

Transcriptome Profiling Reveals the Molecular Mechanisms Governing Postharvest Senescence in Fresh Bamboo Shoots (*Chimonobambusa quadrangularis*) upon SNP Treatment

Jinyang Xu

Guiyang University

Ning Ji

jining552100@163.com

Guiyang University

Rui Wang

Guiyang University

Ni Zhang

Guiyang University

Renchan Liu

Guiyang University

Yuxin Li

Guiyang University

Jiqing Lei

Guiyang University

Research Article

Keywords: fresh bamboo shoots (*Chimonobambusa quadrangularis*), NO, transcriptome, postharvest senescence

Posted Date: March 7th, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-3924305/v1>

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

[Read Full License](#)

Additional Declarations: Competing interest reported. The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ning Ji

reports financial support was provided by Guiyang University. Ning Ji reports financial support was provided by Guizhou Provincial Department of Science and Technology. Ning Ji reports financial support was provided by Guiyang Science and Technology Bureau.

Abstract

Nitric oxide (NO) is a crucial physiological molecule that plays a regulatory role in maintaining the postharvest quality of fruits and vegetables. While previous studies have acknowledged the potential of NO in preserving the postharvest quality of bamboo shoots, the precise mechanism behind this regulatory function remains elusive. In this particular investigation, we aimed to elucidate the underlying mechanism by identifying key genes involved in NO-mediated regulation of postharvest senescence in bamboo shoots (*Chimonobambusa quadrangularis*). To achieve this, we integrated physiological data with transcriptome data. Notably, our study employed a $0.25 \text{ mmol}\cdot\text{L}^{-1}$ SNP (NO) soaking treatment, which significantly demonstrated its capability to delay senescence, as well as inhibit browning and lignification in bamboo shoots. Transcriptome analysis revealed a total of 5077 genes exhibiting differential expression between the NO treatment group and the control group. Several of these genes were associated with the biosynthesis of lignin, ethylene, and abscisic acid, all of which were notably suppressed. In addition, the expression of genes linked to reactive oxygen metabolism was significantly altered, resulting in a reduction in reactive oxygen species accumulation. Based on our experimental findings, it is evident that NO treatment effectively retards the postharvest lignification and browning of fresh bamboo shoots. This is achieved through the inhibition of lignin biosynthesis, regulation of related plant hormone synthesis, and reduction of reactive oxygen species accumulation, collectively contributing to the delay of postharvest senescence in fresh bamboo shoots. The implications of our study shed light on the potential application of NO treatment in preserving the quality of perishable produce during postharvest handling.

1. Introduction

Bamboo shoots are the young buds that emerge through the germination of underground rhizomes of bamboo. They are renowned for their high nutritional value and are widely consumed as a crispy, tender, and delectable vegetable in Asian cuisine (Yang et al. 2011). *Chimonobambusa quadrangularis*, a bamboo species predominantly cultivated in southwest China, is particularly esteemed for its fresh shoots, offering exceptional taste, flavor, and nutritional benefits (Chen et al. 2018). Nonetheless, these shoots have a limited storage life and are highly vulnerable to postharvest senescence due to robust physiological metabolism. Senescence, an inevitable and irreversible process, leads to alterations in color, texture, and nutrient composition of fruits and vegetables (Tang et al. 2020). Postharvest quality is affected by browning and lignification, which are key indicators of bamboo shoot senescence (Yu et al. 2021). In recent years, various preservation methods, such as modified atmosphere packaging (Song et al. 2013), low-temperature storage (Li et al. 2018), and irradiation treatment (Wang et al. 2019a), have been developed to decelerate the senescence of bamboo shoots during storage. Nevertheless, the regulatory mechanism governing postharvest senescence in fresh bamboo shoots remains inadequately understood, necessitating the development of more effective storage technologies to ensure their preservation.

Nitric oxide (NO) serves as a signaling molecule capable of diffusing and penetrating cell membranes, thus participating in diverse plant life activities. It plays a crucial role in biological processes, including senescence, abiotic stress, and biotic stress in fruits and vegetables (Dai et al. 2021). In recent years, Sodium nitroprusside (SNP), an NO donor, has found widespread use in preserving various fruits and vegetables, as it is believed to inhibit the lignification process (Sun et al. 2021). The lignin biosynthesis pathway involves phenylalanine biosynthesis, phenylalanine metabolism, and phenylpropanoid metabolism. It is widely accepted that lignin accumulation leads to plant lignification in most model plants (Wang et al. 2021; Liu et al. 2019). Key enzymes involved in lignin synthesis encompass Phenylalanine ammonia lyase (PAL), Peroxidase (POD), 4-coumaric acid CoA ligase (4CL), Cinnamoyl CoA reductase (CCR), Cinnamyl alcohol dehydrogenase (CAD), and Branched acid mutase (CM) (Zhang et al. 2021). Qi et al (Qi et al. 2020) reported that NO treatment in bamboo shoots inhibited PAL, CAD, POD, and laccase activities, thus delaying lignification, and underscoring the critical role of NO in plant lignin accumulation.

Plant hormones represent a distinct class of signaling molecules exclusively found in plant cells, and they play a pivotal regulatory role in various biological functions of plants. They are closely associated with plant growth, development, and senescence as they specifically bind to receptor proteins in specific tissues, thus orchestrating plant growth and development. Moreover, fluctuations in hormone levels exert a certain influence on plant growth and senescence. The six most significant plant hormones in plants are ethylene, abscisic acid, auxin, cytokinin, gibberellin, and salicylic acid. Notably, nitric oxide (NO) has the capacity to regulate the biosynthesis of certain plant hormones, such as ethylene and abscisic acid (ABA), thereby enhancing the storage quality of postharvest fruits and delaying senescence (Zhang et al. 2020). Ethylene is responsible for promoting fruit and vegetable ripening and cell senescence, with its metabolism potentially affecting bamboo shoots, despite not being climacteric fruits and vegetables (Luo et al. 2007). In this regard, NO treatment has been observed to inhibit ACS synthase and ACO activity involved in ethylene biosynthesis (Mukherjee 2019). Fruits and vegetables postharvest ABA also plays a crucial role in cell senescence and stress response (Chen et al. 2020). Upon ABA induction, reactive oxygen species (ROS) accumulate in fruit tissues, leading to senescence and browning (Wang et al. 2019b). However, NO can counteract this process by reducing ROS levels and regulating the ABA signaling pathway, ultimately inhibiting ABA biosynthesis (Prakash et al. 2019).

The appearance and color of fruits and vegetables play a crucial role in determining their quality, a significant factor for consumers. Browning, which reduces the quality of these commodities (Zuo et al. 2021), is primarily attributed to enzymatic browning. During postharvest storage, phenolic compounds in fruits and vegetables undergo oxidation to form quinones when they come into contact with polyphenol oxidase (PPO). Subsequently, dehydration, polymerization, and other reactions take place, resulting in the undesirable browning phenomenon. In organisms, phenols and quinones typically exist in equilibrium, but oxidative damage to the cell membrane of bamboo shoots during postharvest storage disrupts this balance, leading to a significant conversion of phenols into quinones and thus accelerating the enzymatic browning of bamboo shoots (Barberis et al. 2019). A critical factor contributing to cell oxidative damage is the presence of reactive oxygen species (ROS). By increasing ROS levels,

malondialdehyde (MDA) accumulates and cell membrane permeability increases, ultimately hastening postharvest senescence (Lin et al. 2020). However, by activating the scavenging ability of reactive oxygen species in bamboo shoots, rapid senescence during storage can be effectively delayed, while also inhibiting the occurrence of browning. This strategy proves to be beneficial for maintaining the overall quality of bamboo shoots.

Presently, the impact of nitric oxide (NO) on the senescence mechanism of bamboo shoots during storage remains obscure. In this study, we put forth the hypothesis that treating bamboo shoots with SNP (sodium nitroprusside) can effectively delay senescence and uphold their overall quality by mitigating lignin accumulation and tissue browning. To explore the association between exogenous NO treatment and lignin biosynthesis as well as browning, we rely on a combination of physiological and molecular sequencing data. Additionally, the investigation entails the identification of differentially expressed genes during storage and an analysis of enzyme activities linked to the postharvest senescence inhibition induced by SNP treatment. The outcomes of this study yield novel insights into the aging mechanism of *Chimonobambusa quadrangularis* shoots following their storage period.

2. Materials and Methods

2.1. Plant Material

Bamboo shoots (*Chimonobambusa quadrangularis*) were collected from Taibai Town in Suiyang County, Zunyi City, Guizhou Province, China (28° 40' 50.40" N, 107° 09' 26.00" E). Fresh shoots of similar length, free from mechanical injury, pests, and diseases, were selected as experimental materials. Randomly divide 60 kg bamboo shoots into two groups: CK group and SNP group. The concentration selection was based on preliminary studies including 0.25, 0.5, or 1.0 mmol·L⁻¹ SNP. The corresponding experimental results were presented in the supplementary materials, and 0.25 mmol·L⁻¹ SNP was selected as the appropriate treatment concentration. This study used two treatment methods, namely the control group (soaked in distilled water for 2 minutes) and the 0.25 mmol·L⁻¹ SNP group (soaked for 2 minutes). After all fresh bamboo shoots are ventilated and dried, they are stored at a temperature of (1.0 ± 0.3)°C and a humidity of (90 ± 5)%. Each bag of 2.5 ± 0.5 kg fresh bamboo shoots is stored in a 0.02mm PE self controlled atmosphere bag (Preliminary experiments have been conducted, and the specific data is attached). After pre cooling for 24 hours in the cold storage, tie the self controlled atmosphere bag of all samples. Randomly sampled at days 15, 30, 45, and 60 for relevant indicator analysis. For further biochemical analysis, bamboo shoot samples were stored at -80°C in liquid nitrogen .

After 45 days of storage, the hardness, browning index, weight loss rate and other physiological indicators related to quality of SNP treatment began to be significantly better than those of CK treatment. Therefore, RNA extraction was extracted and sequenced from fresh bamboo shoots stored for 45 days. CK represents bamboo shoots soaked in distilled water, and SNP represents bamboo shoots soaked in 0.25mol·L⁻¹ SNP.

2.2. Determination of respiratory intensity, weight loss rate, soluble protein content and free amino acid content

The respiratory rate was measured using the standing method (Zhang et al. 2018). Two kilograms of bamboo shoots were randomly selected, weighed, and placed in a 30 L sealed plastic box. The bamboo shoots were allowed to stand at 25°C for 2 hours, measuring the respiratory intensity of bamboo shoots using a residual oxygen meter (Checkpoint 3 Premium, Mocon Inc., Minneapolis, MN, USA).

Measuring the weight loss rate of bamboo shoots during storage using the weighing method (Xu et al. 2021). The initial weight of each treatment was recorded on the first day, and the final weight was recorded at the end of each storage interval.

$$\text{weight loss (\%)} = \frac{(m_0 - m_n)}{m_n} \quad (1)$$

Where m_0 and m_n represent the initial weight and final weight of bamboo shoots, respectively.

Using the BROUWER method to determine the soluble protein content in bamboo shoots with slight modifications (Brouwer et al. 2023). Weigh 1.0g bamboo shoot sample and grind it into homogenate in 5 mL distilled water. Centrifuge it in a centrifuge at 4 °C and 10000 r·min⁻¹ for 20 minutes. Take 1 mL supernatant and mix it with 5 mL Coomassie brilliant blue G-250 solution. After 1.5 minutes, measure the content of soluble protein at the wavelength of 595 nm.

Using the XU method to determine the free amino acid content of bamboo shoots and slightly (Xu et al. 2019). Weigh 5.0g of bamboo shoot sample, add 20 mL of 10% acetic acid solution for grinding, take homogenate distilled water to a constant volume of 50 mL after grinding, shake up and filter, take 2 mL of filtrate, add Ninhydrin and ascorbic acid solution, fully mix and heat in 95 °C water bath for 20 min. After cooling, add a 95% ethanol solution and shake, dilute to 20 mL with 60% ethanol, and measure the absorbance value at 570 nm using no filtrate as the blank control.

2.3. Determination of browning index (BI), PPO activity and total phenol content

To standardize the colorimeter, standard white and black ceramics were used. The colorimeter measures the L^* , a^* , and b^* parameters. The middle part of bamboo shoots without shell was measured, and each treatment was repeated 10 times. The CIE- $L^* a^* b^*$ color system, an international standard, was used for the test. BI, an important color change parameter, represents the browning after treatment and during storage. The calculation formula was as follows: (2) Measurements were taken every 15 d.

$$BI = \frac{[100 \times (X - 0.31)]}{0.172} \quad X = \frac{a^* + 1.75 \times L^*}{5.645 \times L^* + A^* - 3.012 \times b^*} \quad (2)$$

PPO activity adopts Trichloroacetic acid method perform the measurement and make slight modifications (He et al. 2017). Weigh 3.0 g of bamboo shoot sample and grind it into a homogenate in 10 ml $0.05\text{mmol}\cdot\text{L}^{-1}$ sodium phosphate buffer in an ice bath. Centrifuge it in a centrifuge at 4°C for $10000\text{ r}\cdot\text{min}^{-1}$ for 30 minutes (DragonLabS Inc., Beijing, China). Take 5 mL of supernatant, add 7.8 ml of $0.1\text{mmol}\cdot\text{L}^{-1}$ buffer solution(sodium phosphate) and 2 mL $0.2\text{ mol}\cdot\text{L}^{-1}$ catechol solution, shake them evenly, add 2 mL of 20% Trichloroacetic acid solution (Macklin Inc., Shanghai, China) after 10 minutes of water bath at 37°C , measure the absorbance value at 420 nm, and use $0.1\text{mmol}\cdot\text{L}^{-1}$ sodium phosphate buffer solution instead of enzyme solution as blank.

