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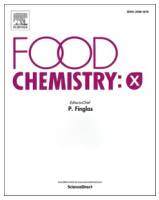

Hydrogen peroxide induced changes in the levels of disease-resistant substances and activities of disease-resistant enzymes in relation to the storability of longan fruit

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ABSTRACT

The influences of hydrogen peroxide (H_2O_2) on the storability and metabolism of disease-resistant substances in fresh longan were investigated. Compared to the control samples, H_2O_2-treated longan exhibited a higher index of fruit disease, pericarp browning, and pulp breakdown, a higher rate of fruit weight loss, but lower chromaticity values (L^*, a^* and b^*) in pericarp appearance, and a lower commercially acceptable fruit rate. Additionally, H_2O_2-treated longan showed a lower lignin content, lower activities of enzymes including phenylalnine ammonia lyase (PAL), cinnamate 4-hydroxylase (C4H), 4-coumaryl coenzyme A ligase (4-CL), cinnamate dehydrogenase (CAD), peroxidase (POD), chitinase (CHI), and β-1,3-glucanase (GLU). These data collectively suggest that H_2O_2 negatively impacted the storability of fresh longan. This can be attributed to H_2O_2's role in reducing the levels of disease-resistant substances and suppressing the activities of disease-resistant enzymes, implying that H_2O_2 reduced the postharvest storability of longan by compromising its disease resistance.

1. Introduction

Longan is one of the most favorite fruits in the world, specifically in Thailand, China, Pakistan, Vietnam, and Australia (Lin et al., 2017; Yu et al., 2022). Longan has attractive taste and flavor, as well as high nutritional value (Liu et al., 2022). It is especially rich in bioactive compounds, vitamins, and dietary fiber, making it a popular choice as medicine and food dual-purpose fruit for consumers (Y.X. Lin et al., 2020; Y.Z. Lin et al., 2020). The consumption and production of longan fruit in China have increased substantially over the last decade (Lin et al., 2018; Y.X. Lin et al., 2020). However, the reduced storability of fresh longans, leading to issues like pulp breakdown and fruit disease, significantly limits their transportation, storage, and market potential (Y.H. Chen et al., 2020; Li et al., 2023; Lin et al., 2023). Consequently, it is very important to understand the factors contributing to the reduced storability in fresh longan after harvest.

The intensity of disease-resistant metabolism, as determined by the levels of disease-resistant substances and the activities of disease-resistant enzymes, is associated with the storability of fresh products (Ge et al., 2019; Zeng et al., 2021). Researchers have elucidated that the lowered levels of disease-resistant substances and the weakened activities of disease-resistant enzymes could decrease fruit disease resistance, leading to the increased disease occurrences and the reduced storability of fresh products, such as apples (Ge et al., 2019), cherry tomatoes (Li et al., 2019), strawberries (Wei et al., 2018), and peaches (Wang et al., 2018). Additionally, prior studies illustrated that the levels of reactive oxygen species (ROS) in fruit tissues play a crucial role in disease resistance, which is affected by the levels of disease-resistant substances and activities of disease-resistant enzymes, and ultimately affecting the storability of postharvest fruit (Deng et al., 2015). During storage, lower activities of disease-resistant enzymes, including phenylalnine ammonia lyase (PAL), cinnamate 4-hydroxylase (C4H), 4-coumaryl coenzyme A ligase (4-CL), cinnamate dehydrogenase (CAD), peroxidase (POD), chitinase (CHI), and β-1,3-glucanase (GLU), could reduce the contents of

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disease-resistant substances and lead to a declined ability of disease resistance, and thus reduce the storability of harvested fruit (Li et al., 2019; Tang et al., 2021). However, there is a lack of documentation concerning the metabolism of disease-resistant substances in relation to the storability of postharvest longan. Therefore, there is a need to better understand the metabolism of disease-resistant substances in postharvest longan and its connection with the storability of fresh longan. This understanding can gain insight into the regulation of the occurrences of pulp breakdown and fruit disease in longan.

Low levels of ROS can effectively activate stress responses to adverse conditions such as senescence, cold damage, and pathogen infestation in postharvest fruits (Lin et al., 2021). However, the dysregulation of ROS metabolism, such as the outburst of $O_2^{\cdot-}$, ·OH, and H_2O_2, can further damage the cellular structure of fruits (Lin et al., 2017). Our preliminary works have consistently shown that H_2O_2 could accelerate the deterioration of quality and reduce the storability of longan fruit during storage (Lin et al. 2016; Lin et al., 2019; Y.X. Lin et al., 2020; Y.Z. Lin et al., 2020). Nevertheless, the alteration of disease-resistant substance metabolism in H_2O_2-affected fresh longan remains unexplained. Accordingly, we investigated the influences of H_2O_2 on the activities of disease-resistant enzymes (CAD, CHI, 4-CL, GLU, C4H, PAL, and POD), the levels of disease-resistant substances such as lignin, and the storability parameters including fruit disease index, commercially acceptable fruit rate, fruit weight loss rate, pericarp browning index, pericarp appearance color parameters, and pulp breakdown index in postharvest fresh longan. The object of this study is to reveal the mechanism by which ROS affects the storability of fresh longan with regard to disease-resistant substance metabolism.

2. Materials and methods

2.1. Longan fruit and postharvest treatment

'Fuyan' longan fruit, a famous variety cultivar from South China, was harvested at the Fujian Nan'an fruit orchard in China. Longans were harvested at a commercial level of ripeness, with a chromaticity value (b^*) of 53.73. Longans were transported to our laboratory within 3 h using a refrigerator car at 4 °C. The obtained longans were uniform in maturity, color, size, and shape, and were free from any diseases or defects. The initial quality indices were measured by taking 150 longans on day 0. The remaining 5000 longans were divided into two groups, each containing 2500 fruits. One group (the control group) was immersed in distilled water for 20 min, while the other group was soaked for 20 min in a solution of 1.96 mol/L H_2O_2 based on our previous work (Lin et al., 2019). After air-drying, the longans were packed in polyethylene fresh-keeping bags with a thickness of 15 μm (50 fruits per bag, 50 bags for each group), and stored at 15 °C with 80 % relative humidity for 10 d. During the storage, three selected bags (50 longan fruit per bag) from each group were used to estimate the weight loss rate of longan fruit. Additionally, for each group, three bags (150 fruit) were sampled randomly every two days of storage to determine the following indices related to storability and the metabolism of disease-resistant substances during storage.

