing reactive oxygen species. *Plant Molecular Biology*. 116: 19.
26. Liu Z, Wang H, Wang J, Lv J, Xie B, Luo S, Wang S, Zhang B, Li Z, Yue Z. 2022. Physical, chemical, and biological control of black rot of brassicaceae vegetables: A review. *Frontiers in Microbiology*. 13: 1023826.
27. Liu Z, Wang J, Yue Z, Wang J, Dou T, Chen T, Li J, Dai H, Yu J. 2024. Study of cabbage antioxidant system response on early infection stage of *Xanthomonas campestris* pv. *campestris*. *BMC Plant Biology*. 24: 324.
28. Mm B.1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry*. 72: 248-254.
29. Munir S, Shahzad AN, Rai A, Petrov V, Gechev T, Shokat S, Qureshi MK. 2025. Reactive oxygen species production and signal transduction in response to stress triggered by Alternaria elicitors in Brassicaceae. *Plant Molecular Biology*. 115: 113.
30. Nambara E, Van WS. 2021. Plant hormone functions and interactions in biological systems, 287-289. *Plant Journal*.
31. Ngadze E, Coutinho TA, Icishahayo D, Van der Waals J. 2014. Effect of calcium soil amendments on phenolic compounds and soft rot resistance in potato tubers. Crop protection. 62: 40-45.
32. Orynbayev AT, Dzhalilov FS, Ignatov AN. 2020. Improved efficacy of formulated bacteriophage in control of black rot caused by *Xanthomonas campestris* pv. *campestris* on cabbage seedlings. *Archives of Phytopathology and Plant Protection*. 53: 379-394.
33. Pan X, Welti R, Wang X. 2010. Quantitative analysis of major plant hormones in crude plant extracts by high-performance liquid chromatography–mass spectrometry. *Nature protocols*. 5: 986-992.
34. Park S, Arasu MV, Jiang N, Choi SH, Lim YP, Park JT, AlDhabi NA, Kim SJ. 2014. Metabolite profiling of phenolics, anthocyanins and flavonols in cabbage (*Brassica oleracea* var. *capitata*). *Industrial Crops and Products*. 60: 8-14.
35. Rubel MH, Abuyusuf M, Nath UK, Robin AHK, Jung HJ, Kim HT, Park JI, Nou IS. 2020. Glucosinolate profile and glucosinolate biosynthesis and breakdown gene expression manifested by black rot disease infection in cabbage. *Plants*. 9: 1121.
36. Saleem S, Ragasova LN, Tekielska D, Fidurski M, Sekara A, Pokluda R. 2023. Serendipita

indica as a plant growth promoter and biocontrol agent against black rot disease in cabbage grown in a phytotron. *Agriculture*. 13: 2048.

37. Shabnam N, Tripathi I, Sharmila P, Pardha SP. 2016. A rapid, ideal, and eco-friendlier protocol for quantifying proline. *Protoplasma*. 253: 1577-1582.

38. Sies H, Belousov VV, Chandel NS, Davies MJ, Jones DP, Mann GE, Murphy MP, Yamamoto M, Winterbourn CJ. 2022. Defining roles of specific reactive oxygen species (ROS) in cell biology and physiology. *Nature Reviews Molecular Cell Biology*. 23: 499-515.

39. Singh B, Sharma S, Singh B. 2010. Antioxidant enzymes in cabbage: variability and inheritance of superoxide dismutase, peroxidase and catalase. *Scientia Horticulturae*. 124: 9-13.

40. Singh J, Upadhyay A, Bahadur A, Singh B, Singh K, Rai M. 2006. Antioxidant phytochemicals in cabbage (*Brassica oleracea* L. var. *capitata*). *Scientia Horticulturae*. 108: 233-237.

41. Singh S, Dey S, Bhatia R, Batley J, Kumar R. 2018. Molecular breeding for resistance to black rot [*Xanthomonas campestris* pv. *campestris* (Pammel) Dowson] in Brassicas: recent advances. *Euphytica*. 214: 196.

42. Sood M. 2025. Reactive oxygen species (ROS): plant perspectives on oxidative signalling and biotic stress response. *Discover Plants*. 2: 187.