Using GONG's method to determine the total phenolic content of bamboo shoots with slight modifications (Gong et al. 2018). Weigh 4.0 g of bamboo shoot sample (m), 20 mL of 75% anhydrous ethanol was added, and ground into a homogenate in an ice bath. The mixture was brought to a constant volume of 50 mL and allowed to stand for 2 hours in dark at 25°C , followed by centrifugation at 10°C at $10000\text{ r}\cdot\text{min}^{-1}$ for 10 minutes (DragonLabS Inc., Beijing, China). Take 3 mL of the supernatant and add it to 5 mL of Folin phenol reagent, avoiding light for a sufficient reaction of 0.5 minutes. Add 6 mL of 12% Na_2CO_3 solution (Macklin Inc., Shanghai, China) and dilute it to 50 mL with distilled water. Measure the absorbance (A) at 760 nm after avoiding light for 1 hour at 25°C . Calculate the total phenol content using the following standard curve equations and formulas:

$$Y = 0.365x + 0.0165$$

$$R^2 = 0.09972$$
(3)

$$M = \frac{(A - 0.1688) \times 25 \times 25}{0.2112 \times m \times 1000}$$
(4)

2.4. Determination of APX activity, SOD activity, ASA content and MDA content

Using Petriccione's method to determine the APX activity of bamboo shoots with slight modifications (Petriccione et al. 2018). Weigh 3.0 g of bamboo shoot samples and place them in a pre-cooled mortar. Add 20 mL of pre-cooled extraction buffer ($200\text{ mmol}\cdot\text{L}^{-1}$ potassium phosphate buffer, $0.2\text{ mmol}\cdot\text{L}^{-1}$ EDTA, $2\text{ mmol}\cdot\text{L}^{-1}$ ascorbic acid, 25% PVPP), grind them in an ice bath to form a homogenate, and centrifuge them in a centrifuge at 4°C for 20 minutes. Take 0.6 mL of the supernatant as the enzyme extraction solution, add 6 mL of reaction buffer ($50\text{mmol}\cdot\text{L}^{-1}$ potassium phosphate buffer, $0.2\text{mmol}\cdot\text{L}^{-1}$ EDTA, $2\text{ mmol}\cdot\text{L}^{-1}$ ascorbic acid) and mix thoroughly. Finally, add 0.5 mL of $20\text{mmol}\cdot\text{L}^{-1}\text{ H}_2\text{O}_2$ and measure the absorbance value at 290nm. The APX activity unit is expressed as $\text{U}\cdot\text{g}^{-1}\cdot\text{min}^{-1}$.

Using the method of Qi et al. to determine the SOD activity in bamboo shoots (Qi et al. 2022). Weigh 3.00 g of bamboo shoot sample and place it in a pre-cooled mortar. Add 10 mL of distilled water that has been pre cooled at 4°C , grind it into a homogenate under ice bath conditions, and filter it in a low temperature environment of 4°C away from light. Take 2 mL of filtrate and add 4.7 mL of $0.3\text{ mol}\cdot\text{L}^{-1}$ Tris HCl

solution (containing $3.0 \text{ mmol} \cdot \text{L}^{-1}$ ethylenediamine tetraacetic acid) and 0.3 mL of $4.0 \text{ mol} \cdot \text{L}^{-1}$ pyrogallol. Mix well and measure the absorbance value at 325 nm .

Using the SHU method to determine the content of ascorbic acid in bamboo shoots with slight modifications (Shu et al. 2020). Weigh 5.0 g of bamboo shoot sample and grind it into a homogenate under ice bath conditions in a $30 \text{ g} \cdot \text{L}^{-1}$ oxalic acid solution. Filter the homogenate and dilute to 250 mL with $30 \text{ g} \cdot \text{L}^{-1}$ oxalic acid solution. Using a pipette, take 30 mL in a conical flask. Titrate it with a calibrated 2,6-dichlorophenol indophenol solution to a red color that does not change color within 15 seconds.

The content of MDA was determined by the thio Barbituric acid method with improvements. Weigh 3.0 g (FW) of bamboo shoot sample, add 10 mL (V_t) of $100 \text{ g} \cdot \text{L}^{-1}$ trichloroacetic acid (TCA), grind the homogenate, and centrifuge at 5°C for 30 minutes at $12000 \text{ r} \cdot \text{min}^{-1}$. Collect the supernatant and store it at low temperature for later use. Take 5 mL (V_s) of the supernatant and add 5 mL of 0.5% TBA solution to obtain the reaction solution (V_a). After mixing, react in a 100°C water bath for 30 minutes, cool down, and then centrifuge again for 30 minutes at $6000 \text{ r} \cdot \text{min}^{-1}$. Take the supernatant and measure the absorbance at 532 nm , 600 nm , and 450 nm . Calculate the MDA content using the following formula (5):

$$\text{MDA content}(\mu\text{mol} \cdot \text{kg}^{-1}) = \frac{[6.452 \times (A_{532} - A_{600}) - 0.559 \times A_{450}] \times V_t \times V_a}{V_s \times FW} \quad (5)$$

2.5. Determination of hardness, PAL activity, lignin content and POD activity

The hardness of the peeled bamboo shoots was tested by placing them horizontally on a texture analyzer (SMS Inc., London, England) and using a P/2 N probe to determine the middle part of bamboo shoots. The testing depth was set at 8 mm , and the speed before, during, and after measurement was $5 \text{ mm} \cdot \text{s}^{-1}$. The triggering force was set at 0.049 Newton .

Using the FUKUSHIMA method to test the lignin content in bamboo shoots with slight modifications (Fukushima et al. 2021). Weigh and dry 100.00 mg of bamboo shoot sample in a 60°C oven to constant weight. Place the dried sample into a reaction tube and add 1000 in sequence μL acetyl bromide reagent, $40 \mu\text{L}$ Mix evenly with L perchloric acid. Place the reaction tube in an 80°C water bath for 40 minutes, and then add $600 \mu\text{L}$ $3 \text{ mol} \cdot \text{L}^{-1}$ sodium hydroxide solution + glacial acetic acid solution $600 \mu\text{L}$ After fully mixing and terminating the reaction, centrifuge for 5 minutes in a transcription centrifuge at $10000 \text{ r} \cdot \text{min}^{-1}$, Take the supernatant and measure the absorbance value at 280 nm .

PAL activity adopted β - Determination of mercaptoethanol method with slight modifications (Kahramanoğlu et al. 2020). Weigh 5.0 g of bamboo shoot sample and add 15 mL $150 \text{ mmol} \cdot \text{L}^{-1}$ extraction buffer (per liter containing 30 g of PVPP, $45 \mu\text{L}$ β -Mercaptoethanol, 3 mmol ethylenediamine tetraacetic acid), ground into a homogenate under ice bath conditions. Transfer the homogenate into a

centrifuge tube and centrifuge at 4 °C for 12000 r·min⁻¹ for 20 minutes (DragonLabS Inc., Beijing, China). Collect the supernatant and store it as the crude enzyme extract at 4°C temperature for future use. Take 1 mL of crude enzyme extract and put it into a test tube. Quickly add 8 mL 100 mmol·L⁻¹ buffer(boric acid borax) and 2 mL 30 mmol·L⁻¹ L-phenylalanine (Macklin Inc., Shanghai, China), shake evenly, and 290 nm determination of absorbance value. After the measurement is completed, place the test tube in a 35 °C water bath for 0.8 hour and measure the absorbance value at 290nm as the reaction termination value. The activity is expressed in units of U·g⁻¹·min⁻¹.

Determination of POD activity in bamboo shoots using LIU method with slight modifications (Liu et al. 2018). Weigh 3.0g of bamboo shoot samples and place them in a pre-cooled mortar. Add 10 mL 200 mmol·L⁻¹ extraction buffer (per liter containing 30g PVPP, 2% Triton X-100, 2mmol PEG), and grind them into a homogenate under ice bath conditions. Transfer the homogenate into a centrifuge tube and centrifuge at 4 °C for 10000 r·min⁻¹ for 30 minutes (DragonLabS Inc., Beijing, China). Collect the supernatant as an enzyme extract. Suck 1 mL of media area into the reaction tube and add 8 mL of 30 mmol·L⁻¹ guaiacol solution, 400 μ L 0.5 mol·L⁻¹ H₂O₂ (Macklin Inc., Shanghai, China) was mixed evenly, and the absorbance value was measured at 470nm.

2.6. RNA extraction and library construction

Total RNA was extracted from fresh bamboo shoots (*Chimonobambusa quadrangularis*) using the RNAprep pure plant kit. The extracted nucleic acid concentration was measured using a Nanodrop2000 spectrophotometer, and the integrity was assessed using Agilent 2100 and LabChip GX. The first strand of cDNA was synthesized using mRNA as a template and six-base random primers. A cDNA library was constructed according to the recommended protocol. Six cDNA libraries were created, and all libraries were sequenced using the Illumina HiSeq 2500 system according to standard procedures.

2.7. De novo sequence assembly and gene annotation

The Illumina HiSeq platform was employed to generate the original reads, which were then subjected to sequence alignment and subsequent analysis using HISAT2 (hierarchical index of transcripts) (Kim et al. 2015). The moso bamboo genome was utilized as a reference for sequence alignment and analysis, which can be obtained at <http://bamboo.bamboogdb.org/#/download>. The reads were assembled using StringTie and compared with genome annotation information to identify new transcripts (Pertea et al. 2015). Gene annotation was performed using various databases, including NCBI, NR, GO, COG, KEGG, and Swiss-Prot. The biological repetitive correlations were assessed by calculating Spearman's correlation coefficient (r) (Fonseca et al. 2014).

2.8. Differential gene (DEGs) detection

FPKM (fragments per kilobase of transcript per million fragments mapped) (Florea et al. 2013) was utilized as an indicator of gene expression, and differences were analyzed using DESeq2 (Love et al. 2014). Fold Change ≥ 4 and FDR < 0.01 were employed as screening criteria for gene differential expression analysis. Using Fold Change, we determined the difference in expression levels between the

two groups. Furthermore, we calculated the false discovery rate (FDR) by adjusting the p-value of the significant difference.

2.9. RT-PCR

According to Wu et al bamboo shoots were treated using melting peak and dissociation curve specificity analysis (Wu et al. 2017). Three biological replicates were used for all qRT-PCR analyses.using Actin as an internal reference gene. See Table 2 for the list of related genes. The relative expression level was calculated using the $2^{-\Delta\Delta C_t}$ method.

2.9. Statistical Analysis

A completely randomized design was used to determine the mean and standard deviation (SD) of the experiments. $P < 0.05$ is considered statistically significant in a one-way ANOVA using IBM SPSS version 21 (IBM, Armonk, New York, USA).

3. Results

3.1. Respiratory intensity, free amino acid content, soluble protein content, weight loss rate changes

As presented in Fig. 1-A, the respiration intensity of bamboo shoots exhibited an upward trend during storage, with no significant difference observed in the early stages. However, the respiration intensity of fresh bamboo shoots treated with SNP reached its lowest level during the middle and late storage periods. In comparison to other treatments, respiration intensity was significantly lower at 45 and 60 days ($P < 0.05$). This indicates that the SNP treatment effectively suppressed postharvest respiration of fresh bamboo shoots. During storage, bamboo shoots consumed nutrients and lost their soluble protein content, as shown in Fig. 1-B. At 60 days, however, the soluble protein content of the SNP treatment was 1.74-fold greater than that of the CK treatment. This observation suggests that the SNP treatment better preserved the nutrient content of fresh bamboo shoots. During storage, bamboo shoots gradually increase their free amino acid content (Fig. 1-C). The nutrients in fruits and vegetables will be lost postharvest, nutrients are broken down into amino acids. As compared to SNP, the CK treatment produced significantly more free amino acids during mid and late storage stages. According to Fig. 1-D, bamboo shoots lose weight over time. The weight loss rate of SNP treatment is significantly lower than that of CK treatment in the middle and later stages of storage. The SNP treatment mitigates weight loss in fresh bamboo shoots during storage. Overall, these findings strongly suggest that the application of SNP treatment inhibits the respiration intensity and metabolic activity of bamboo shoots during storage, retards nutrient decline, and suppresses the increase in weight loss rate.

3.2. PPO activity, total phenol content, browning index, appearance and color changes

In storage, polyphenol oxidase (PPO) facilitates phenolic compound oxidation, causing enzymatic browning of postharvest fruits and vegetables. As well, PPO oxidizes phenolic substances, including chlorogenic acid, which leads to lignification (Wang et al. 2019a). During the early stages of storage, the PPO activity of bamboo shoots treated with SNP was significantly lower than that of CK treatment. As seen in Fig. 2-A, PPO activity in the SNP treatment was only 65.31% of that seen in the control treatment after 30 days. The changes in phenolic content during storage are shown in Fig. 2-B. During storage, there were significant differences in phenolic substances in bamboo shoots before and after storage, but there was no significant difference between SNP treatment and CK treatment. A variation in the browning index of bamboo shoots (*Chimonobambusa quadrangularis*) during storage can be seen in Fig. 2-C. Browning index increased continuously between treatments during the initial 0–15 day period, with no significant difference between them. However, at 45 d, the SNP treatment displayed a significantly lower browning index compared to the control treatment. According to Fig. 2-D, this finding supports ZHANG's (Zhang et al. 2023) findings that fresh bamboo shoots change in appearance during storage .

3.3. The changes of APX activity, SOD activity, ASA content and MDA content

Shown in Fig. 3-A, ascorbate peroxidase (APX) activity in bamboo shoots decreased rapidly at first, then increased gradually with storage time. Notably, The SNP treatment group's APX activity exceeded that of the control group throughout the storage period, which is in agreement with CHEN et al's findings (Chen et al. 2013). Regarding fresh bamboo shoots, Fig. 3-B illustrates an initial increase in superoxide dismutase (SOD) activity, followed by a subsequent decrease. However, the SNP treatment demonstrated a significant increase in SOD activity after 30–60 days of treatment. This increase in SOD activity in bamboo shoots treated with SNP indicates an enhancement in their antioxidant capacity. In Fig. 3-C, the ascorbic acid content consistently remained at its highest level in the SNP treatment group during storage, surpassing the CK treatment. There was a significant increase in ascorbic acid content in the SNP treatment group after 15 days ($P < 0.05$) versus the CK treatment group. Consequently, bamboo shoots treated with SNP exhibited better preservation of ascorbic acid levels compared to those treated with CK. Figure 3-D shows that both the control and SNP treatment groups had an increase in malondialdehyde (MDA) levels during storage. However, the increase in MDA content was effectively inhibited by SNP treatment. Specifically, At 45 days, the MDA content was 33.02% higher in the control group compared with the SNP group. In summary, SNP treatment can stimulate SOD and APX activities, maintain ascorbic acid content, inhibit MDA accumulation, and slow down oxidative damage of bamboo shoots during storage.

3.4. Changes of PAL activity, POD activity, lignin content and hardness

Figure 4-C shows that, during storage, phenylalanine ammonia-lyase's (PAL's) activity initially increased before declining. Notably, the treatment with SNP consistently exhibited the lowest PAL activity throughout the storage period, displaying a significant difference from other treatments at 60 d ($P < 0.05$).