2.2. Determination of the indices of fruit disease and pericarp browning, and commercially acceptable fruit rate

Fifty longans were sampled to evaluate the indices of fruit disease and pericarp browning, and commercially acceptable fruit rate based on the methods outlined in our previous works (Chen et al., 2015; Y.H. Chen et al., 2020). In detail, fruit disease was estimated by detecting the extent of the total lesion area on the surface of fifty individual fruits based on the following visual appearance scale: 0, No lesion; 1, lesion area <1/4; 2, 1/4 ≤ lesion area <1/2; 3, 1/2 ≤ lesion area <3/4; and 4, lesion area ≥ 3/4. The disease index was calculated as ∑(disease scale / the highest scale × proportion of corresponding fruit within each class).

Pericarp browning was estimated by detecting the extent of the total browning area of the inner pericarp of fifty individual fruits based on the following visual appearance scales: 0, no browning; 1, browning area <1/4; 2, 1/4 ≤ browning area <1/2; 3, 1/2 ≤ browning area <3/4; 4, browning area ≥ 3/4; and 5, complete browning. The browning index was calculated as ∑(browning scale × proportion of corresponding fruit within each class).

Fifty longans were sampled to estimate the rate of commercially acceptable fruit based on the method of Chen et al. (2015). Longan fruit that were not infected by pathogenic bacteria and had no surface browning were classified as commercially acceptable. The commercially acceptable fruit rate was calculated as (the number of commercially acceptable fruit/total number of fruit) × 100.

2.3. Assessments of weight loss rate of fresh longan

Three fixed bags (50 fruit per bag) of longan fruit were used to evaluate the weight loss rate of longan during storage, referring to the work of Chen et al. (2015). The weight loss rate (%) was calculated as: $(W_0\text{-}W) \div W_0 \times 100$, where W_0 = initial fruit weight at storage day 0, kg; W = fruit weight at different storage days, kg. The result was denoted as %.

2.4. Determination of longan pericarp appearance color parameters

Based on our previous work of Liu et al. (2021), the pericarp appearance chromaticity values (L^*, a^*, and b^*) of four places on the equatorial area of ten individual longans were detected using a colorimeter (Konica Minolta Inc., Japan).

2.5. Assay of pulp lignin amount in longan

Lignin amount was detected referring to our works of Jiang et al. (2018) and Wu et al. (2017) with some alteration. Longan pulp powders (50 g) from 30 longans were comminuted with liquid nitrogen, and then dried to constant weight at 100 °C in a bake oven. Then 2 g of dried longan pulp were added in 20 mL of boiled water. Afterwards, the above liquid was used to assay lignin content. The unit of lignin amount was indicated with g kg^{-1}.

2.6. Detections of pulp disease resistance enzyme activities in longan

Referring to our previous works (Jiang et al., 2018; Lin et al., 2013, 2016; Sun et al., 2023; Tang et al., 2021), 5 g of pulp samples from ten longans were taken to extract the disease-resistance enzyme solutions and assess the activities of disease-resistance enzymes, including CHI, GLU, PAL, C4H, 4-CL, CAD, and POD. One activity unit of CHI and GLU denoted the amount of enzyme catalyzing the generation of 1 mg *N*-acetylglucosamine per hour and 1 mg glucose per hour, respectively. Similarly, one activity unit of PAL, C4H, 4-CL, CAD, and POD denoted the quantity of enzymes inducing a 0.01 absorbance change at 290, 340, 333, 340, and 470 nm per minute, respectively.

The protein contents of disease-resistance enzyme solutions were assayed by the protocol of Bradford (1976). U mg^{-1} protein was adopted to express the unit of the aforementioned enzyme activities.

2.7. Data statistical

Measurements of the aforementioned indices were conducted in triplicates. Each data point in the figure was expressed as mean ± standard error (n = 3). SPSS 22.0 software (IBM Inc., Chicago, USA) was used to analyze the experimental data. $^*P < 0.05$ and $^{**}P < 0.01$ indicated the level of significant differences between the control and hydrogen peroxide-treated longans at the same storage days, according to the independent samples *t*-test.

A heat-map of Pearson correlation was drawn using the R package

ggcorrplot based on the methods of Chen et al. (2022), Chen et al. (2023) and Zhang et al. (2023). The mark * or ** in the Heat-map of Pearson correlation indicates the notable ($P < 0.05$) correlations or highly notable ($P < 0.01$) correlations between the measured parameters, respectively.

3. Results

3.1. The storability parameters

Fig. 1A displayed that the fruit disease index in the control and H_2O_2-treated samples raised quickly with the prolonged storage times. The fruit disease index in the control group rose slowly throughout the entire storage period, while the fruit disease index of H_2O_2-treated samples increased quickly from the start of storage to day 2, followed by a slow rise from days 2–4, and another rapid increase from days 4 to 10.

The pericarp browning index in both control samples and H_2O_2-treated samples increased quickly from 0 to 10 d (Fig. 1B). Compared with the control samples, the H_2O_2-treated samples maintained a higher pericarp browning index with the prolonged storage times, with a notable difference from day 4 to 10 ($P < 0.05$).

As depicted in Fig. 1C, the commercially acceptable rate in control samples decreased steadily from the start of storage to day 4, followed by a rapid decline from days 4 to 10. Contrasted to the control samples, the commercially acceptable rate of H_2O_2-treated samples decreased quickly as the storage time increased. The H_2O_2-treated samples consistently showed a lower commercially acceptable rate compared to the control longan, with significant differences observed during storage days 4 to 10 ($P < 0.05$). Especially on day 10, the commercially acceptable rate was 18.67 % higher for H_2O_2-treated samples than the control. The result implies that H_2O_2 treatment reduced the commercial acceptability of longan fruit.

The weight loss rate in both control samples and H_2O_2-treated samples increased gradually from 0 to 8 d, followed by a rapid increase from 8 to 10 d (Fig. 1D). Compared with the control samples, H_2O_2-treated samples consistently maintained a higher weight loss rate as the storage time increased, with a significant difference from 8 to 10 d ($P < 0.05$).