43. Sun S, Liu A, Li Z, Guo T, Chen S, Ahammed GJ. 2023. Anthocyanin synthesis is critical for melatonin-induced chromium stress tolerance in tomato. *Journal of Hazardous Materials*. 453: 131456.

44. Swanson S, Gilroy S. 2010. ROS in plant development. *Physiologia Plantarum*. 138: 384-392.

45. Tiwari K, Singh A, Mal P. 2003. Effect of drip irrigation on yield of cabbage (*Brassica oleracea* L. var. *capitata*) under mulch and non-mulch conditions. *Agricultural Water Management*. 58: 19-28.

46. Ullah C, Schmidt A, Reichelt M, Tsai CJ, Gershenzon J. 2022. Lack of antagonism between salicylic acid and jasmonate signalling pathways in poplar. *New Phytologist*. 235: 701-717.

47. Wang J, Mao S, Liang M, Zhang W, Chen F, Huang K, Wu Q. 2022. Preharvest methyl jasmonate treatment increased glucosinolate biosynthesis, sulforaphane accumulation, and antioxidant activity of broccoli. *Antioxidants*. 11: 1298.

48. Wang J, Wang J, Luo S, Li W, Dou T, Liu X, Zheng L, Liu X, Liu Z, Yu J. 2026. Hydrogen sulfide modulation of quality traits and antioxidants in broccoli sprouts. *LWT*. 119429.

49. Wang J, Wang J, Luo S, Yue Z, Li J, Chen T, Dai H, Liu X, Wang G, Liu ZC. 2026. Enhancement of postharvest quality and antioxidative ability in broccoli sprouts by preharvest application of hydrogen sulfide. *Postharvest Biology and Technology*. 232: 113956.

50. Wang J, Wang J, Yue Z, Chen T, Li J, Dai H, Yu J, Liu ZC. 2025. Insights into hydrogen sulfide defense against black rot of cabbage at morphological, cellular and transcriptional metabolic levels. *Plant Physiology and Biochemistry*. 227: 110129.

51. Weyers JD, Paterson NW. 2001. Plant hormones and the control of physiological processes. *New Phytologist*. 152: 375-407.

52. Xu J, Wang X, Zu H, Zeng X, Baldwin IT, Lou Y, Li R. 2021. Molecular dissection of rice phytohormone signaling involved in resistance to a piercing-sucking herbivore. *New Phytologist*. 230: 1639-1652.

53. Yang L, Li B, Zheng XY, Li J, Yang M, Dong X, He G, An C, Deng XW. 2015. Salicylic acid biosynthesis is enhanced and contributes to increased biotrophic pathogen resistance in Arabidopsis hybrids. *Nature Communications*. 6: 7309.

54. Yue Z, Zhang G, Ercisli S, Wang J, Wang J, Li J, Chen T, Liu ZC. 2025. Identification and functional characterization of MYB genes regulating polyphenol biosynthesis in cabbage for resistance to *Xanthomonas campestris* pv. *campestris*. *Plant Physiology and Biochemistry*. 222: 109714.
55. Zhang M, Li W, Zhang T, Liu Y, Liu L. 2024. *Botrytis cinerea*-induced F-box protein 1 enhances disease resistance by inhibiting JAO/JOX-mediated jasmonic acid catabolism in Arabidopsis. *Molecular Plant*. 17: 297-311.
56. Zhang P, Jackson E, Li X, Zhang Y. 2025. Salicylic acid and jasmonic acid in plant immunity. *Horticulture Research*. 12: uhaf082.
57. Zhang Y, Xu S, Ding P, Wang D, Cheng YT, He J, Gao M, Xu F, Li Y, Zhu Z. 2010. Control of salicylic acid synthesis and systemic acquired resistance by two members of a plant-specific family of transcription factors. *Proceedings of the National Academy of Sciences*. 107: 18220-18225.
58. Zhu C, Li X, Zhang M, Wang S, Jing B, Hu C, Thomas HR, Zhou Y, Yu J, Hu Z. 2025. ERF. D2 negatively controls drought tolerance through synergistic regulation of abscisic acid and jasmonic acid in tomato. *Plant Biotechnology Journal*. 23: 3363-3381.