Specifically, the PAL activity of the SNP treatment was only 69.89% of that observed in the CK treatment. POD activity shows an upward trend in the early stage of storage, followed by a gradual decrease, as shown in Fig. 4-B. This result is consistent with the study by XU et al (Xu et al. 2023). The POD activity of SNP treatment continued to decrease and was significantly lower than that of CK treatment after 45 and 60 days of storage, accounting for only 63.59% and 58.22% of the activity observed in the CK treatment, respectively. As shown in Fig. 4-C, the lignin content showed an upward trend during storage, with no significant difference between CK treatment and SNP treatment at 0–30 days. However, the SNP treatment effectively attenuated the accumulation of lignin at 45–60 d, displaying a significant difference compared to the CK treatment ($P < 0.05$). Throughout the storage duration, the hardness of bamboo shoots continuously increased, with the SNP treatment showing a deceleration in the hardness increment during the later stages of storage. At the time of harvest, the hardness of bamboo shoots measured 915.17 g. After 60 d, the hardness of the CK treatment increased by 1079.54 g, while the hardness of the SNP treatment increased by 991.94 g (Fig. 4-A). This increase in hardness was attributed to the lignification process, a phenomenon that is also observed in mangosteen fruit (Yufang et al. 2001). Based on these results, SNP treatment may suppress the activity of enzymes involved in lignification biosynthesis, inhibiting the increase in lignin content, such as PAL and POD, thereby retarding the hardness increase of bamboo shoots during storage.

3.5. Global analysis of transcriptome data

We obtained 41.67 Gb of Clean Data from 6 samples. Each sample yielded approximately 5.85 Gb of Clean Data, with a Q30 base percentage of 93.75% or higher. The Clean Reads of each sample were then compared to the designated bamboo genome sequence, resulting in a comparison efficiency ranging from 66.93–70.05%. According to Fig. 5, 5067 differentially expressed genes (2816 up-regulated and 2251 down-regulated) were identified between the NO treatment group and the control group. It is evident from these results that NO treatment affected the expression levels of numerous genes in bamboo shoots.

3.6. Transcriptome alterations in bamboo shoots (*Chimonobambusa quadrangularis*) treated with SNP

Induced delayed postharvest senescence of bamboo shoots was investigated in this study. In order to achieve this objective, GO enrichment analysis was used to analyze differentially expressed genes in SNP and CK treatments. The distribution of these differential genes across three main categories, namely biological process, molecular function, and cellular component, is visually presented in Fig. 6. Furthermore, the top 30 most abundant GO categories in both SNP and CK treatments were further subdivided into specific functional subcategories. Notably, significant categories encompassed cellular processes, metabolic processes, single-organism processes, organelles, and catalytic activity. Furthermore, KEGG enrichment analysis was performed to understand the specific functions of differentially expressed genes between SNP and CK treatments within metabolic pathways. Figure 7 provides a graphical representation of the 20 most enriched metabolic pathways. Several pathways stood out due to their high enrichment of differential genes, including mannose-type O-glycan

biosynthesis, ribosome, flavonoid biosynthesis, and brassinosteroid biosynthesis. Molecular mechanisms underpinning NO's impact on bamboo shoot postharvest senescence were revealed by these comprehensive analyses. In addition to highlighting specific biological processes and cellular components, a number of molecular functions and metabolic pathways are also highlighted. Providing insight into the regulatory effects of NO on bamboo shoot senescence.

3.7. SNP affects differential genes in aging

Among the 5077 differentially expressed genes influenced by SNP treatment, as presented in Table 1, a total of 49 genes were discerned to be associated with the senescence of bamboo shoots. Particularly noteworthy, among these differentially expressed genes, 20 were found to be implicated in lignin biosynthesis, 16 genes in plant hormone biosynthesis, and 13 genes in reactive oxygen species metabolism.

In the context of lignin biosynthesis, multiple genes were identified and duly annotated. These genes encompassed Shikimate kinase (PH02Gene06459), Tryptophan synthase β chain (PH02Gene15732), Tryptophan synthase α chain (PH02Gene20304), Tyrosine aminotransferase (PH02Gene39337), 4-coumaric acid CoA ligase (PH02Gene26838), Coniferyl aldehyde dehydrogenase (PH02Gene25533), scopolamine glucosyltransferase (PH02Gene36322), cinnamyl alcohol dehydrogenase (PH02Gene26814), and two genes annotated as chorismate mutating enzyme. Following SNP treatment (Table 1, Fig. 8-A), a discernible down-regulation in the expression of the aforementioned genes was observed.

In the plant hormone biosynthesis pathway, several specific genes play crucial roles. Flavin dehydrogenase (PH02Gene00021) and exfoliated aldehyde oxidase (PH02Gene30643, PH02Gene43244) are involved in the abscisic acid synthesis pathway. Serine-O-acetyltransferase (PH02Gene27443), homocysteine S-methyltransferase (PH02Gene01123, PH02Gene42555, PH02Gene42561), and ACC synthase (PH02Gene01947) serve as key components of the ethylene synthesis pathway. For gibberellin synthesis, critical genes include Gibberellin 3 β -Dioxygenase (PH02Gene30496), gibberellin-44-dioxygenase (PH02Gene40136), and gibberellin-2 β -dioxygenase (PH02Gene36729). Upon SNP treatment, the expression of these genes exhibited distinct responses. Specifically, in Table 1 and Fig. 8-B, the expression of genes involved in the gibberellin synthesis pathway decreased under the influence of SNP treatment. In contrast, the expression of aldehyde dehydrogenase (NAD⁺) (PH02Gene17054, PH02Gene37309, PH02Gene37333) and amidase (PH02Gene16240, PH02Gene35506) in the auxin synthesis pathway increased in response to the same treatment.

In the realm of active oxygen metabolism, the expression levels of peroxidase genes (PH02Gene02731, PH02Gene25959, PH02Gene46530) and lipoxygenase gene (PH02Gene47636) notably decreased upon treatment with SNP, as evidenced by the data presented in Table 1 and Fig. 8-C. In contrast, the expression of several other genes involved in this metabolic pathway exhibited a significant increase under the same SNP treatment, namely ascorbate peroxidase genes (PH02Gene00102, PH02Gene07059, PH02Gene18614, PH02Gene43093), superoxide dismutase gene (PH02Gene35117), catalase gene

(PH02Gene16155), glutathione synthase gene (PH02Gene27678), and glucose-6-phosphate 1-dehydrogenase genes (PH02Gene11326, PH02Gene19105), as indicated by the data in Table 1 and Fig. 8-C.

Table 1
Annotation of Aging Genes

Gene id	Gene name	Gene description	Significant
lignin biosynthesis			
PH02Gene06459	MtSK	Shikimate kinase	Down
PH02Gene15732	trpB	Tryptophan synthase β chain	Down
PH02Gene20304	trpA	Tryptophan synthase α chain	Down
PH02Gene24639	CM	Branched acid mutase	Down
PH02Gene35239	CM	Branched acid mutase	Down
PH02Gene39337	TAT	Tyrosine aminotransferase	Down
PH02Gene44264	C4H	Trans cinnamate 4-monooxygenase	Down
PH02Gene46974	C4H	Trans cinnamate 4-monooxygenase	Down
PH02Gene26838	4CL	4-coumaric acid CoA ligase	Down
PH02Gene25533	CALDH	Coniferous aldehyde dehydrogenase	Down
PH02Gene14706	CCR	Cinnamoyl CoA reductase	Down
PH02Gene26814	CAD	Cinnamyl alcohol dehydrogenase	Down
PH02Gene02731	POD	Peroxidase	Down
PH02Gene19041	HCT	Mangrove acid o-hydroxycinnamoyl transferase	Down
PH02Gene20074	HCT	Mangrove acid o-hydroxycinnamoyl transferase	Down
PH02Gene25511	CCR	Cinnamoyl CoA reductase	Down
PH02Gene25959	POD	Peroxidase	Down
PH02Gene32168	HCT	Mangrove acid o-hydroxycinnamoyl transferase	Down
PH02Gene36322	TOGT1	Scopolamine glucosyltransferase	Down
PH02Gene46530	POD	Peroxidase	Down
Plant hormone biosynthesis			
PH02Gene00021	ABA2	Flavin dehydrogenase	Down
PH02Gene30643	AA03	Absciscic aldehyde oxidase	Down
PH02Gene43244	AA03	Absciscic aldehyde oxidase	Down
PH02Gene27443	SAT	Serine O-Acetyltransferase	Down
PH02Gene01123	BHMT2	Homocysteine S-methyltransferase	Down

Gene id	Gene name	Gene description	Significant
PH02Gene42555	BHMT2	Homocysteine S-methyltransferase	Down
PH02Gene42561	BHMT2	Homocysteine S-methyltransferase	Down
PH02Gene01947	ACS	1-aminocyclopropane-1-carboxylic acid synthase 1/2/6	Down
PH02Gene30496	GA3ox	Gibberellin 3 β - Dioxygenase	Up
PH02Gene40136	GA20ox	Gibberellin-44 dioxygenase	Up
PH02Gene36729	GA2ox	Gibberellin 2 β - Dioxygenase	Up
PH02Gene17054	ALDH(NAD ⁺)	Aldehyde dehydrogenase (nad ⁺)	Down
PH02Gene37309	ALDH(NAD ⁺)	Aldehyde dehydrogenase (nad ⁺)	Down
PH02Gene37333	ALDH(NAD ⁺)	Aldehyde dehydrogenase (nad ⁺)	Down
PH02Gene16240	Cas	Amidase	Down
PH02Gene35506	Cas	Amidase	Down
Active oxygen metabolism			
PH02Gene02731	POD	Peroxidase	Down
PH02Gene25959	POD	Peroxidase	Down
PH02Gene46530	POD	Peroxidase	Down
PH02Gene00102	APX	Ascorbic acid peroxidase	Up
PH02Gene07059	APX	Ascorbic acid peroxidase	Up
PH02Gene18614	APX	Ascorbic acid peroxidase	Up
PH02Gene43093	APX	Ascorbic acid peroxidase	Up
PH02Gene35117	SOD	Superoxide dismutase	Up
PH02Gene16155	CAT	catalase	Up
PH02Gene47636	LOX	Lipoxygenase	Down
PH02Gene27678	Gss	Glutathione Synthase	Up
PH02Gene11326	G6PD	Glucose-6-phosphate 1-Dehydrogenase	Up
PH02Gene19105	G6PD	Glucose-6-phosphate 1-Dehydrogenase	Up

3.8. SNP regulates the expression level of aging key genes

We conducted qRT-PCR analysis on 12 key differential genes involved in the regulation of bamboo shoot senescence, with the primary objective of further corroborating the findings from transcriptome sequencing. These 12 genes encompass PH02Gene02731 (POD), PH02Gene06459 (MtSK), PH02Gene26814 (CAD), PH02Gene26838 (4CL), and PH02Gene35239 (CM), all of which are associated with the lignin biosynthesis pathway. Additionally, we investigated PH02Gene01947 (ACS) and PH02Gene30643 (AA03), which are related to plant hormone biosynthesis. Furthermore, our investigation included PH02Gene35117 (SOD), PH02Gene43093 (APX), PH02Gene16155 (CAT), PH02Gene27678 (GSS), and PH02Gene47636 (LOX), known to be involved in the reactive oxygen metabolism pathway. The fluorescence quantitative data demonstrated a substantial agreement between the gene expression levels obtained from RNA-Seq and those observed in qRT-PCR (Fig. 9). This concurrence effectively validates the reliability and accuracy of the transcriptome results obtained in this study.

Table 2
Specific primer sequences and conditions for real-time PCR analysis

Species	Gene	Primer sequences	Size (bp)	Annealing (°C)
Phyllostachys edulis	Actin	F:TGCCCTTGATTATGAGCAGG R:AACCTTTCTGCTCCGATGGT	108	60
Phyllostachys edulis	PH02Gene35117(SOD)	F:CTTTCCACTCGCTCCTCCTC R:TGATACGGGCGTTCACTGTT	107	60
Phyllostachys edulis	PH02Gene43093(APX)	F:CACCAACCGATGAGAAGAA R:GAGTAATTGGCAGCAACGA	103	60
Phyllostachys edulis	PH02Gene01947(ACS)	F:AACCAACTTTTCGCTGGACCT R:CTTGGAATTGGCTATCCTC	109	60
Phyllostachys edulis	PH02Gene02731(POD)	F:CTTCGTCTTTCTCCTCGCATT R:TCTCAAGGTTTGGGCAGATG	95	60
Phyllostachys edulis	PH02Gene06459(MtSK)	F:CCTCAATGCGGCGATTAGTT R:CAAGGGCACATCCAACCAA	107	60
Phyllostachys edulis	PH02Gene16155(CAT)	F:TTTTCGGAGCCGTCAATCG R:AGCTCGGAACTCCTCACCA	131	60
Phyllostachys edulis	PH02Gene26814(CAD)	F:GACAGTGACTTTCTTCAACATC R:TTGGTGTTGCCGTAGTTGATGTA	279	60
Phyllostachys edulis	PH02Gene26838(4CL)	F:GAATGACCCAGAATCCACAAAG R:ACTTGGAACCCCTTGTAATTGA	141	60
Phyllostachys edulis	PH02Gene27678(GSS)	F:TTCCTGGGCTTGGTTCCTTA R:ACATTAAACTCAGCACATGC	158	60
Phyllostachys edulis	PH02Gene30643(AA03)	F:AGGTTACCGACCGATTGTTGAT R:CATCTGGGTGCTTATCTCCTTTC	107	60
Phyllostachys edulis	PH02Gene35239(CM)	F:AAGGCTGGTGAGGAAAGGAAGT R:GTGACTCCTGGAACCTTGCCTCT	131	60
Phyllostachys edulis	PH02Gene47636(LOX)	F:TTCGCCAACAAGCCTTATCTG R:TCAGACTTCGGGTCTTTGGTG	260	60

4. Discussion

4.1. Physiological metabolism

Bamboo shoots, being the buds of bamboo, exhibit a robust physiological metabolism. A fruit or vegetable's physiological metabolism is adversely affected by postharvest damage. Extensive research has shown that respiratory intensity serves as an intuitive indicator for evaluating the physiological metabolism of such produce postharvest. Postharvest fruits and vegetables lose nutrients due to respiration during storage, resulting in deteriorated quality and accelerated senescence (Li et al. 2019b). Postharvest fruits and vegetables can be delayed from senescence by SNP treatment by inhibiting their physiological metabolism (Rabiei et al. 2019). Fresh bamboo shoot respiration rate was significantly reduced after SNP (NO) treatment, compared with the control group (CK treatment) (Fig. 1-A). This indicates that NO treatment successfully inhibits the physiological metabolism of bamboo shoots postharvest. According to the results, NO treatment effectively delays the decline in soluble protein content and weight loss during storage (Fig. 1-B, Fig. 1-D). The study also observed an upward trend in free amino acid concentrations during later stages of storage (Fig. 1-C). This can be attributed to the loss of endogenous proteins and external nutrients, as was found by LI et al (Li et al. 2014). Observation of continuous decreases in soluble protein content in this study is consistent with these results.

In conclusion, the application of NO treatment has demonstrated its efficacy in effectively inhibiting the cellular respiration of bamboo shoots during storage, thereby mitigating the decline in soluble protein and other essential nutrients. Consequently, this treatment serves to curb the escalation of weight loss rate throughout the storage duration, ensuring the preservation of superior quality in bamboo shoots, even during the later stages of storage, and Delaying Postharvest the senescence of bamboo shoots.