Chromaticity L^* value (Fig. 2A) and a^* value (Fig. 2B) in both control and H_2O_2-treated samples decreased rapidly as storage time extended·H_2O_2-treated samples consistently maintained lower chromaticity L^* and a^* values as the storage time increased, with a significant difference observed from 2 to 6 d and from 8 to 10 d, respectively ($P < 0.05$). Compared with the control samples, the chromaticity L^* and a^* value was 2.43 % and 6.58 % lower in H_2O_2-treated samples on day 10, respectively.

Fig. 2C exhibits that the chromaticity b^* value in both control and H_2O_2-treated samples declined quickly with prolonged storage times. Compared with the control samples, H_2O_2-treated samples consistently maintained a lower chromaticity b^* value as storage time extended, with a markedly difference observed from 6 to 10 d ($P < 0.01$).

3.2. The lignin content

Fig. 3A illustrates a sharp and sustained increase in the lignin content from 0 to 10 d. The lignin content in H_2O_2-treated samples increased slowly within 0 to 6 d, but decreased rapidly thereafter. Compared with the control samples, H_2O_2-treated samples maintained a lower lignin content as the storage period extended, with a noticeable difference from 4 to 10 d ($P < 0.05$). Compared with the control, the lignin content of H_2O_2-treated samples showed a maximum difference of 15.20 % on day 6. These results indicate that H_2O_2 treatment accelerated the

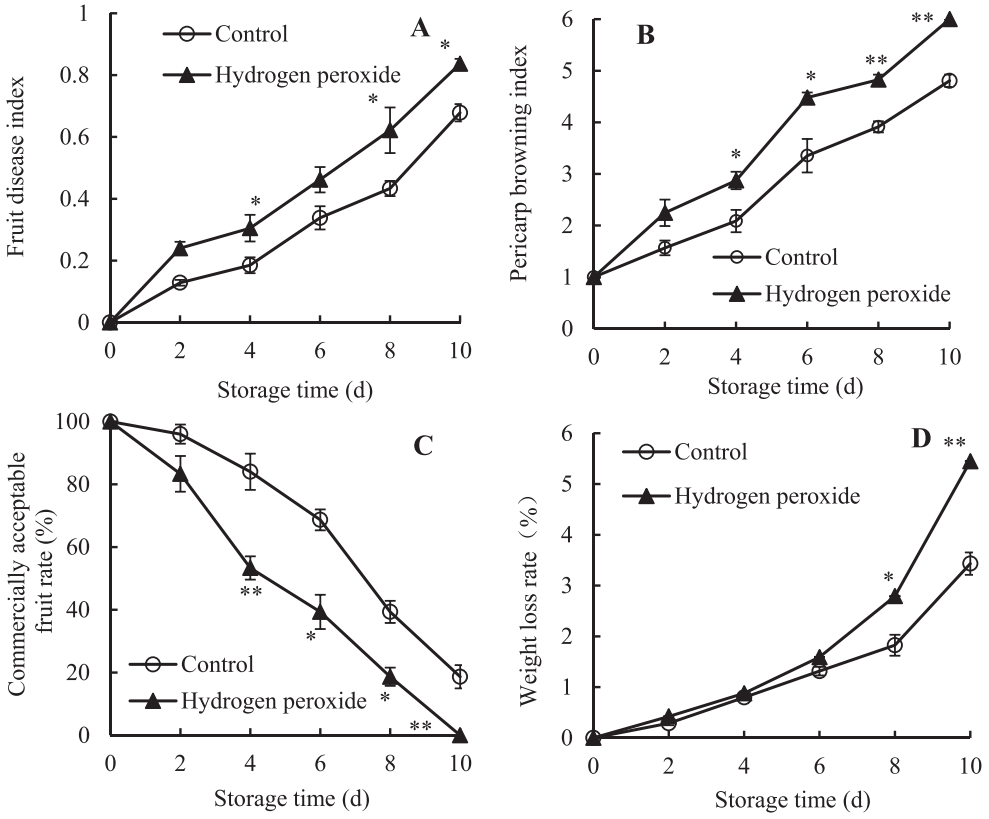

Fig. 1. Influences of hydrogen peroxide treatment on fruit disease index (A), pericarp browning index (B), commercially acceptable fruit rate (C), and weight loss rate (D) of harvested longan fruits. ▲, hydrogen peroxide treatment; ○, control. Each value is expressed as mean ± standard error (n = 3). *$P < 0.05$ and **$P < 0.01$ indicated the level of significant differences between the control and hydrogen peroxide-treated longans at the same storage days, according to the independent samples *t*-test.

