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ORIGINAL ARTICLE

Effect of Se application on selenium accumulation and fruit quality in pear (*Pyrus ussuriensis*)

Chi Yuan[1] · Haidong Bu[1,2] · Jiaming Zhao[1] · Jiaojiao Liu[1] · Guobao Wang[3] · Hui Yuan[1] · Aide Wang[1]

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Abstract

Selenium (Se) is an essential trace element for both animals and plants. Se treatment can increase fruit Se concentration and shelf life. However, the mechanism underlying Se-delayed fruit ripening is still unclear. 'Nanhong' pear (*Pyrus ussuriensis*) is a typical climacteric fruit with high ethylene production and a rapid drop in firmness during the ripening process. In this research, two groups of Se (A and B treatments) were used to treat 'Nanhong' pear fruit. The results showed that these treatments could greatly increase the Se content but decreased the titratable acid content. Treatment A significantly decreased ethylene production, and the key genes controlling ethylene production, *PuACSs* and *PuERF2,* were inhibited by Se treatment. Our findings suggest that PuERF2 may play an important role in Se-mediated ethylene reduction. In addition, treatment A significantly decreased the stone cell content, and one lignin biosynthesis gene, *PuC4H,* was downregulated by treatment A, indicating that *PuC4H* may be the key gene responsible for stone cell reduction under Se treatment. Our findings provide a new medium to extend pear shelf life and improve fruit quality, which is beneficial to the development of the pear industry.

Keywords Pear · Selenium · Fruit quality · Ethylene · Stone cell

Introduction

Selenium (Se) is an essential trace element for both animals and plants; however, Se deficiency in the diet is now a global problem (Schiavon et al. 2020). Around one billion people worldwide may be Se deficiency (Trippe and Pilon-Smits 2021), including those in many areas in China (Dinh et al. 2018). Se deficiency in the human body may be related to some serious medical complications, such as hypothyroidism (Arthur et al. 1992), cataracts, cardiomyopathy, and even cancer (Natasha et al. 2018; Newman et al. 2019). Diets are the major Se source for humans, but the Se contents in staple food are very low and are unable to meet the requirement for health (Zhou et al. 2020). Therefore, biofortification of Se-enriched food is very important for increasing the Se concentration in food and will be helpful for human health (White and Broadley 2009). Foliar spraying and soil application are both effective means to increase the Se content in food, and the latter is much more effective (Deng et al. 2019).

Low and moderate Se concentrations in plants can promote growth and ameliorate the adverse effects of environmental stresses (Hamilton 2004; Zhu et al. 2016), such as drought (Hasanuzzaman and Fujita 2011), water (Wang 2011), and salt (Hasanuzzaman et al. 2011). Se has been used to alleviate Cd-inhibited plant growth in cucumber (Sun et al. 2020). Se is generally effective in decreasing ethylene production and phenylalanine ammonia lyase (PAL) activity in lettuce and chicory (Malorgio et al. 2009). Furthermore, the effects of Se on fruit physiology has been raising concern. For example, Se makes tomato fruit more resistant to postharvest decay and increases the concentration of non-enzymatic antioxidants (Zhu et al. 2016; Schiavon et al.

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Chi Yuan and Haidong Bu contributed equally to this work.

✉ Hui Yuan
huiyuan@syau.edu.cn

✉ Aide Wang
awang@syau.edu.cn

[1] Key Laboratory of Fruit Postharvest Biology, Liaoning Province, College of Horticulture, Shenyang Agricultural University, Shenyang 110866, China

[2] Mudanjiang Branch of Heilongjiang Academy of Agricultural Sciences, Mudanjiang, China

[3] College of Biological and Agricultural Engineering, Weifang University, Weifang 261061, China

2013). Se can decrease the rate of ethylene biosynthesis in tomato, leading to a delay in fruit ripening (Pezzarossa et al. 2014). Foliar Se treatment can decrease ethylene production by repressing the expression of *ACS* and *ACO* in tomato fruit (Zhu et al. 2017). Moreover, Se treatment increases the Se concentration in fruit and prolong the shelf life by delaying the reduction of flesh firmness and fruit ripening in peach and pear (Pezzarossa et al. 2012). In apple, foliar application of Se could retard flesh firmness reduction and fruit ripening by lowering ethylene biosynthesis rate (Babalar et al 2019). However, the mechanism of how Se delays fruit ripening is still unclear.