4.2. Enzymatic browning

The appearance color is commonly employed as an instinctive parameter for evaluating the quality of postharvest fruits and vegetables. Enzymatic browning plays a crucial role in altering the appearance color, particularly in bamboo shoots postharvest. This browning process occurs when phenolic substances react with PPO under aerobic conditions, forming quinones that subsequently undergo oxidation and lead to browning (Ali et al. 2020). Phenols are mainly distributed in vacuoles within plant cells, while PPO is predominantly found in the cytoplasm. The presence of a cell membrane creates a spatial barrier that partially inhibits enzymatic browning in fruits and vegetables (Wei et al. 2022). Nevertheless, the accumulation of reactive oxygen species (ROS) resulting from harvest damage and postharvest storage disrupts the cell membrane, exacerbating enzymatic browning (Li et al. 2017). Due to the distinctive harvesting method of bamboo shoots, postharvest damage is inevitable. Consequently, the PPO content of fresh bamboo shoots rapidly increases during storage. However, prior studies on cherries by AGHDAM have indicated that treatment with NO effectively inhibits the rise in PPO activity and delays enzymatic browning (Aghdam et al. 2019). In our own research, we observed an ascending trend in the browning index of fresh bamboo shoots (Fig. 2-C). In the later stage of storage, the browning index of bamboo shoots treated with NO was lower than that treated with CK and there was a significant

difference, suggesting that NO treatment can effectively suppress postharvest browning during bamboo shoot storage. This observation aligns with the changes observed in appearance color (Fig. 2-D). In summary, NO treatment proves to be an effective measure in inhibiting enzymatic browning, reducing postharvest browning, and delaying the senescence of fresh bamboo shoots during storage.

4.3. Active oxygen metabolism

ROS, an acronym for reactive oxygen species, is an oxygen-containing substance formed during the process of aerobic metabolism in postharvest fruits and vegetables. It exhibits potent oxidation capabilities and active chemical properties, primarily originating from mitochondria. Upon the transfer of electrons to oxygen molecules during aerobic metabolism, plants produce a toxic and active oxygen-containing substance known as ROS, where MDA serves as its primary representative(Xie et al. 2022).The rapid accumulation of ROS during the storage period of postharvest fruits and vegetables can cause lipid peroxidation of the cell membrane in the body of fruits and vegetables, resulting in membrane damage and cellular structure disruption. This damage facilitates direct interactions between PPO and phenolic compounds, exacerbating enzymatic reactions and ultimately leading to browning(Dokhanieh and Aghdam 2016). To prevent browning and delay senescence in postharvest fruits and vegetables, maintaining sufficient levels of non-enzymatic antioxidants and promoting the activity and gene expression of enzymes involved in reactive oxygen metabolism are crucial(Wang et al. 2022). In this regard, treatment with exogenous NO has been shown to modulate the activity of key non-enzymatic antioxidants and antioxidant enzymes, thus facilitating the removal of reactive oxygen species within postharvest fruits and vegetables(Jiménez-Muñoz et al. 2021).

Numerous studies have extensively demonstrated the involvement of various enzymes, namely POD, SOD, CAT, APX, and LOX, in the metabolism of reactive oxygen species (ROS). The cellular ROS level is intricately dependent on the capacity of these enzymes to produce and scavenge ROS(Wang et al. 2017a). In the present investigation, under NO treatment, 13 genes associated with reactive oxygen metabolism exhibited distinct expression patterns. The MDA content of NO treatment was significantly lower than that of CK treatment in the later stage of bamboo shoot storage (Fig. 3-D, Table 1). These results clearly indicate the considerable impact of NO treatment on ROS metabolism. CAT, APX, and SOD enzymes are believed to delay ROS accumulation by clearing peroxides. (Rabiei et al. 2019). This study further elucidates the upregulation of related genes by NO treatment, including APX (PH02Gene43093, PH02Gene18614, PH02Gene07059, PH02Gene00102), SOD (PH02Gene35117), and CAT (PH02Gene16155) (Table 1). Furthermore, the activities of APX and SOD were significantly higher in the NO-treated group at 45 d (Fig. 3-A, Fig. 3-B), suggesting that NO stimulation enhances the expression or activity of APX, SOD, and CAT genes, which aligns with prior research by LI et al (Madebo et al. 2022; Li et al. 2019a).Previously, LOX has been shown to play a role in peroxide metabolism by generating ROS, leading to oxidative damage of cell membranes (Mirshekari et al. 2020).The transcriptome data of this study showed that the LOX gene (PH02Gene47636) expression in the NO treated group was significantly inhibited after 45 days of storage, indicating that NO can attenuate ROS production by suppressing LOX gene expression. In addition, we found that in the later stage of storage, the ascorbic acid content of

bamboo shoots treated with NO was significantly higher than that treated with CK (Fig. 3-C). This finding suggests that NO treatment can preserve crucial non-enzymatic antioxidants, such as ascorbic acid, which in turn delays the accumulation of MDA, this is consistent with the change in MDA content (Fig. 3-D). To sum up, our findings indicate that NO treatment induces alterations in key enzyme activities and gene expressions involved in active oxygen metabolism. Additionally, NO treatment helps preserve the levels of non-enzymatic antioxidants, inhibits ROS accumulation, decelerates the oxidative damage of cell membrane lipids, and impedes the browning of bamboo shoots during storage.

4.4. Lignification

Lignification plays a critical role in the postharvest deterioration of fruits and vegetables, leading to a substantial increase in their hardness and significantly compromising their taste. Moreover, this process negatively impacts the quality and market value of bamboo shoots. To address this issue, effective measures are required for the storage and preservation of bamboo shoots that can mitigate postharvest lignification (Yang et al. 2023). Following harvest, lignin progressively accumulates and deposits in the plant cell walls, thickening the secondary walls of bamboo shoot cells and causing the lignification of fruits and vegetables (Wang et al. 2023). Therefore, it becomes crucial to inhibit the biosynthesis of lignin. A key enzyme in this process is Phenylalanine ammonia-lyase (PAL), responsible for converting phenylalanine to trans-cinnamic acid, which significantly influences lignin production (Kong 2015). This study demonstrates that treatment with NO (nitric oxide) effectively inhibits the increase in hardness, lignin content, and browning index in bamboo shoots (Fig. 4-D, Fig. 4-C, Fig. 2-C). Additionally, it significantly suppresses PAL activity during the early stages of storage (Fig. 4-A), thus confirming this observation. These findings highlight the potential of NO treatment to retard lignification and browning processes in bamboo shoots during storage, corroborating previous reports by Qi et al. (Qi et al. 2020). As a result, NO treatment shows promise in delaying the senescence of bamboo shoots during storage.

Lignin accumulation is widely recognized as the primary factor leading to postharvest lignification of bamboo shoots. The phenylpropanoid metabolism serves as a crucial metabolic pathway responsible for lignin production. Previous research has indicated that key enzymes, such as POD, C4H, 4CL, CCR, and CAD, play vital roles in the production of lignin in bamboo shoots, with these genes being prominently featured in the phenylpropanoid metabolic pathway (ZHENG et al. 2020). Currently, the majority of investigations on the preservation of NO in bamboo shoots focus on the enzymatic activity and gene expression of the aforementioned enzymes. However, there is a scarcity of studies examining the comprehensive regulation of NO on the entire pathway (Yang et al. 2010; Wang et al. 2017b). Notably, the treatment of NO was found to elicit differential expression of 20 lignin biosynthesis genes (Fig. 8-A, Table 1), signifying its significant impact on lignin biosynthesis.

In the phenylalanine biosynthesis pathway, the treatment with NO significantly repressed the expression of three genes: MtSK (PH02Gene06459), tyrosine transaminase (PH02Gene39337), and CM (PH02Gene24639, PH02Gene35239). MtSK is responsible for catalyzing the phosphorylation of shikimic acid (SA) to form shikimic acid 3-phosphate (Reddy et al. 2020), while CM facilitates the decarboxylation of prebenzoic acid to yield phenylpyruvic acid (Pittard and Yang 2008). Shikimate 3-phosphate and

phenylpyruvate are intermediate products in the formation of phenylalanine, which serves as a vital precursor for lignin synthesis(Winkel-Shirley 2001). These findings suggest that NO inhibits phenylalanine biosynthesis and restricts lignin synthesis. Moving on to the phenylpropanoid metabolic pathway, our study revealed that CAD (PH02Gene26814), POD (PH02Gene02731, PH02Gene25959, PH02Gene46530), CCR (PH02Gene14706, PH02Gene25511), and 4CL (PH02Gene26838) were found to be enriched. CAD plays a critical role in the catalytic synthesis of various lignin monomers and serves as a key enzyme in phenylpropanoid metabolism. Consequently, NO treatment resulted in the downregulation of the CAD gene expression(Singh et al. 2010), leading to a decrease in the synthesis of lignin monomers and retarding lignification. On the other hand, CCR converts cinnamoyl coenzyme A into the corresponding cinnamaldehyde(Thévenin et al. 2011). Our study also demonstrated that NO treatment inhibited the expression of the CCR gene, preventing the formation of cinnamaldehyde and thus slowing down lignification. Additionally, cinnamaldehyde acts as an intermediate product in lignin production and exhibits oxidative properties that induce apoptosis(Hong et al. 2016). Furthermore, 4CL plays a crucial role in converting cinnamic acid derivatives into pivotal enzymes in the lignin branch point, thereby influencing the synthesis of phenylpropanoid derivatives(Zhang et al. 2019). After NO treatment, the expression of the 4CL gene and lignin production were significantly reduced. Prior research has shown that the increase in POD activity and gene expression leads to the lignification of plant tissues(Meloni et al. 2003). This observation aligns with our findings that NO treatment inhibits both POD activity and gene expression at 45 d, effectively preventing the rise in lignin content (Fig. 4-B, Fig. 4-C, Table 1). Overall, these results demonstrate that NO treatment suppresses the activity and gene expression of crucial enzymes in the phenylpropanoid metabolic pathway, impeding lignin accumulation, and inhibiting bamboo shoot lignification during storage.

4.5. Phytohormone

Fruits and vegetables' postharvest ripening is significantly influenced by ethylene, an essential plant hormone. However, its significance as a maturation signal for non-climacteric fruits, such as bamboo shoots, remains relatively unexplored. Nevertheless, mounting evidence suggests that ethylene indeed plays a role in the ripening process of non-climacteric fruits. For example, MA et al (Ma et al. 2021) demonstrated that inhibiting ethylene biosynthetic enzymes and signal component transcripts in pepper effectively halts the postharvest senescence of pepper. Similarly, A similar regulation of ripening and senescence has been demonstrated for postharvest fruits and vegetables by Absciscic acid (ABA) (Dong et al. 2023), while auxin, gibberellin, and cytokinin may have the opposite effect of delaying ripening and senescence. The ethylene production in bamboo shoots is triggered by postharvest stress and injury, resulting in bamboo shoot senescence. Further research has revealed that ethylene also plays an important role in fruit ripening and senescence (Gu et al. 2002). The enzyme ACC synthase (ACS) plays a critical role in regulating ethylene biosynthesis and production (Jiang and Fu 2000). In fact, studies have indicated that NO treatment significantly inhibits the expression of the ACS (PH02Gene01947) gene, thus reducing endogenous ethylene synthesis. Similarly, the primary hormone ABA has been found to play a pivotal role in fruit ripening, and LIU et al. also reported similar results in their study (LIU et al. 2007). Absciscic acid (ABA) plays a leading role in fruit ripening (Gupta et al. 2020). Relevant studies have shown

a positive correlation between ABA content and the hardness of fruits and vegetables, which may result in lignification (Carvajal et al. 2017). In this study, we found that NO treatment significantly inhibited gene expression of related enzymes in the ABA biosynthesis pathway, such as flavin dehydrogenase (PH02Gene00021) and exfoliated aldehyde oxidase (PH02Gene30643, PH02Gene43244) (Table 1). This suggests that NO treatment effectively hinders the internal mechanism responsible for ABA synthesis. Conversely, after NO treatment, the expression of enzymes involved in gibberellin biosynthesis, such as gibberellin 3 β -dioxygenase (PH02Gene30496), gibberellin-44 dioxygenase (PH02Gene40136), and gibberellin 2 β -dioxygenase (PH02Gene36729), increased significantly compared to the control treatment. This indicates that NO treatment can induce the expression of these key enzyme genes, leading to increased endogenous gibberellin biosynthesis and delayed senescence in fresh bamboo shoots. Moreover, in this study, the expression levels of acetaldehyde dehydrogenase (NAD⁺) (PH02Gene17054, PH02Gene37309, PH02Gene37333) and amidase (PH02Gene16240, PH02Gene35506), which are key genes in auxin biosynthesis, were found to be significantly lower after NO treatment compared to the control treatment. This suggests that NO treatment can modulate the expression of these key genes involved in auxin biosynthesis, thereby regulating the biosynthesis of endogenous auxin and delaying senescence in fresh bamboo shoots.

5. Conclusion

In this study, the analysis of physiological data revealed an increasing trend in hardness and browning index of bamboo shoots (*Chimonobambusa quadrangularis*) during storage, indicating an ongoing process of lignification and browning. Transcriptome data analysis further demonstrated that the treatment with nitric oxide (NO) inhibited the activity of key enzymes and gene expression involved in lignin synthesis, thereby decelerating lignin accumulation and preventing bamboo shoot lignification. Additionally, the accumulation of reactive oxygen species was found to promote tissue browning. Interestingly, The results of this study indicate that NO treatment can regulate the expression of reactive oxygen species metabolism related enzymes and their genes expression, thereby enhancing the ability of bamboo shoots to scavenge reactive oxygen species and inhibit MDA accumulation. Moreover, our results indicate that NO can effectively delay bamboo shoot senescence during storage by regulating plant hormones, such as ethylene and ABA biosynthesis. Finally, this study provides a comprehensive summary of the potential molecular regulation mechanism underlying NO treatment and its role in delaying the senescence of fresh bamboo shoots (Fig. 10). The present findings contribute to a better understanding of the processes involved in bamboo shoot storage and offer valuable insights into the application of NO treatment to preserve their freshness.

Declarations

Competing Interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ning Ji reports financial support was provided by Guiyang University. Ning Ji reports financial support was provided by Guizhou Provincial Department of Science and Technology. Ning Ji reports financial support was provided by Guiyang Science and Technology Bureau.

Funding:

This research was funded by the Guiyang Science and Technology Talent Plan Project (ZhuKeHeTong[2023]48 – 20), the Guiyang University Doctoral Scientific Research Startup Fund (GYU-KY-[2024]), the Guizhou Provincial Key Technology R&D Program(QianKeHeZhiCheng[2020]1Y139) and the Guizhou Provincial Science and Technology Plan Project (QianKeZhongYinDi[2020]4018).