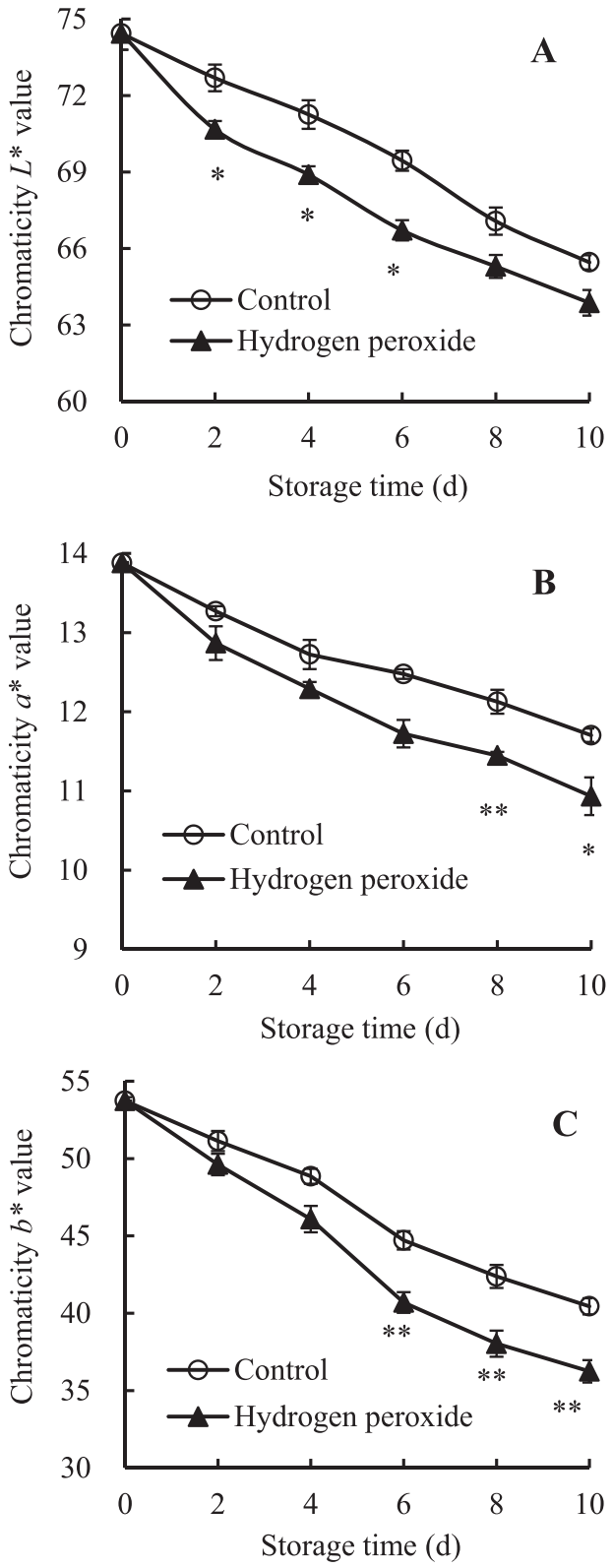

Fig. 2. Influences of hydrogen peroxide treatment on values of chromaticity L^* (A), chromaticity a^* (B), and chromaticity b^* (C) of harvested longan fruits. ▲, hydrogen peroxide treatment; ○, control. Each value is expressed as mean ± standard error (n = 3). $^*P < 0.05$ and $^{**}P < 0.01$ indicated the level of significant differences between the control and hydrogen peroxide-treated longans at the same storage days, according to the independent samples *t*-test.

reduction of the lignin content in longan pulp.

3.3. CHI and GLU activities

The CHI activity in the pulp of control longans increased progressively from 0 to 6 d, and gradually declined afterward (Fig. 3B). The CHI activity in the pulp of longans treated with H_2O_2 increased slowly within 0 to 4 d, followed by a rapid enhancement from days 4 to 6, and a subsequent decline. Compared with the control samples, H_2O_2-treated samples maintained lower CHI activity with prolonged storage times, with an obvious discrepancy from 4 to 10 d ($P < 0.05$), and an extremely significant difference on day 10 ($P < 0.01$).

The GLU activity in the pulp of control samples gradually ascended within days 0–4, and rapidly enhanced from days 4 to 6, but declined progressively afterwards (Fig. 3C). Nevertheless, the GLU activity in the pulp of H_2O_2-treated longans increased slowly from 0 to 4 d, then quickly from days 4 to 6, and dropped slowly from days 6 to 8, but declined quickly afterwards. Statistical analysis demonstrated that the GLU activity in the pulp of longans treated with H_2O_2 was always lower than that of the control longans, with significantly lower activities observed from 4 to 6 d, on day 10 ($P < 0.05$), and an extremely significant difference on day 8 ($P < 0.01$).

3.4. The activities of PAL, C4H, 4-CL, CAD, and POD

The PAL activity in the pulp of control longans enhanced speedily from 0 to 6 d, declined quickly during 6 to 8 d, and then declined slowly (Fig. 3D). Nevertheless, the PAL activity in the pulp of H_2O_2-treated longans increased quickly within 0 to 2 d, and gradually from 2 to 6 d, decreased quickly during days 6–8, followed by a slow reduction. Compared with the control samples, H_2O_2-treated samples maintained lower PAL activity in the pulp with prolonged storage times and displayed a markedly lower level from 4 to 10 d ($P < 0.05$).

The C4H activity in the pulp of control and H_2O_2-treated longans enhanced slowly from 0 to 4 d, rapidly from 4 to 6 d, and then gradually declined (Fig. 3E). Compared with the control samples, H_2O_2-treated samples showed lower C4H activity in the pulp as storage time increased, with a markedly lower activity observed from 6 to 10 d ($P < 0.05$). Moreover, the C4H activity in the pulp of H_2O_2-treated longans declined to the lowest level at the end of storage, which was 30.45 % lower than the control.

The pulp 4-CL activity in control longans ascended rapidly within 0–2 d, gradually elevated during 2–4 d, slowly enhanced from 4 to 6 d, and then gradually declined (Fig. 3F). Nevertheless, the 4-CL activity in the pulp of longans treated with H_2O_2 increased slowly during 0 to 4 d, and gradually declined afterwards. Compared with the control samples, H_2O_2-treated samples showed lower 4-CL activity in the pulp with prolonged storage times and displayed markedly lower activities from 4 to 10 d ($P < 0.05$).

The CAD activity in the pulp of control longans increased progressively within 0 to 6 d, raised slowly from 6 to 8 d, but progressively decreased afterwards (Fig. 3G). Nevertheless, the CAD activity in the pulp of H_2O_2-treated longans increased slowly from 0 to 8 d, followed by a speedy decline. Compared with the control samples, H_2O_2-treated samples kept lower CAD activity in the pulp with the prolonged storage times and displayed evidently lower activities from 4 to 10 d ($P < 0.05$).

The pulp POD activity in the control and H_2O_2-treated samples increased in as storage time progressed (Fig. 3H). More importantly, compared with the control samples, H_2O_2-treated samples exhibited lower POD activity in the pulp as storage times increased, with remarkably lower activities observed from 4 to 10 d ($P < 0.05$). Specifically, on day 10, the POD activity in H_2O_2-treated samples was only 80 % of that in the control samples.