'Nanhong' pear (*Pyrus ussuriensis*) is a red bud sport variety of 'Nanguo' pear. The fruit of 'Nanhong' pear is typical climacteric fruit, and ethylene is the main factor controlling the ripening process (Yuan et al. 2020). During ripening, the fruits produce high amounts of ethylene, and firmness drops rapidly. 'Nanhong' pear fruits quality declined, including a rapid increase in the stone cell content and a decrease in the aroma, which seriously influence the shelf life and economic benefits of 'Nanhong' pear (Liu 2019). Thus, finding a way to improve fruit quality is very important for 'Nanhong' pear. As an important trace element, Se is increasingly used for vegetables, fruits, and food crops to produce selenium-rich foods (Nawaz et al. 2017). However, little is known about whether Se treatment can increase the Se content and fruit quality of 'Nanhong' pear.

Here, we used Se to treat 'Nanhong' pear and found that the Se content increased in the Se-treated fruits. In addition, both the ethylene production and the stone cell content decreased. Our results showed that Se treatment could improve the quality of 'Nanhong' pear fruit, which provides new insights for improving fruit quality.

Materials and methods

Plant materials and treatments

'Nanhong' pear (*Pyrus ussuriensis* Maxim.) was grafted on 'Shanli' (*Pyrus ussuriensis* Maxim.) and grown at the experimental farm of Shenyang Agricultural University (Shenyang, China). The experimental farm had a sandy loam soil and the pH was 7.2. The soil contains 1.98% of organic matters, 0.085% of total nitrogen, 3 and 56 mg/kg of available phosphorus and potassium, respectively. The trees were planted at 2.0 m × 4.0 m spacing. We designed two treatments, and distilled water was used as a control. Treatment A was a 7000-fold dilution of a mixture of 0.1% nano-selenium fertilizer (Hengshui Gemei Micronutrient Co., Ltd., Hengshui, China), 40% ethephon (an ethylene precursor compound; Sigma, http://www.sigmaaldrich.com/), and a 1000-fold dilution of 1% sodium selenite (10102-18-8, Nanjing Chemical Reagent Co., Ltd., Nanjing, China). Treatment B was a 5000-fold dilution of a mixture of 0.1% nano-selenium fertilizer, 40% ethephon, and a 1000-fold dilution of 1% sodium selenite. The treatments were used to spray the trees, including leaves and fruits, at 60, 75, and 95 days after flowering. Three trees were selected as one biological replicate and every treatment included three biological replicates. After harvest (139 days after flowering), the fruits were transported to the laboratory and stored at room temperature for 15 days; sampling was conducted every 5 days. At each sampling time, fruits were used to measure ethylene production and other indexes, and then the fruits were sliced, frozen in liquid nitrogen, and stored at - 80 °C for later use.

Measurement of fruit firmness

The fruit firmness measurement was carried out according to Yuan et al. (2017) using a portable pressure tester (FT-327, Facchini, Italy) fitted with an 11-mm-diameter probe. Each fruit was cut into four thin discs (approximately 2.5 cm in diameter) from opposite sides. The probe was pressed into the cut surface of the fruit to a depth of 8–9 mm. Five fruits were used per sample.

Measurement of soluble solids and the sugar content

For the measurement of soluble solids, the fruit flesh was ground into a powder and filtered through a cell strainer (Cat. no. CSS010040, Jet Biofil, https://www.jetbiofil.com), and then the soluble solids remaining on the filter were measured by a sugar meter (PAL-1, Atago, Tokyo, Japan). Measurement of the sugar content was carried out using an HPLC 1260 Infinity Series (Agilent Technologies, Santa Clara, CA, USA) according to Li et al. (2020b). First, 1 g of each sample was placed in a 50 ml centrifuge tube to which 10 ml 80% (v/v) ethanol was added. The sample was incubated at 80 °C for 30 min and then centrifuged at 12,000 rpm for 5 min. The supernatant was transferred into a new tube, and the above steps were repeated twice to ensure complete extraction. The supernatant was dried by distillation, and then 1 ml distilled water was used to dissolve the sugar. The solution was passed through a 0.45 mm membrane, and then the soluble sugar content was measured by HPLC (Agilent 1260). The specific methods were as follows: 3 μm, 7.8 × 300 mm Carbomix Ca-NP column (Sepax Technologies, Inc., Newark, DE, USA); column temperature of 80 °C; refractive index detector temperature of 35 °C; and an injection volume of 10 ml. The standards for sugar content measurement were sucrose (CAS:57-50-1), D-(+)-Glucose (14431-43-7), D-(-)-Fructose and D-Sorbitol (CAS:50-70-5), respectively. Nine fruits were collected at each sampling

time and were randomly divided into three groups as three biological replicates.