Author Contribution

Conceptualization and methodology: Jinyang.Xu. and Ning.Ji.; investigation: Jinyang.Xu., Ning.Ji., Rui.Wang., Yuxing.Li., and Jiqing.Lei.; formal analysis: Jinyang.Xu., Ni.Zhang., and Renchan.Liu.; data curation: Jinyang.Xu. and Ning.Ji.; writing-original draft preparation: Jinyang.Xu.; writing-review and editing: Jinyang.Xu. and Ning.Ji. All authors have read and agreed to the published version of the manuscript.

References

1. Aghdam MS, Kakavand F, Rabiei V, Zaare-Nahandi F & Razavi FJSH (2019) γ -Aminobutyric acid and nitric oxide treatments preserve sensory and nutritional quality of cornelian cherry fruits during postharvest cold storage by delaying softening and enhancing phenols accumulation. 246, 812-817.
2. Ali S, Khan AS, Anjum MA, Nawaz A, Naz S, Ejaz S & Hussain SJFc (2020) Effect of postharvest oxalic acid application on enzymatic browning and quality of lotus (*Nelumbo nucifera* Gaertn.) root slices. 312, 126051.
3. Barberis A, Cefola M, Pace B, Azara E, Spissu Y, Serra PA, Logrieco AF, D'hallewin G, Fadda AJPB & Technology (2019) Postharvest application of oxalic acid to preserve overall appearance and nutritional quality of fresh-cut green and purple asparagus during cold storage: A combined electrochemical and mass-spectrometry analysis approach. 148, 158-167.
4. Brouwer B, Paillart MJ, Bruins ME, Wissink E, Vries MNd, Mensink M, Bode-Mocking H, Liese W, Geerdink P & Echtelt EMHvJJoFS (2023) The impact of wounding and postharvest storage conditions on retention of soluble protein in sugar beet leaves. 88(4), 1580-1594.
5. Carvajal F, Palma F, Jiménez-Muñoz R, Jamilena M, Pulido A, Garrido DJPB & Technology (2017) Unravelling the role of abscisic acid in chilling tolerance of zucchini during postharvest cold storage. 133, 26-35.

6. Chen G, Bu F, Chen X, Li C, Wang S & Kan JJJobm (2018) Ultrasonic extraction, structural characterization, physicochemical properties and antioxidant activities of polysaccharides from bamboo shoots (*Chimonobambusa quadrangularis*) processing by-products. 112, 656-666.
7. Chen H, Ling J, Wu F, Zhang L, Sun Z, Yang HJL-FS & Technology (2013) Effect of hypobaric storage on flesh lignification, active oxygen metabolism and related enzyme activities in bamboo shoots. 51(1), 190-195.
8. Chen K, Li GJ, Bressan RA, Song CP, Zhu JK & Zhao YJJoipb (2020) Absciscic acid dynamics, signaling, and functions in plants. 62(1), 25-54.
9. Dai H, Ji S, Zhou X, Wei B, Cheng S, Zhang F, Wang S & Zhou QJSH (2021) Postharvest effects of sodium nitroprusside treatment on membrane fatty acids of blueberry (*vaccinium corymbosum*, cv. Bluecrop) fruit. 288, 110307.
10. Dokhanieh AY & Aghdam MSJSH (2016) Postharvest browning alleviation of *Agaricus bisporus* using salicylic acid treatment. 207, 146-151.
11. Dong W, Cao S, Zhou Q, Jin S, Zhou C, Liu Q, Li X, Chen W, Yang Z & Shi LJFiPS (2023) Hydrogen-rich water treatment increased several phytohormones and prolonged the shelf life in postharvest okras. 14, 1108515.
12. Florea L, Song L & Salzberg SLJF (2013) Thousands of exon skipping events differentiate among splicing patterns in sixteen human tissues. 2.
13. Fonseca NA, Marioni J & Brazma AJPo (2014) RNA-seq gene profiling-a systematic empirical comparison. 9(9), e107026.
14. Fukushima R, Kerley M, Ramos M, Kallenbach RJAFS & Technology (2021) The acetyl bromide lignin method accurately quantitates lignin in forage. 276, 114883.
15. Gong K, Chen L, Li X, Liu KJJJoFP & Preservation (2018) Lignin accumulation and biosynthetic enzyme activities in relation to postharvest firmness of fresh waxy corn. 42(1), e13333.
16. Gu Q, Zhu M, Wang X & Pan JJJoZU (2002) Studies on postharvest physiology and storage of bamboo shoots (*Phyllostachys praecox* f. *prevernalis*). 28, 169-174.
17. Gupta MK, Lenka SK, Gupta S, Rawal RKJPP & biochemistry (2020) Agonist, antagonist and signaling modulators of ABA receptor for agronomic and post-harvest management. 148, 10-25.
18. He J, Ren Y, Chen C, Liu J, Liu H & Pei YJJoFS (2017) Defense responses of salicylic acid in mango fruit against postharvest anthracnose, caused by *Colletotrichum gloeosporioides* and its possible mechanism. 37(1), e12294.
19. Hong SH, Ismail IA, Kang SM, Han DC & Kwon BMJPR (2016) Cinnamaldehydes in cancer chemotherapy. 30(5), 754-767.
20. Jiang Y & Fu JJPGR (2000) Ethylene regulation of fruit ripening: molecular aspects. 30, 193-200.
21. Jiménez-Muñoz R, Palma F, Carvajal F, Castro-Cegrí A, Pulido A, Jamilena M, Romero-Puertas MC, Garrido DJPB & Technology (2021) Pre-storage nitric oxide treatment enhances chilling tolerance of

- zucchini fruit (*Cucurbita pepo* L.) by S-nitrosylation of proteins and modulation of the antioxidant response. 171, 111345.
22. Kahramanoğlu İ, Chen C, Chen Y, Chen J, Gan Z & Wan CJJoFQ (2020) Improving storability of “nanfeng” mandarins by treating with postharvest hot water dipping. 2020, 1-12.
 23. Kim D, Langmead B & Salzberg SLJNm (2015) HISAT: a fast spliced aligner with low memory requirements. 12(4), 357-360.
 24. Kong J-QJRa (2015) Phenylalanine ammonia-lyase, a key component used for phenylpropanoids production by metabolic engineering. 5(77), 62587-62603.
 25. Li C, Suo J, Xuan L, Ding M, Zhang H, Song L, Ying YJPB & Technology (2019a) Bamboo shoot-lignification delay by melatonin during low temperature storage. 156, 110933.
 26. Li C, Xuan L, He Y, Wang J, Zhang H, Ying Y, Wu A, Bacic A, Zeng W & Song LJP (2018) Molecular mechanism of xylogenesis in moso bamboo (*Phyllostachys edulis*) shoots during cold storage. 11(1), 38.
 27. Li L, He X, Sun J, Li C, Ling D, Sheng J, Zheng F, Liu G, Li J & Tang YJJoFQ (2017) Responses of phospholipase D and antioxidant system to mechanical wounding in postharvest banana fruits. 2017.
 28. Li T, Zhang J, Gao X, Chen J, Zheng Y, Gao Y, Qiu LJPB & Technology (2019b) The molecular mechanism for the ethylene regulation of postharvest button mushrooms maturation and senescence. 156, 110930.
 29. Li Y, Ishikawa Y, Satake T, Kitazawa H, Qiu X, Rungchang SJPB & Technology (2014) Effect of active modified atmosphere packaging with different initial gas compositions on nutritional compounds of shiitake mushrooms (*Lentinus edodes*). 92, 107-113.
 30. Lin Y, Chen G, Lin H, Lin M, Wang H & Lin YJIJoBM (2020) Chitosan postharvest treatment suppresses the pulp breakdown development of longan fruit through regulating ROS metabolism. 165, 601-608.
 31. LIU M-c, SONG W-h, ZHU S-h & Jie ZJASiC (2007) Effects of nitric oxide and exogenous ethylene treatments on ethylene biosynthesis in Feicheng peach. 6(3), 290-295.
 32. Liu W, Zhang J, Jiao C, Yin X, Fei Z, Wu Q & Chen KJHR (2019) Transcriptome analysis provides insights into the regulation of metabolic processes during postharvest cold storage of loquat (*Eriobotrya japonica*) fruit. 6.
 33. Liu X, Lu Y, Yang Q, Yang H, Li Y, Zhou B, Li T, Gao Y, Qiao LJPB & Technology (2018) Cod peptides inhibit browning in fresh-cut potato slices: A potential anti-browning agent of random peptides for regulating food properties. 146, 36-42.
 34. Love MI, Huber W & Anders SJGb (2014) Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. 15(12), 1-21.
 35. Luo Z, Xu X, Cai Z & Yan BJFC (2007) Effects of ethylene and 1-methylcyclopropene (1-MCP) on lignification of postharvest bamboo shoot. 105(2), 521-527.

36. Ma L, Wang Q, Li L, Grierson D, Yuan S, Zheng S, Wang Y, Wang B, Bai C, Fu AJPB & Technology (2021) UV-C irradiation delays the physiological changes of bell pepper fruit during storage. 180, 111506.
37. Madebo MP, Ayalew Y, Zheng Y & Jin PJFRI (2022) Nitric oxide and its donor sodium-nitroprusside regulation of the postharvest quality and oxidative stress on fruits: a systematic review and meta-analysis. 1-29.
38. Meloni DA, Oliva MA, Martinez CA, Cambraia JJE & botany e (2003) Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. 49(1), 69-76.
39. Mirshekari A, Madani B, Yahia EM, Golding JB, Vand SHJJotSoF & Agriculture (2020) Postharvest melatonin treatment reduces chilling injury in sapota fruit. 100(5), 1897-1903.
40. Mukherjee SJNO (2019) Recent advancements in the mechanism of nitric oxide signaling associated with hydrogen sulfide and melatonin crosstalk during ethylene-induced fruit ripening in plants. 82, 25-34.
41. Pertea M, Pertea GM, Antonescu CM, Chang T-C, Mendell JT & Salzberg SLJNb (2015) StringTie enables improved reconstruction of a transcriptome from RNA-seq reads. 33(3), 290-295.
42. Petriccione M, Pagano L, Forniti R, Zampella L, Mastrobuoni F, Scortichini M, Mencarelli FJPB & Technology (2018) Postharvest treatment with chitosan affects the antioxidant metabolism and quality of wine grape during partial dehydration. 137, 38-45.
43. Pittard J & Yang JJEP (2008) Biosynthesis of the aromatic amino acids. 3(1), 10.1128/ecosalplus.1123.1126. 1121.1128.
44. Prakash V, Singh VP, Tripathi DK, Sharma S, Corpas FJJE & Botany E (2019) Crosstalk between nitric oxide (NO) and abscisic acid (ABA) signalling molecules in higher plants. 161, 41-49.
45. Qi X, Ji Z, Lin C, Li S, Liu J, Kan J, Zhang M, Jin C & Qian CJFc (2020) Nitric oxide alleviates lignification and softening of water bamboo (*Zizania latifolia*) shoots during postharvest storage. 332, 127416.
46. Qi X, Zhao J, Jia Z, Cao Z, Liu C, Li J, Su Y, Pan Y, He C & Xu YJH (2022) Potential metabolic pathways and related processes involved in pericarp browning for postharvest pomegranate fruits. 8(10), 924.
47. Rabiei V, Kakavand F, Zaare-Nahandi F, Razavi F & Aghdam MSJSH (2019) Nitric oxide and γ -aminobutyric acid treatments delay senescence of cornelian cherry fruits during postharvest cold storage by enhancing antioxidant system activity. 243, 268-273.
48. Reddy MR, Krishnasamy SK & Kathiravan MJBC (2020) Identification of novel scaffold using ligand and structure based approach targeting shikimate kinase. 102, 104083.
49. Shu P, Min D, Ai W, Li J, Zhou J, Li Z, Zhang X, Shi Z, Sun Y, Jiang YJPB & Technology (2020) L-Arginine treatment attenuates postharvest decay and maintains quality of strawberry fruit by promoting nitric oxide synthase pathway. 168, 111253.
50. Singh R, Rastogi S, Dwivedi UNJCRiFS & Safety F (2010) Phenylpropanoid metabolism in ripening fruits. 9(4), 398-416.

51. Song L, Chen H, Gao H, Fang X, Mu H, Yuan Y, Yang Q & Jiang YJCCJ (2013) Combined modified atmosphere packaging and low temperature storage delay lignification and improve the defense response of minimally processed water bamboo shoot. 7(1), 1-9.
52. Sun M, Yang X-L, Zhu Z-P, Xu Q-Y, Wu K-X, Kang Y-J, Wang H, Xiong A-SJPP & Biochemistry (2021) Comparative transcriptome analysis provides insight into nitric oxide suppressing lignin accumulation of postharvest okra (*Abelmoschus esculentus* L.) during cold storage. 167, 49-67.
53. Tang N, An J, Deng W, Gao Y, Chen Z, Li ZJPB & Technology (2020) Metabolic and transcriptional regulatory mechanism associated with postharvest fruit ripening and senescence in cherry tomatoes. 168, 111274.
54. Thévenin J, Pollet B, Letarnec B, Saulnier L, Gissot L, Maia-Grondard A, Lapierre C & Jouanin LJMp (2011) The simultaneous repression of CCR and CAD, two enzymes of the lignin biosynthetic pathway, results in sterility and dwarfism in *Arabidopsis thaliana*. 4(1), 70-82.
55. Wang B, Wu C, Wang G, He J & Zhu SJSH (2021) Transcriptomic analysis reveals a role of phenylpropanoid pathway in the enhancement of chilling tolerance by pre-storage cold acclimation in cucumber fruit. 288, 110282.
56. Wang C, Gao Y, Tao Y, Wu X, Zhibo CJIFS & Technologies E (2017a) Influence of γ -irradiation on the reactive-oxygen metabolism of blueberry fruit during cold storage. 41, 397-403.
57. Wang D, Li L, Xu Y, Limwachiranon J, Li D, Ban Z, Luo ZJJJoA & Chemistry F (2017b) Effect of exogenous nitro oxide on chilling tolerance, polyamine, proline, and γ -aminobutyric acid in bamboo shoots (*Phyllostachys praecox* f. *prevernalis*). 65(28), 5607-5613.
58. Wang J, Jiang J, Wang J, Wang Z, Yang X, Jia LJRP & chemistry (2019a) The influence of gamma irradiation on the storage quality of bamboo shoots. 159, 124-130.
59. Wang L, Chen Y, Wu M, Dai F, Ye M, Chen F, Qi Y, Luo Z, Huang HJPB & Technology (2023) Involvement of lignin deposition and cell wall degradation in stem senescence of Chinese flowering cabbage during storage. 198, 112256.
60. Wang W, Ni Z-J, Thakur K, Cao S-Q & Wei Z-JJCOiFS (2022) Recent update on the mechanism of hydrogen sulfide improving the preservation of postharvest fruits and vegetables. 100906.
61. Wang Y, Mo Y, Li D, Xiang C, Jiang Z & Wang JJFc (2019b) The main factors inducing postharvest lignification in king oyster mushrooms (*Pleurotus eryngii*): Wounding and ROS-mediated senescence. 301, 125224.
62. Wei D, Yang J, Xiang Y, Meng L, Pan Y & Zhang ZJFiN (2022) Attenuation of postharvest browning in rambutan fruit by melatonin is associated with inhibition of phenolics oxidation and reinforcement of antioxidative process. 9, 905006.
63. Winkel-Shirley BJPp (2001) Flavonoid biosynthesis. A colorful model for genetics, biochemistry, cell biology, and biotechnology. 126(2), 485-493.
64. Wu L, Ma N, Jia Y, Zhang Y, Feng M, Jiang C-Z, Ma C & Gao JJPP (2017) An ethylene-induced regulatory module delays flower senescence by regulating cytokinin content. 173(1), 853-862.