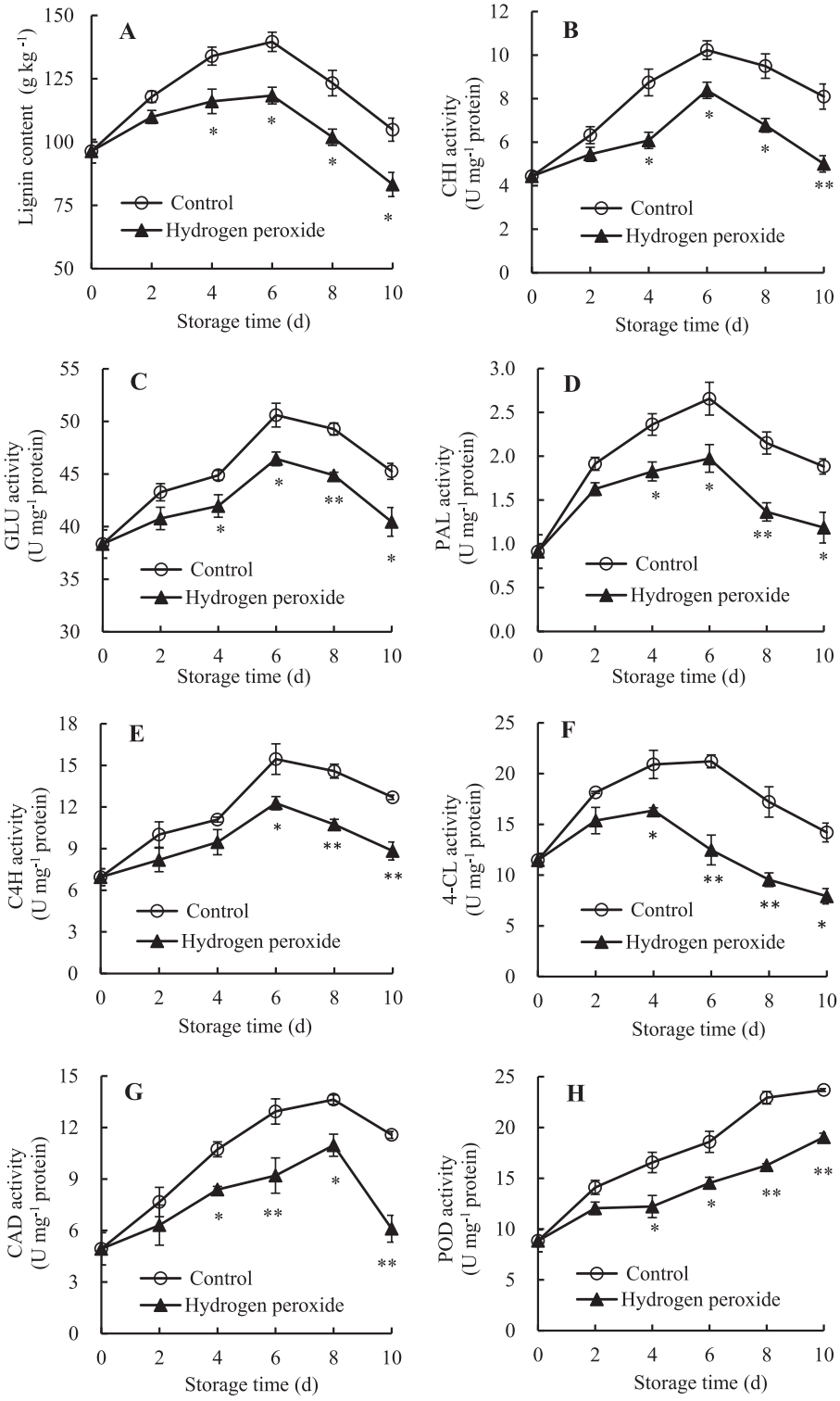

Fig. 3. Influences of hydrogen peroxide treatment on content of lignin (A), the activities of CHI (B) and GLU (C), PAL (D), C4H (E), 4-CL (F), CAD (G), and POD (H) in pulp of harvested longan fruits. ▲, hydrogen peroxide treatment; ○, control. Each value is expressed as mean ± standard error (n = 3). *$P < 0.05$ and **$P < 0.01$ indicated the level of significant differences between the control and hydrogen peroxide-treated longans at the same storage days, according to the independent samples *t*-test.

4. Discussion

4.1. H_2O_2 induced changes in storability parameters of postharvest longans

Postharvest longan is susceptible to fruit disease, pulp breakdown, and pericarp browning (Lin et al., 2023; Yu et al., 2022). During storage, these symptoms can seriously reduce storability and cause economic losses in longan fruit (Liu et al., 2021; Liu et al., 2022). Pulp breakdown, a major issue in postharvest longan, can decrease the edible quality of fresh longan (Y.X. Lin et al., 2020; Y.Z. Lin et al., 2020; Y.Z. Lin et al., 2020). The commercially acceptable fruit rate is an indicator of fruit

quality based on the criteria related to disease, pulp breakdown, and pericarp browning, which are not tolerated in longan (Chen et al., 2015). Additionally, weight loss of longan increased with the extended storage period, primarily due to juice exosmosis and moisture loss during storage (Y.Z. Lin et al., 2020). Furthermore, color characteristics are used to assess the freshness, storage quality, and commercial grades of fresh produce, influencing consumer purchasing decisions (Liu et al., 2021). Pericarp browning is another principal postharvest factor resulting in the unattractive appearance of postharvest longan (Liu et al., 2021).

This study demonstrated that, during storage, the indices of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), pulp breakdown (Fig. S1), and the rate of weight loss (Fig. 1D) in postharvest longans increased rapidly, but the commercially acceptable fruit rate (Fig. 1C) and chromaticity L^*, a^*, b^* value (Fig. 2) dropped. Meanwhile, correlation analysis displayed that, during storage, the decreased commercially acceptable fruit rate (Fig. 1C) was highly negatively associated with the enhanced indies of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), and pulp breakdown (Fig. S1) in control fruits, with correlation coefficients (r) of −0.956, −0.950, and −0.980, respectively. Besides, the increased rate of weight loss (Fig. 1D) has a clear positive correlation with the enhanced indies of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), and pulp breakdown (Fig. S1) in the control longans, with r values of 0.977, 0.921, and 0.971, respectively. These findings reveal that the increase in weight loss of postharvest longans was associated with the occurrence of extensive juice exudation after pulp breakdown, which provided nutrients for pathogens and accelerated the occurrence of fruit disease and pericarp browning. These factors together decreased the storability and the commercially acceptable rate of fresh longan fruit after harvesting.