Measurement of ethylene production

One or two fruits were enclosed in an airtight container (0.86 l, 24 °C) equipped with septa, and 1 ml gas was sampled using a syringe. The ethylene production was measured with a gas chromatograph (Agilent 7890A, Santa Clara, USA) according to Tan et al. (2013). Five fruits per sample were measured.

Measurement of the stone cell content

The stone cell contents were measured using the hydrochloric acid treatment method according to Lee et al. (2006) with slight modification as follows: 10 g of each sample was mixed and diluted with distilled water. Solutions were allowed to settle for 30 min, after which the supernatant was decanted; the above steps were repeated twice. The sediment was suspended in 0.5 M/L HCl for 30 min, decanted and washed twice using distilled water. Finally, the sediment was dried in an oven at 65 °C, and the stone cell content was measured. Stone cell content (%) = weight of stone cells (g DW)/weight of pulp (g FW) × 100 (Yan et al. 2014). Nine fruits were collected at each sampling time and were randomly divided into three groups as three biological replicates.

Measurement of the titratable acid content

An acid-base titration was used to measure the titratable acid content, with phenolphthalein as an indicator. Nine fruits were collected at each sampling time and were randomly divided into three groups as three biological replicates.

Measurement of Se content

The Se content measurement was performed according to Zao and Burau (1977), with minor modification. The sample was soaked with nitric and perchloric acid (7:1) overnight, after boiling at 100 °C for 12 h, digested at 150 °C until the digests were clear and transparent. Then the digests were diluted with distilled water to 25 ml. Finally, the digests were analyzed by ICP-MS (inductively coupled plasma mass spectrometry). Nine fruits were collected at each sample point, and were divided into three groups randomly as three biological replicates.

Quantitative RT-PCR

Total RNAs of each sample point were extracted according to Li et al. (2017), with little modification. 1 μg of total RNA was used to synthesize first-strand cDNA using a PrimeScript First-Strand cDNA Synthesis Kit (Takara, Japan).

Quantitative RT-PCR (qRT-PCR) was performed as described by Bu et al. (2020), and the pear *Actin* gene was used as the internal control (Yuan et al. 2017). The primers for each gene were designed by the online website Primer3 (http://primer3.ut.ee/) and were listed in supplemental Table 1. Three replications were conducted.

Results

The Se content increases in treated pear

In order to clarify whether the application of exogenous Se could increase the Se content in 'Nanhong' pear, we treated 'Nanhong' pear during fruit development. After harvested, the fruits were stored at room temperature for 15 days (Fig. 1A). We then measured the Se content in treated fruits, finding that both treatments A and B greatly increased the Se content in these fruits (Fig. 1B). These results indicated

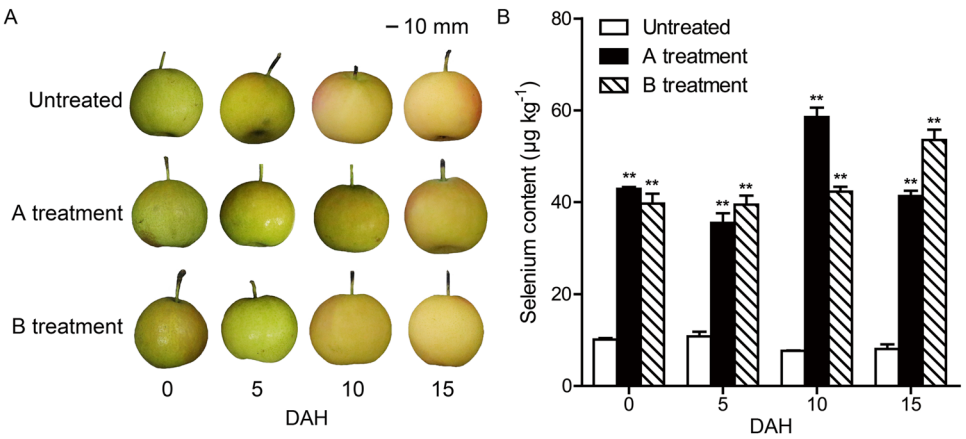

Fig. 1 Exogenous Se treatment increased Se content in Nanhong pear fruits. Nanhong pear fruits of Se treatment were harvested at 139 DAH (days after harvest), and stored for 15 days at room temperature (**A**). Se content of treated fruits was investigated using ICP-MS (B). **Significant differences ($p < 0.01$, Student's t test). Error bars indicated the standard deviation (SD) of 10 fruits. Bar, 10 mm

that our treatments were effective and suitable for the following research.