65. Xie J, Qin Z, Pan J, Li J, Li X, Khoo HE & Dong XJFiPS (2022) Melatonin treatment improves postharvest quality and regulates reactive oxygen species metabolism in “Feizixiao” litchi based on principal component analysis. 13, 965345.
66. Xu D, Zuo J, Fang Y, Yan Z, Shi J, Gao L, Wang Q & Jiang AJFC (2021) Effect of folic acid on the postharvest physiology of broccoli during storage. 339, 127981.
67. Xu J, Ji N, Wang R, Ma C, Lei J, Zhang N, Liu R & Deng YJA (2023) Study on the Regulation Mechanism of 1-MCP Combined with SO₂ Treatment on Postharvest Senescence of Bamboo Shoots (*Chimonobambusa quadrangularis*) in Karst Mountain Area. 13(4), 1122.
68. Xu L, Fang X, Wu W, Chen H, Mu H & Gao HJFC (2019) Effects of high-temperature pre-drying on the quality of air-dried shiitake mushrooms (*Lentinula edodes*). 285, 406-413.
69. Yang B, Han Y, Gao H, Liu R, Xu F, Liu R, Xiao S, Li B, Chen HJPB & Technology (2023) Application of melatonin delays lignification in postharvest water bamboo shoots in association with energy metabolism. 196, 112149.
70. Yang H, Wu F, Cheng JJTJoHS & Biotechnology (2011) Effects of nitric oxide treatment on active oxygen metabolism and flesh lignification in bamboo shoots. 86(5), 499-504.
71. Yang H, Zhou C, Wu F, Cheng JJPB & Technology (2010) Effect of nitric oxide on browning and lignification of peeled bamboo shoots. 57(1), 72-76.
72. Yu L, Pei J, Zhao Y & Wang SJFiPS (2021) Physiological changes of bamboo (*Fargesia yunnanensis*) shoots during storage and the related cold storage mechanisms. 12, 731977.
73. Yufang X, Zisheng L & Du CJZNK (2001) Effect of active oxygen metabolism on excised bamboo shoot lignification.
74. Zhang C, Zang Y, Liu P, Zheng Z & Ouyang JJJob (2019) Characterization, functional analysis and application of 4-Coumarate: CoA ligase genes from *Populus trichocarpa*. 302, 92-100.
75. Zhang D, Xu X, Zhang Z, Jiang G, Feng L, Duan X, Jiang YJPB & Technology (2018) 6-Benzylaminopurine improves the quality of harvested litchi fruit. 143, 137-142.
76. Zhang H, Liu F, Wang J, Yang Q, Wang P, Zhao H, Wang J, Wang C, Xu XJPB & Technology (2021) Salicylic acid inhibits the postharvest decay of goji berry (*Lycium barbarum* L.) by modulating the antioxidant system and phenylpropanoid metabolites. 178, 111558.
77. Zhang W, Cao J, Fan X, Jiang WJTIFS & Technology (2020) Applications of nitric oxide and melatonin in improving postharvest fruit quality and the separate and crosstalk biochemical mechanisms. 99, 531-541.
78. Zhang W, Pan Y, Jiang Y & Zhang ZJSH (2023) Advances in control technologies and mechanisms to treat peel browning in postharvest fruit. 311, 111798.
79. ZHENG J, LI S-e, Maratab A, HUANG Q-h, ZHNEG X-I & PANG L-jJJoIA (2020) Effects of UV-B treatment on controlling lignification and quality of bamboo (*Phyllostachys prominens*) shoots without sheaths during cold storage. 19(5), 1387-1395.

80. Zuo W, Lu L, Su M, Zhang J, Li Y, Huang S, Li C, Wang N, Zhang Z, Chen XJPB & Technology (2021) Analysis of differentially expressed genes and differentially abundant metabolites associated with the browning of Meihong red-fleshed apple fruit. 174, 111437.

Figures

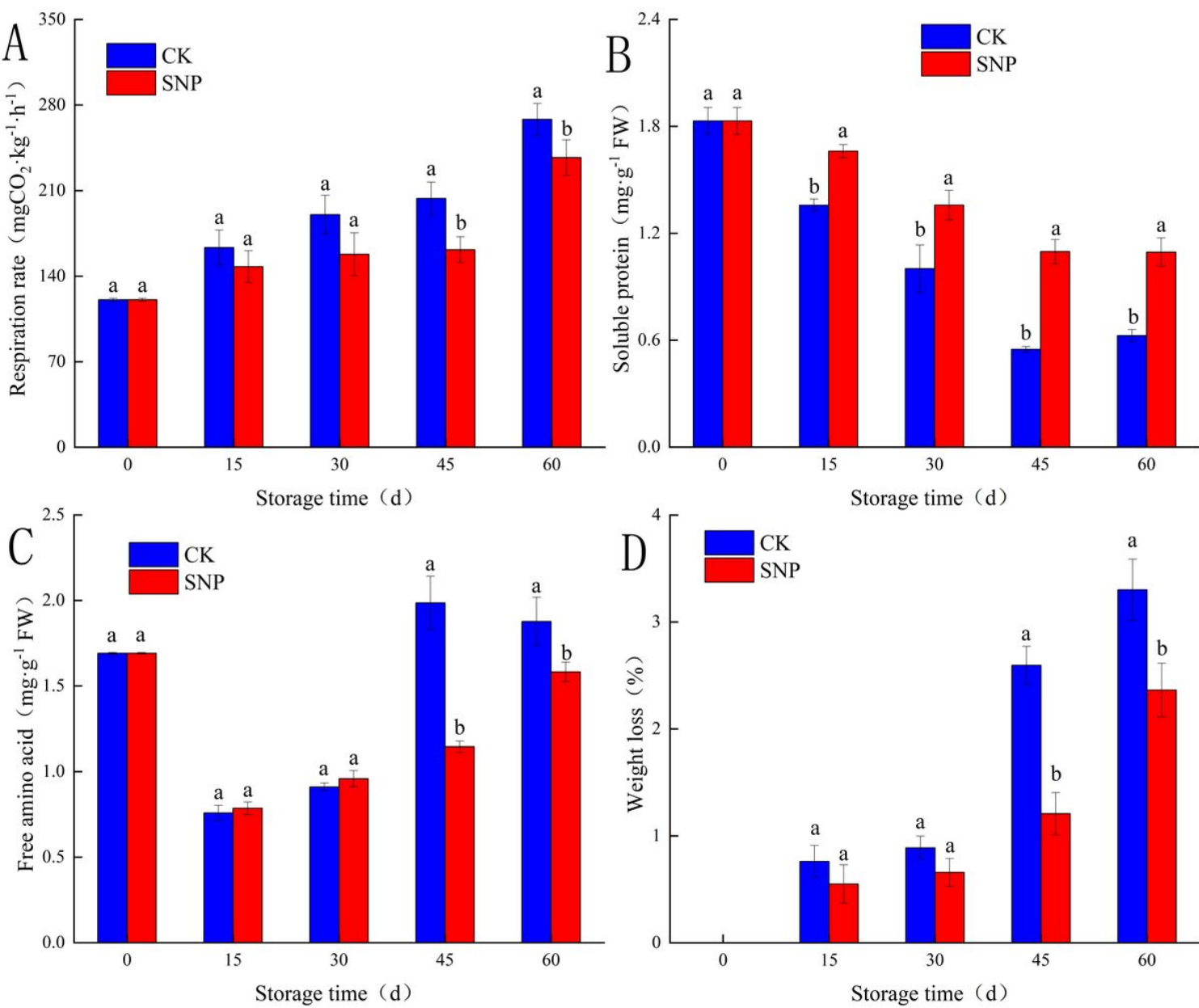


Figure 1

Effects of SNP treatment on respiration rate (A), soluble protein content (B), free amino acid content (C) and weight loss rate (D) of fresh bamboo shoots (*Chimonobambusa quadrangularis*) during storage. Different letters (on the same day) were significantly different (Duncan’smultiple range test, $P < 0.05$).

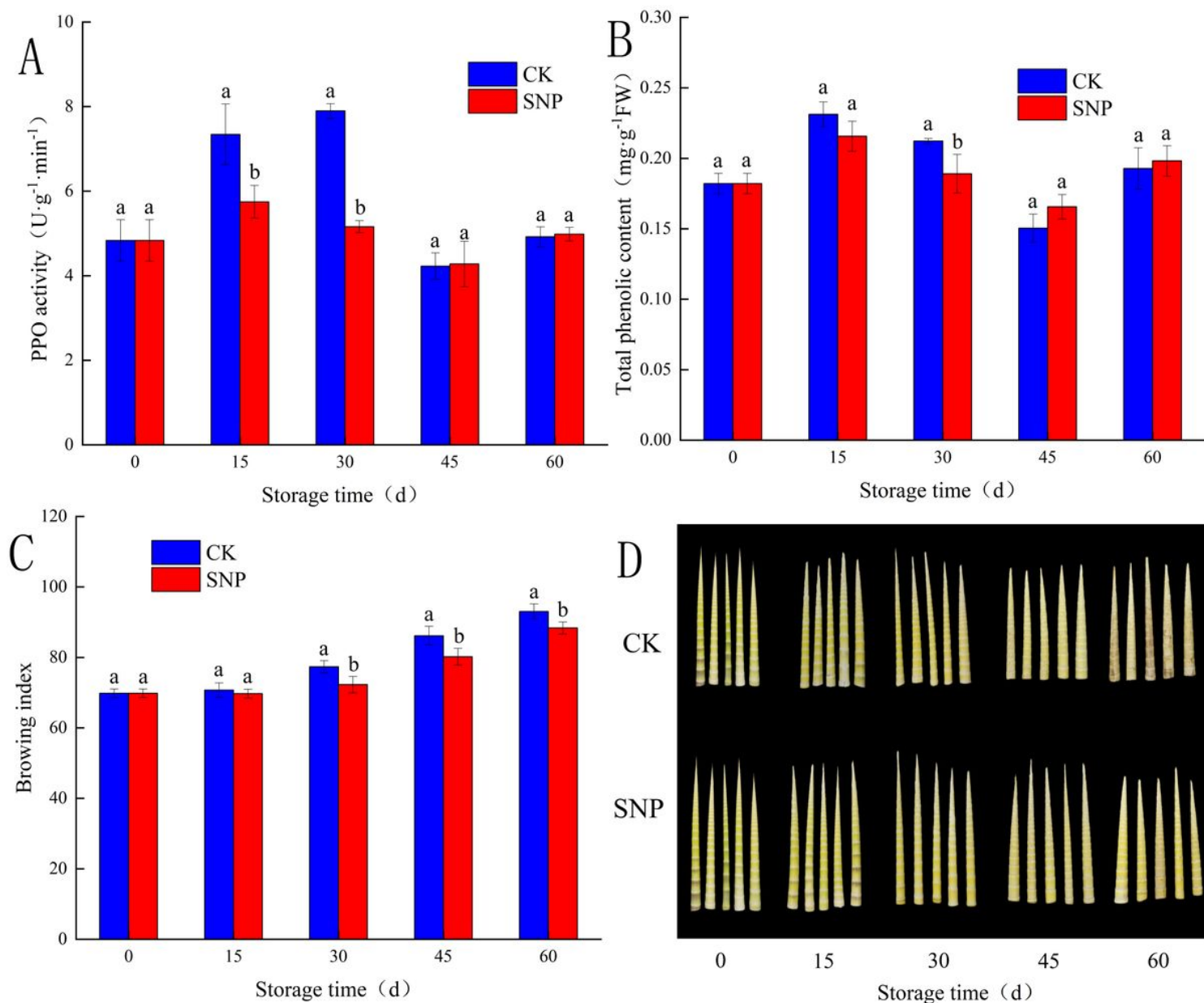


Figure 2

Effects of SNP treatment on PPO activity (A), total phenol content (B), browning index (C) and appearance color (D) of fresh bamboo shoots (*Chimonobambusa quadrangularis*) during storage. Different letters (on the same day) were significantly different (Duncan's multiple range test, $P < 0.05$).