Moreover, the reduced rate of commercially acceptable fruit (Fig. 1C) has a clear positive connection with the reduced value of chromaticity L^* (Fig. 2A), chromaticity a^* (Fig. 2B), and chromaticity b^* (Fig. 2C) in the control fruits, with r values of 0.963, 0.870, and 0.923, respectively. Conversely, the reduced values of chromaticity L^* (Fig. 2A), chromaticity a^* (Fig. 2B), and chromaticity b^* (Fig. 2C) were negatively connected with the raised index of fruit disease (Fig. 1A) in the control fruits, with r values of − 0.967, − 0.923, and − 0.942, respectively. They also showed negative connections with the increased index of pericarp browning (Fig. 1B) with r values of − 0.984, − 0.938, and − 0.990, respectively, and with the enhanced indies of pulp breakdown (Fig. S1) with r values of − 0.984, − 0.931, and − 0.955, respectively. This correlation analysis corroborated that the occurrences of fruit disease, pulp breakdown, and pericarp browning, and the reductions in chromaticity L^*, a^*, and b^* values in pericarp appearance, were associated with the declination in the commercially acceptable fruit rate in postharvest longan.

In addition, the results of this work displayed that, in contrast to the control fruits, H_2O_2-treated samples exhibited a lower rate of commercially acceptable fruit (Fig. 1 C), lower values of chromaticity L^*, a^*, and b^* in pericarp appearance (Fig. 2), but a higher rate of weight loss (Fig. 1D), higher indices of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), and pulp breakdown (Fig. S1) as the storage time extended. These results prove that H_2O_2 treatment accelerated the occurrence of longan fruit disease, pulp breakdown, and pericarp browning, resulting in a lower rate of commercially acceptable fruit, a higher weight loss rate, and ultimately, a decline in the fruit quality and appearance of postharvest longans during storage.

4.2. H_2O_2 induced the changes in the levels of disease-resistance substances and their connection to the storability of postharvest longans

The disease-resistance substances in fresh fruit, including total phenolics, lignin, and flavonoids, play a key role in the fruit's defense system against diseases (Wei et al., 2021). However, the decreased level of these disease-resistance substances can reduce the ability of the disease defense system and disease resistance of postharvest fresh fruit (Zeng et al., 2021; Zheng et al., 2011). Therefore, maintaining higher levels of disease-resistance substances can help preserve the fruit's disease resistance ability and ultimately increase the storage quality of postharvest fresh fruit.

The indices of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), pulp breakdown (Fig. S1) in the control fruits increased with the decline in longan pulp lignin (Fig. 3A), flavonoids (Fig. S2A) and total phenolics content (Fig. S2B). Further correlation analysis reveals that the enhanced indices of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), pulp breakdown (Fig. S1) showed significantly negative connections with the dropped content of pulp lignin (Fig. 3A) in control longans during storage days 6–10, with r values of, − 0.955, − 0.991, and − 0.996, respectively (Fig. 4A). They also showed negative connections with the dropped levels of pulp flavonoids (Fig. S2A) in the control fruits, with r values of − 0.905, − 0.914, and − 0.914, respectively, and with the dropped levels of pulp total phenolics (Fig. S2B) in control fruits, with r values of − 0.934, − 0.978, and − 0.943, respectively (Fig. 4A). This correlation analysis reveals that the decreased ability of disease resistance was associated with the reduction in the levels of disease-resistance substance (lignin, flavonoids, and total phenolics), and consequently promoted the occurrence of diseases, pericarp browning, and pulp breakdown in postharvest longan.

Additionally, the results from this study reveal that, in contrast to the control sample, there were increased indices of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), pulp breakdown (Fig. S1), but lower contents of lignin (Fig. 3A), flavonoids (Fig. S2A), and total phenolics (Fig. S2B) in the pulp of H_2O_2-treated fruit. Furthermore, the correlations between these indicators in longans treated with hydrogen peroxide (Fig. 4B) were similar to those in the control group (Fig. 4A), but with different correlation coefficients. This work discovered that H_2O_2 accelerated the decline in the content of these three disease-resistant substances, reducing disease resistance, and consequently, accelerating the development of longan fruit disease, pericarp browning, and pulp breakdown. These data align with other previous studies showing that lower levels of total phenolics, lignin, and flavonoids could lead to the reduced disease resistance and promote disease occurrence, ultimately resulting in the decreased storage quality in cherry tomatoes (Li et al., 2019), and apples (Ge et al., 2019). Whereas the elevated levels of lignin, flavonoid, and total phenolics were favorable for mitigating disease development and increasing the storage quality in cherry tomatoes (Li et al., 2019), and apples (Ge et al., 2019) when the treatment of melatonin or sodium nitroprusside were applied.

4.3. H_2O_2 induced the changes in the activities of disease-resistance enzymes and their connection to the storability of postharvest longans

The alteration of disease-resistance ability is closely associated with the metabolism of disease-resistant substances, which can influence the storability of fresh products (Sun et al., 2022; Sun et al., 2023; Wei et al., 2021). Furthermore, it has been widely reported that CHI, GLU, PAL, C4H, 4-CL, CAD, and POD are the most featured enzymes and play different roles in the metabolism of disease-resistant substances, commonly regarded as an index to evaluate disease resistance ability (Sun et al., 2023; Tang et al., 2021; Zhu et al., 2022). GLU and CHI can decompose β-1,3-glucan and chitin in the cell walls of fungi, thereby suppressing fungus and inducing host defense responses (Wu et al., 2017). PAL, 4-CL, and C4H are the three key enzymes in the metabolism of disease-resistant substances, which is linked to the synthesis of numerous antibacterial substances, for instance, lignin, flavonoids, and phenolic compounds (Ge et al., 2019; Wang et al., 2018). POD is particularly related to the reinforcement of fruit cell walls by regulating lignin accumulation (Li et al., 2019; Zhao et al., 2009). Therefore, the activities of disease resistance enzymes could play a crucial role in regulating disease resistance ability and consequently influence the storability of longan after harvest.