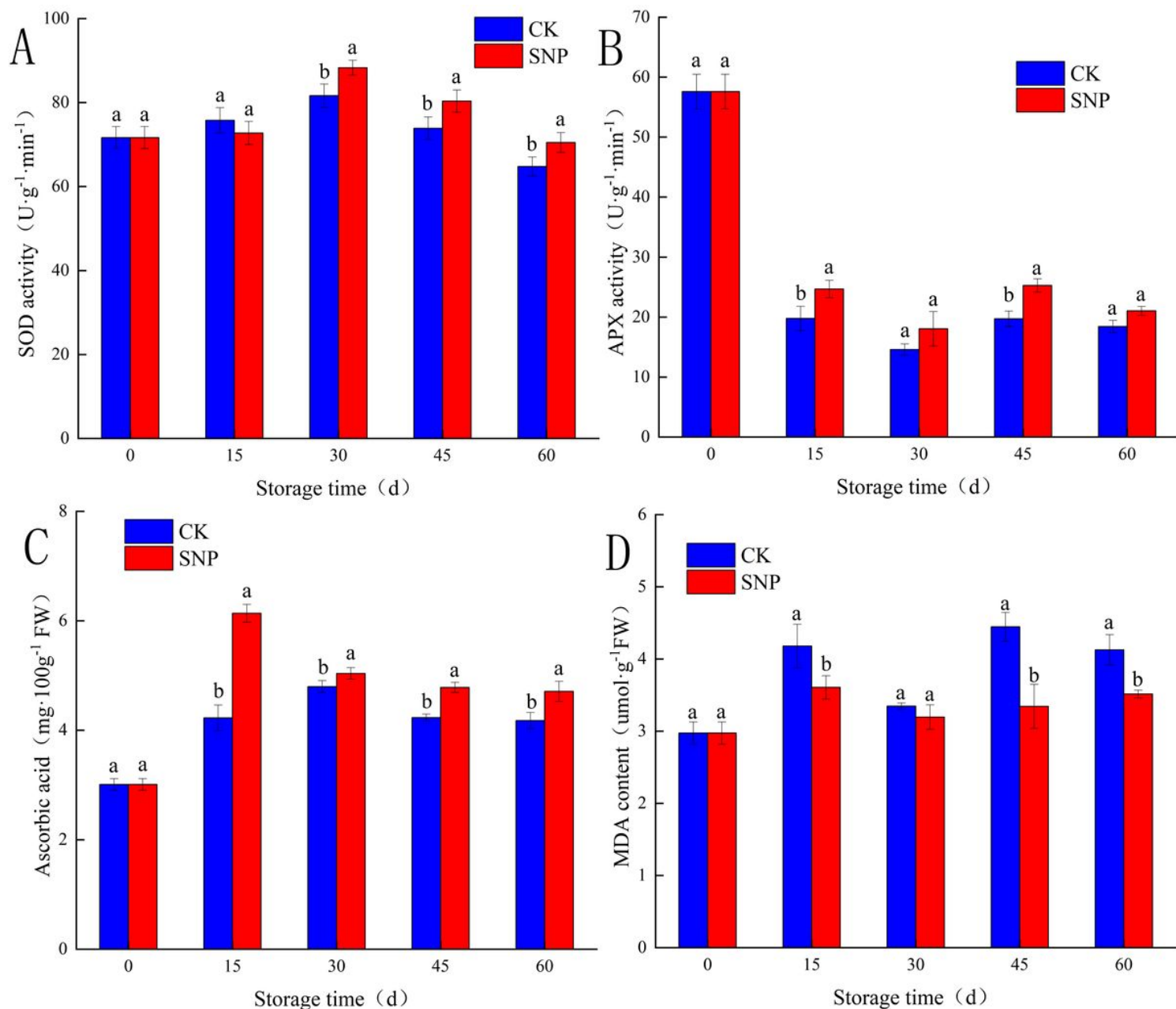


Figure 3

Effects of SNP treatment on SOD (A), APX (B), ascorbic acid content (C) and MDA content (D) of fresh bamboo shoots (*Chimonobambusa quadrangularis*) during storage. Different letters (on the same day) were significantly different (Duncan's multiple range test, $P < 0.05$).

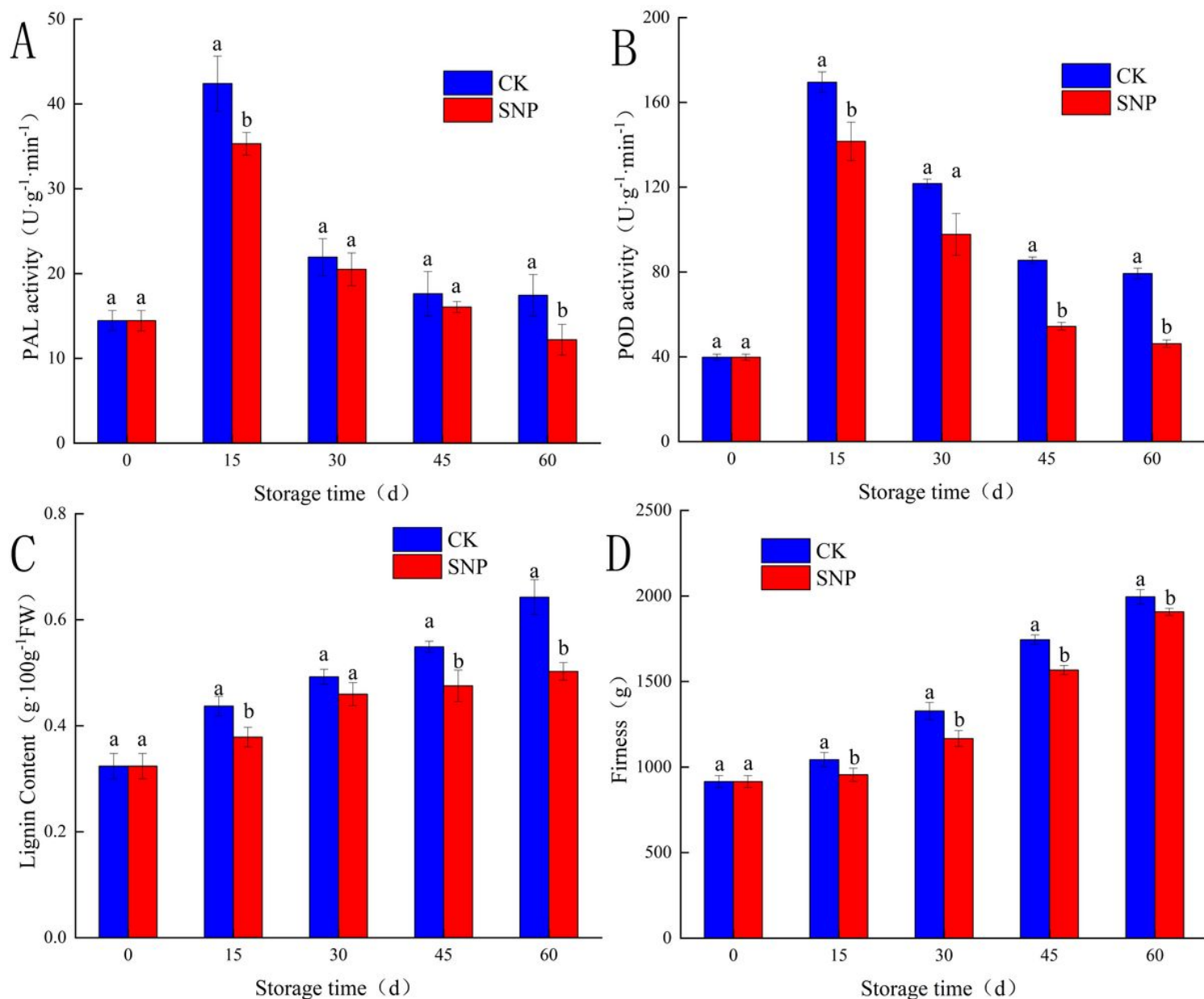


Figure 4

Effects of SNP treatment on PAL (**A**), POD (**B**), lignin content (**C**) and hardness (**D**) of fresh bamboo shoots (*Chimonobambusa quadrangularis*) during storage. Different letters (on the same day) were significantly different (Duncan's multiple range test, $P < 0.05$).

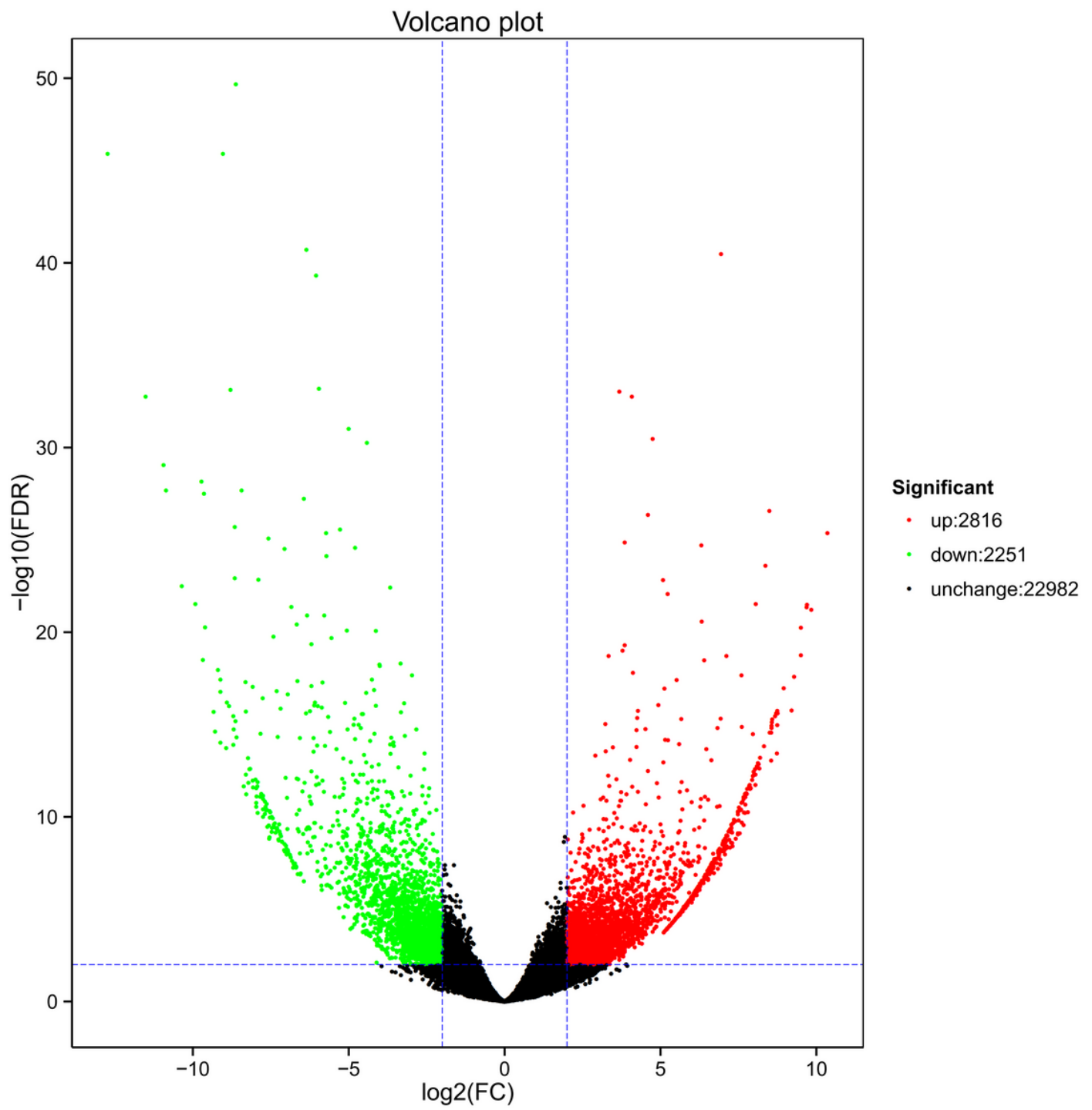


Figure 5

Differential gene volcano map

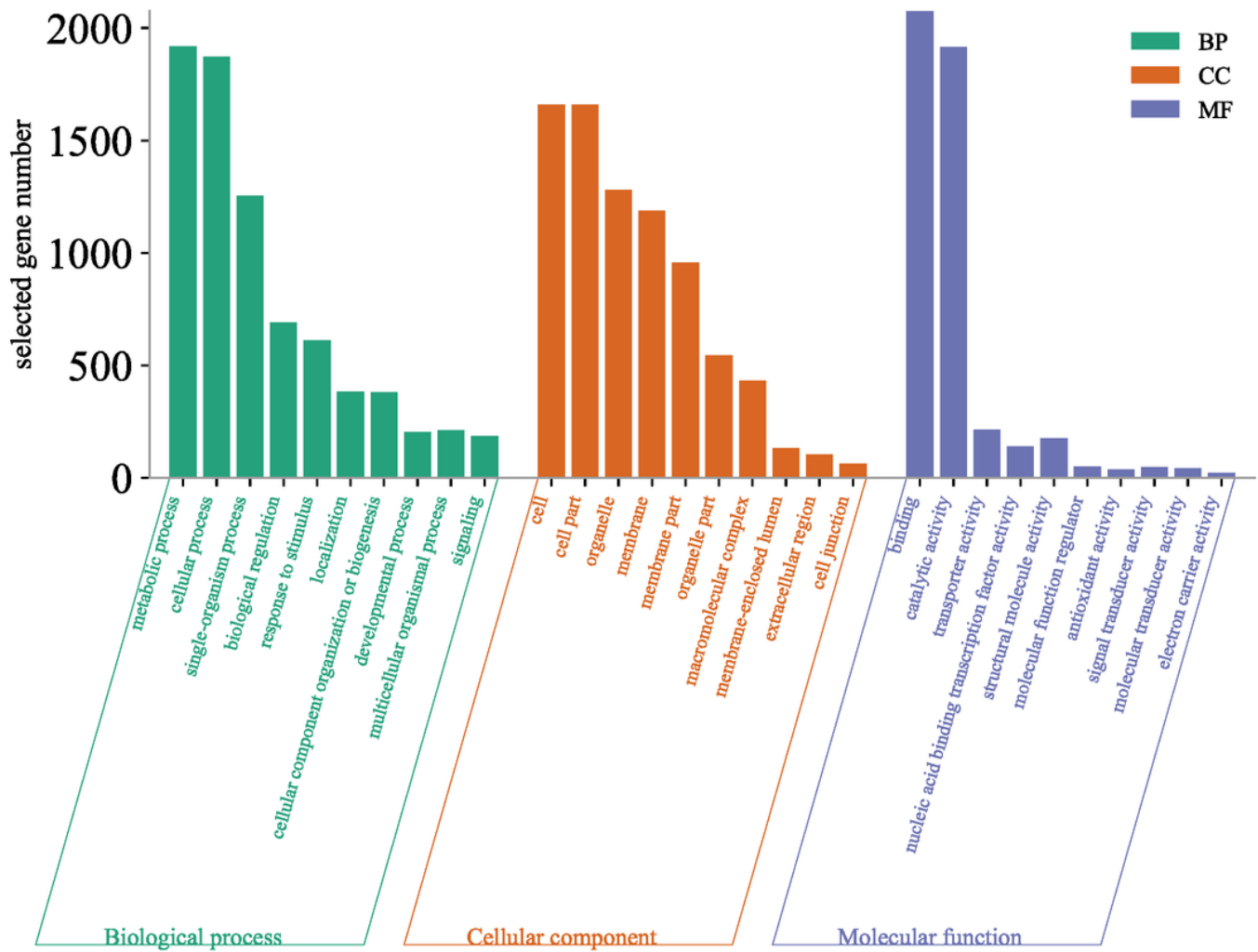


Figure 6

GO enrichment analysis of differential genes

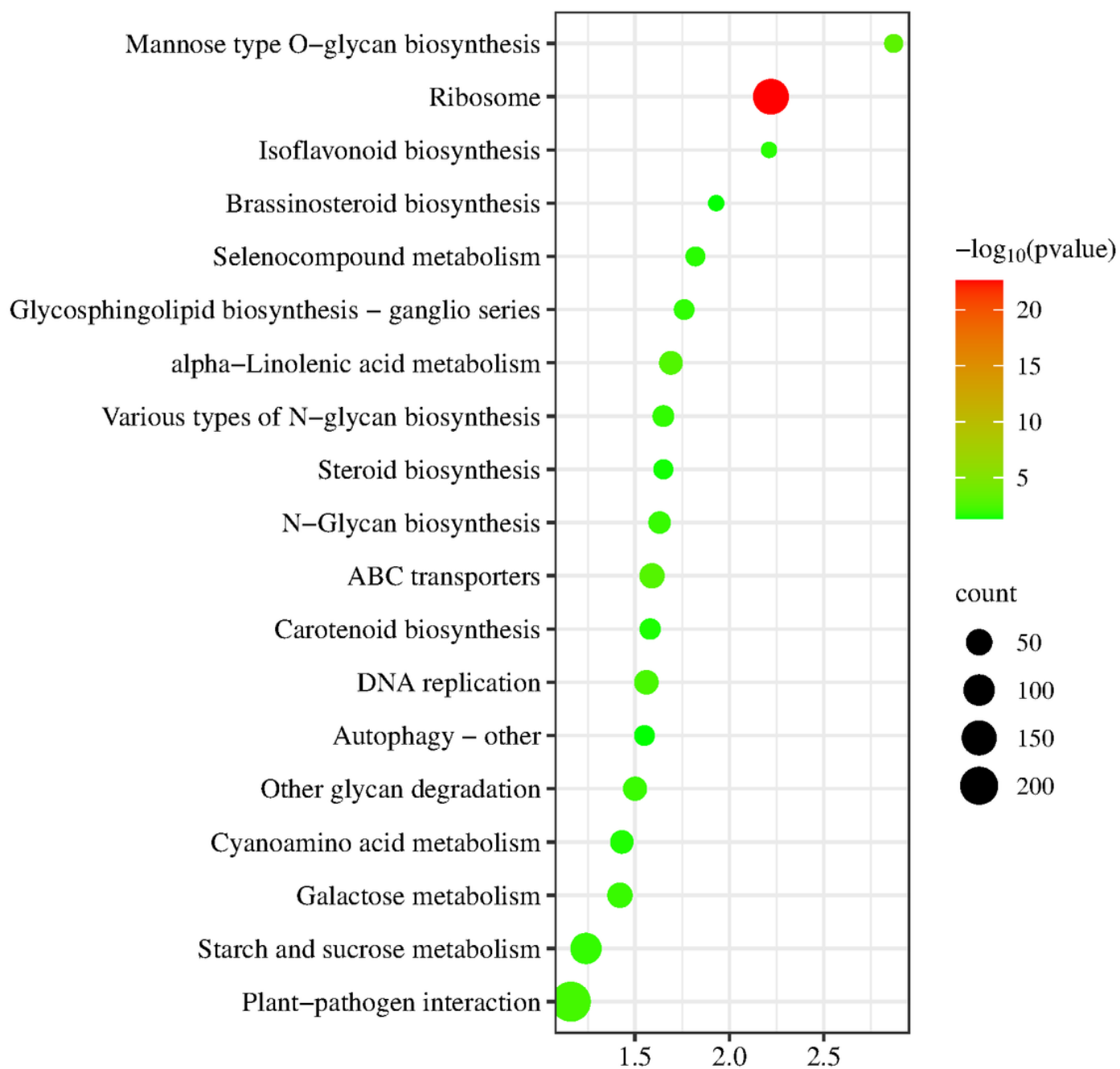


Figure 7

Differential gene KEGG bubble diagram

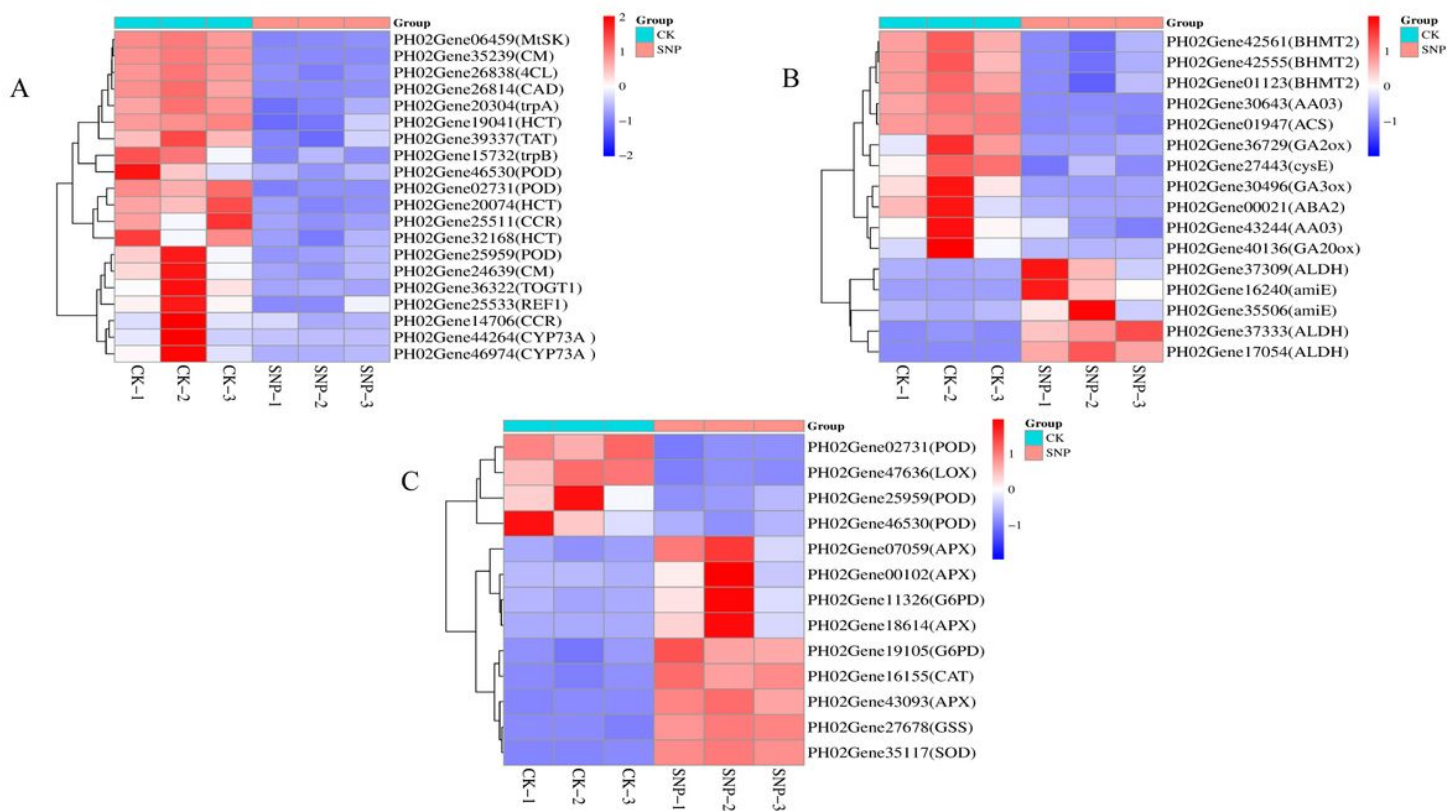


Figure 8

Lignin biosynthesis (**A**), plant hormone biosynthesis (**B**), active oxygen metabolism (**C**) differential gene cluster heat map. The $\log^{10}$ (FPKM+1) values of the genes were used for gene expression normalization and hierarchical cluster analysis.

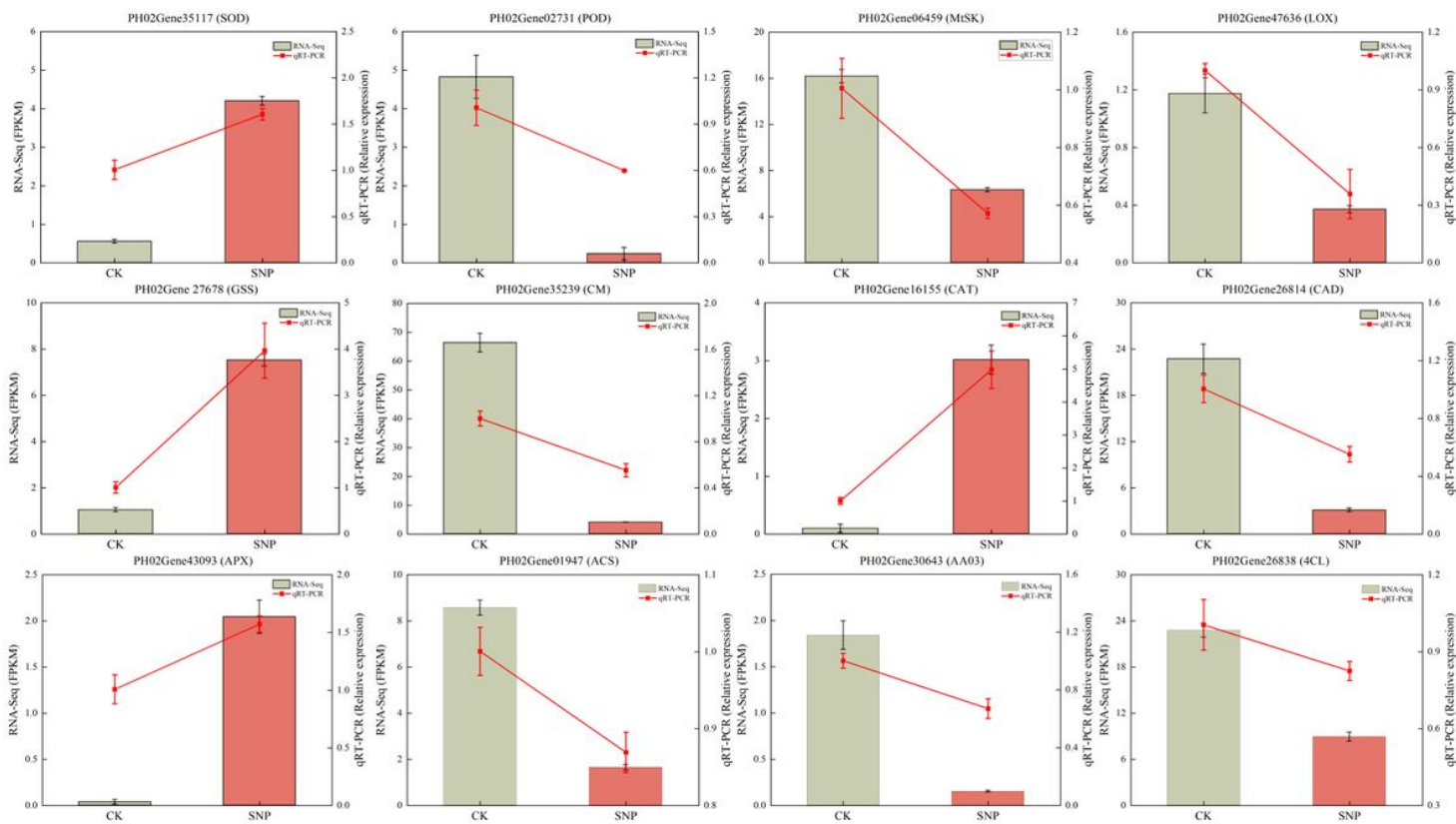


Figure 9

Changes in the expression levels of key aging genes regulated by SNP

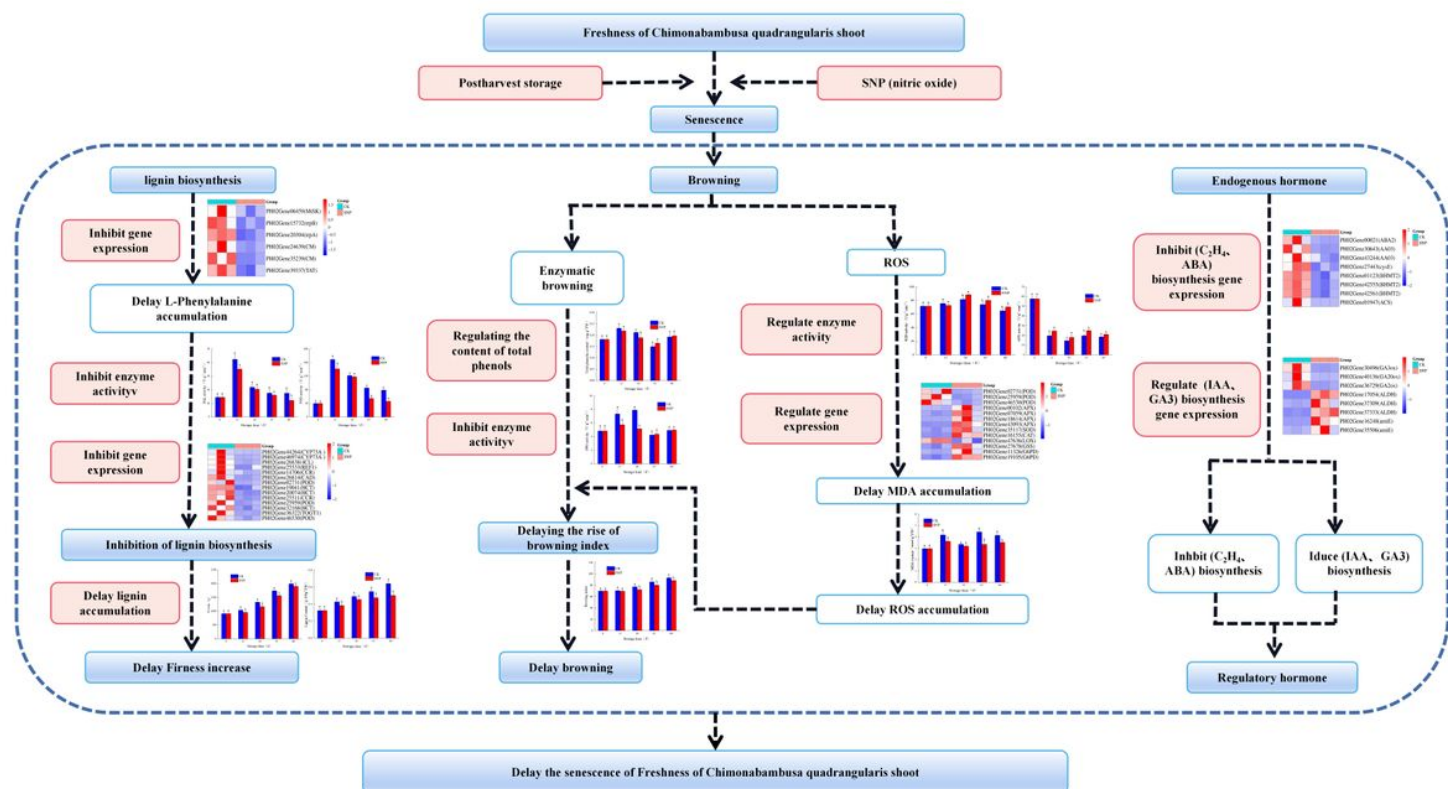


Figure 10

Illustrates a possible molecular regulation mechanism involved in the postharvest senescence of fresh bamboo shoots.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterials.doc](#)
- [SupplementaryMaterials.xlsx](#)