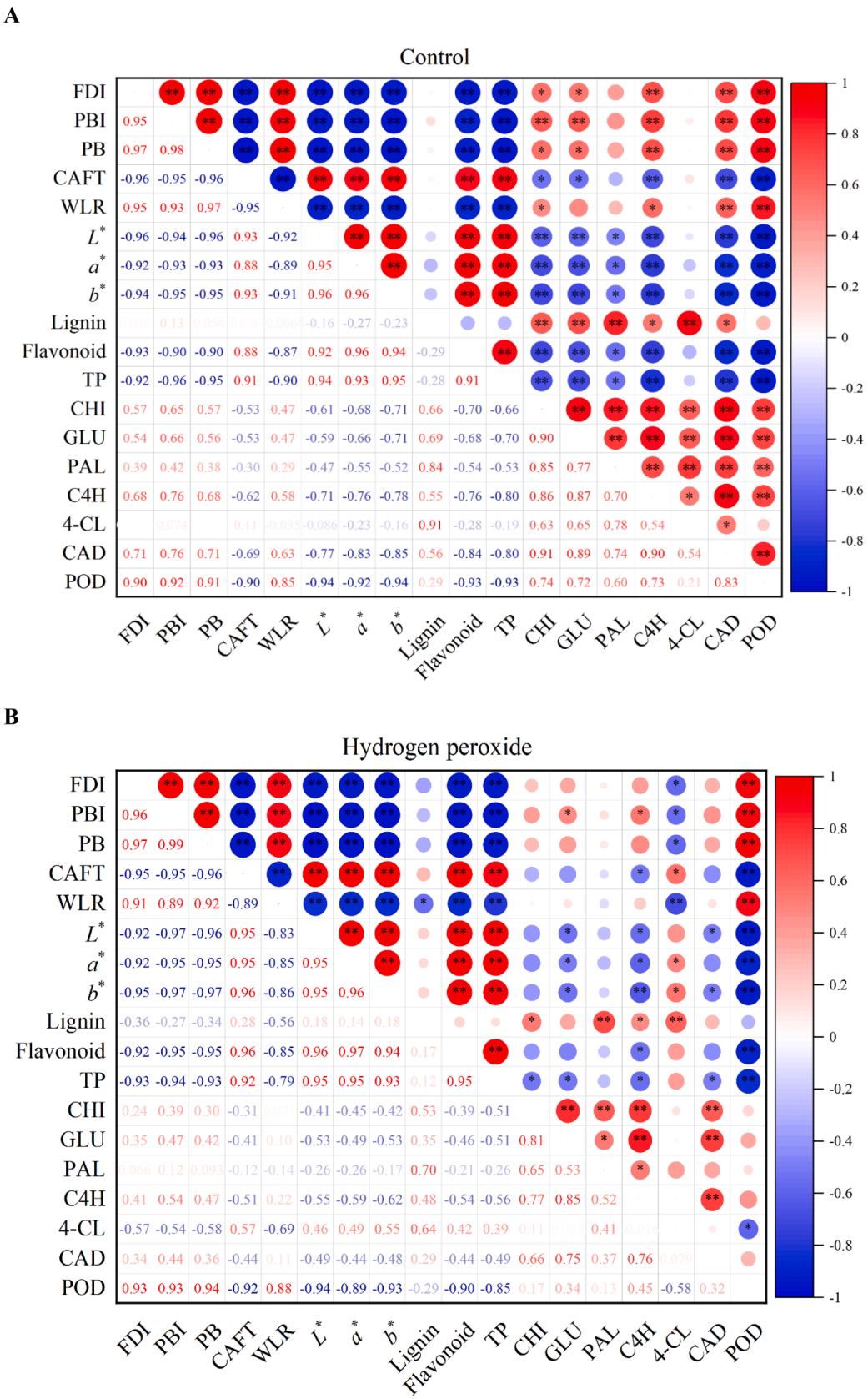

Fig. 4. Heat-map of Pearson correlations based on the measured parameters in longan fruits. Blue presents a negative correlation. Red presents a positive correlation. The mark * or ** indicated the notable ($P < 0.05$) correlations or extremely notable ($P < 0.01$) correlations between these measured parameters, respectively. FDI, fruit disease index; PBI, pericarp browning index; PB, pulp breakdown; CAFT, commercially acceptable fruit rate; WLR, weight loss rate; TP, total phenolics; CHI, chitinase; GLU, β-1,3-glucanase; PAL, phenylalnine ammonia lyase; C4H, cinnamate 4-hydroxylase; 4-CL, 4-coumaryl coenzyme A ligase; CAD, cinnamate dehydrogenase; POD, peroxidase. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This work demonstrates that the activities of CHI (Fig. 3B) and GLU (Fig. 3C) in the pulp of control fruits showed a decreasing tendency with the extension of storage days. Correlation analysis displays that the reduced activities of CHI (Fig. 3B) and GLU (Fig. 3C) demonstrated highly negative correlations with the increased fruit disease index (Fig. 1A) of the control fruit during storage days 6–10, with *r* values of − 0.995 and − 0.999, respectively (Fig. 4A). Additionally, the decreased activities of these enzymes were negatively related to the increased pericarp browning index (Fig. 1B), with *r* values of − 0.998 and − 0.977, respectively. Furthermore, the decreased activities of CHI (Fig. 3B) and GLU (Fig. 3C) were also negatively related to the elevated pulp breakdown index (Fig. S1), with *r* values of − 0.993 and − 0.965, respectively (Fig. 4A). These results confirm that the decreased activities of CHI and GLU could result in a reduced ability of disease resistance, and consequently expediting the occurrence of longan fruit disease, pericarp browning, and pulp breakdown.

Furthermore, compared to the control sample, H_2O_2-treated longans showed lower activities of pulp CHI (Fig. 3B) and GLU (Fig. 3C), but higher indices of fruit disease (Fig. 1A), pericarp browning (Fig. 1B), and pulp breakdown (Fig. S1). Similarly, as shown in Fig. 4, the correlations between these measures in H_2O_2-treated longans were the same as those in the control group, but the coefficients were different. These data prove that H_2O_2 could decrease the activities of CHI and GLU in the pulp of longan after harvest, implying a reduced ability of disease resistance in longan fruit. These results might expedite the occurrence of longan fruit disease, pericarp browning, and pulp breakdown. These data agree with some prior studies showing that lower activities of GLU and CHI could result in decreased ability of disease resistance and promote the occurrence of fruit disease, and reduce storage quality in peaches (Wang et al., 2018), tomatoes (Shu et al., 2021), and strawberries (Wei et al., 2018). Whereas an enhancement in the activities of GLU and CHI was beneficial for mitigating fruit disease development and increasing the storage quality in peaches (Wang et al., 2018), tomatoes (Shu et al., 2021), and strawberries (Wei et al., 2018) by the treatment of tea tree oil or *β*-aminobutyric acid, nitric oxide, and hot air, separately.

Besides, this study also demonstrated that the activities of PAL, C4H, 4-CL, CAD, and POD in the pulp of the control longans illustrated varying trends with the extension of storage time (Fig. 3D-H). The correlation analysis illustrates that the decreased activities of PAL (Fig. 3D), C4H (Fig. 3E), and 4-CL (Fig. 3F) showed clear positive correlations with the reduced lignin content (Fig. 3A) in the control fruit within storage days 6–10, with *r* values of 0.856, 0.970 and 0.987, respectively. They also showed positive connections with the decreased flavonoid content (Fig. S2A) with *r* values of 0.974, 0.951, and 0.995, respectively, and with declined total phenolics content (Fig. S2B) with *r* values of 0.992, 0.914, and 0.998, respectively. Additionally, decreased activities of these enzymes showed clear negative correlations with the increased fruit disease index (Fig. 1A) with *r* values of − 0.830, − 0.998, and − 0.895, respectively. Also, decreased activities of these enzymes were negatively related to the increased pericarp browning index (Fig. 1B) with *r* values of − 0.909, − 0.994, and − 0.955, respectively, and with the raised pulp breakdown index (Fig. S1) with *r* values of − 0.928, − 0.987, and − 0.969, respectively. These results testify that decreased activities of PAL, C4H, and 4-CL could lead to decreased levels of disease-resistance substances and reduced ability of disease resistance, and consequently expediting the occurrence of longan fruit disease, pericarp browning, and pulp breakdown.

Moreover, compared to the control sample, H_2O_2-treated fruits exhibited lower activities of pulp PAL, C4H, 4-CL, CAD, and POD (Fig. 3D-H), lower contents of lignin (Fig. 3A), flavonoids (Fig. S2A) and total phenolics (Fig. S2B), but higher indices of pulp breakdown (Fig. S1) and fruit disease (Fig. 1A). Furthermore, as shown in Fig. 4B, the correlation between the content of disease-resistant substances and the activity of disease-resistant enzymes, as well as their relation to the index of pulp breakdown and fruit disease in H_2O_2-treated longans, was the same as those in the control group, but the coefficients were different. These data prove that H_2O_2 could increase the activity of disease-resistant enzymes (PAL, C4H, 4-CL, CAD, and POD) and decrease the content of disease-resistant substances, thereby diminishing the ability of disease resistance of longan fruit. Some studies reported that the reduced activities of disease-resistance enzymes ineffectively promoted the accumulation of disease-resistance substances, and increased disease incidence in pears (Sun et al., 2022), tomatoes (Zheng et al., 2011), and peaches (Wang et al., 2018). These data prove that H_2O_2 could decrease the activities of disease-resistance enzymes in the pulp of postharvest longans, implying a reduced accumulation of disease-resistance substances. Consequently, these activities would impair the ability of disease resistance and then expedite the occurrence of longan fruit disease, pericarp browning, and pulp breakdown.

Based on the above findings, the probable mechanism of H_2O_2-stimulated occurrences of fruit disease, pulp breakdown, and pericarp browning in postharvest longans was summarized in Fig. 5. This suggests a pathway for modulating the metabolism of disease-resistance substances. However, the molecular mechanisms underlying H_2O_2-stimulated occurrences of fruit disease, pulp breakdown, and pericarp browning in postharvest longans remain unclear. Thus, the molecular mechanisms of H_2O_2-stimulated occurrences of fruit disease, pulp breakdown, and pericarp browning in postharvest longans should be further unraveled by the analyses of metabolomics and transcriptomics.

5. Conclusions

In summary, the heightened occurrence of fruit disease, pulp breakdown, and pericarp browning in H_2O_2-treated longans could be related to the metabolism of its disease-resistant substances·H_2O_2 promoted the deterioration of quality in postharvest longans, which was because H_2O_2 reduced the activities of disease-resistance enzymes (CHI, GLU, PAL, C4H, 4-CL, CAD, and POD) and the levels of disease-resistant

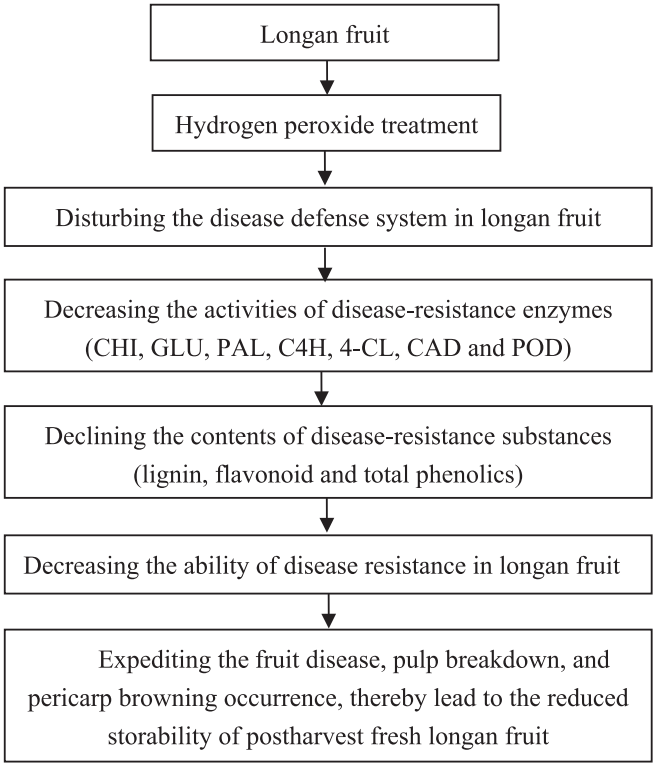

Fig. 5. The probable mechanism of hydrogen peroxide induced the reduced-storability of longans by modulating the metabolism of disease-resistant substances.

substances (lignin, flavonoids, and total phenolics). Consequently, it accelerated the functional loss of the disease defense system and decreased the ability of disease resistance, thereby expediting the occurrence of fruit disease, pulp breakdown, and pericarp browning in postharvest fresh longan.

CRediT authorship contribution statement

Yixiong Lin: Project administration, Investigation, Data curation, Formal analysis, Writing – original draft. **Yifen Lin:** Supervision, Project administration, Writing – review & editing. **Huili Zhang:** Investigation, Data curation, Formal analysis. **Mengshi Lin:** Writing – review & editing. **Lian Chen:** Investigation. **Hui Li:** Investigation. **Hetong Lin:** Supervision, Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2023.100923.

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