Effect of Se on fruit storage quality

Storage quality is one of the most important economic traits of fruits; a good storage quality has a decisive influence on the fruit quality and market value. In order to detect the effect of Se on fruit storage quality, we measured the ethylene production and hardness of the fruits under Se treatment. The results showed that both treatments retained fruit hardness during storage, especially on 10 and 15 DAH (Fig. 2A). The ethylene production was inhibited by these two treatments, especially treatment A (Fig. 2B).

Effect of Se on fruit sensory quality

In order to clarify the influence of Se treatment on the stone cell content, we measured the stone cell content of the pears treated with Se during fruit storage. Because the fruits on 15 DAH were too soft, we only present the results for 0, 5, and 10 DAH. On 0 and 5 DAH, both treatments decreased the stone cell content. On 10 DAH, treatment A decreased the stone cell content, whereas B had the opposite effect (Fig. 3A).

We then analyzed the soluble solid content and found that the soluble solid content continued to increase as the storage time prolonged, with no significant difference between the control and treatments (Fig. 3B). Soluble solid includes sugar, titratable acid (TA), and other components, so we measured the titratable acid content. Both treatments A and B greatly decreased the titratable acid content (Fig. 3C), leading to an increase in the solidity-acid ratio (Fig. 3D). We believed that treatment A was much more effective than treatment B, so we chose treatment A for the following research.

We measured the soluble sugar content in the treated and control fruits. Glucose, fructose, and sorbitol increased in response to Se treatment, but no significant difference was observed for sucrose (Fig. 4).

Effect of Se on expression patterns of ethylene biosynthesis and signal transduction genes

Treatment A inhibited ethylene production (Fig. 2B), so we analyzed the expressions of *PuACS1* and *PuACS4*, which are key enzymes in pear ethylene biosynthesis (Yuan et al. 2020), and we found that the expressions of *PuACS1* and *PuACS4* were inhibited by Se treatment (Fig. 5A and B), showing a similar tendency as that observed for ethylene (Fig. 2B).

PuERF2 was proved to play an important role in pear ethylene signal transduction (Yue et al. 2019), and our result showed that the expression of *PuERF2* was greatly inhibited by Se treatment (Fig. 5C).

Effect of Se on the expression patterns of lignin-related genes

We examined the expressions of the *COMT* (caffeic acid 3-O-methyltransferase), *C4H* (cinnamate-4-hydroxylase), and *CAD* (cinnamyl alcohol dehydrogenase) genes, which are important for lignin biosynthesis. The expression of *PuCOMT* decreased during fruit storage, but it was not inhibited by Se treatment (Fig. 6A). The expression pattern of *PuCAD* was not regular (Fig. 6B). *PuC4H* was greatly inhibited by Se treatment, especially on 10 and 15 DAH (Fig. 6C), indicating that *PuC4H* may be the key gene responsible for stone cell reduction in Se treatment.

Discussion

Se is indispensable for life, and a moderate Se concentration is beneficial to both animals and plants (Zhu et al. 2016, 2017). However, hyper-accumulated levels of Se are toxic to the creatures mentioned above. For adults, the Se

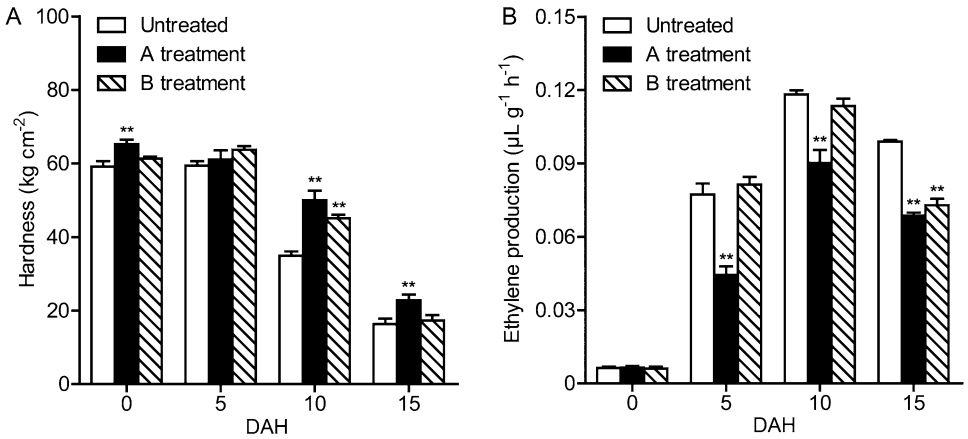

Fig. 2 The influencing of the exogenous Se treatment on Nanhong pear fruits during storage. Hardness (**A**) and ethylene production were measured (**B**), DAH (days after harvest). **Significant differences ($p < 0.01$, Student's t test). Error bars indicate the standard deviation (SD) of 3 biological replicates

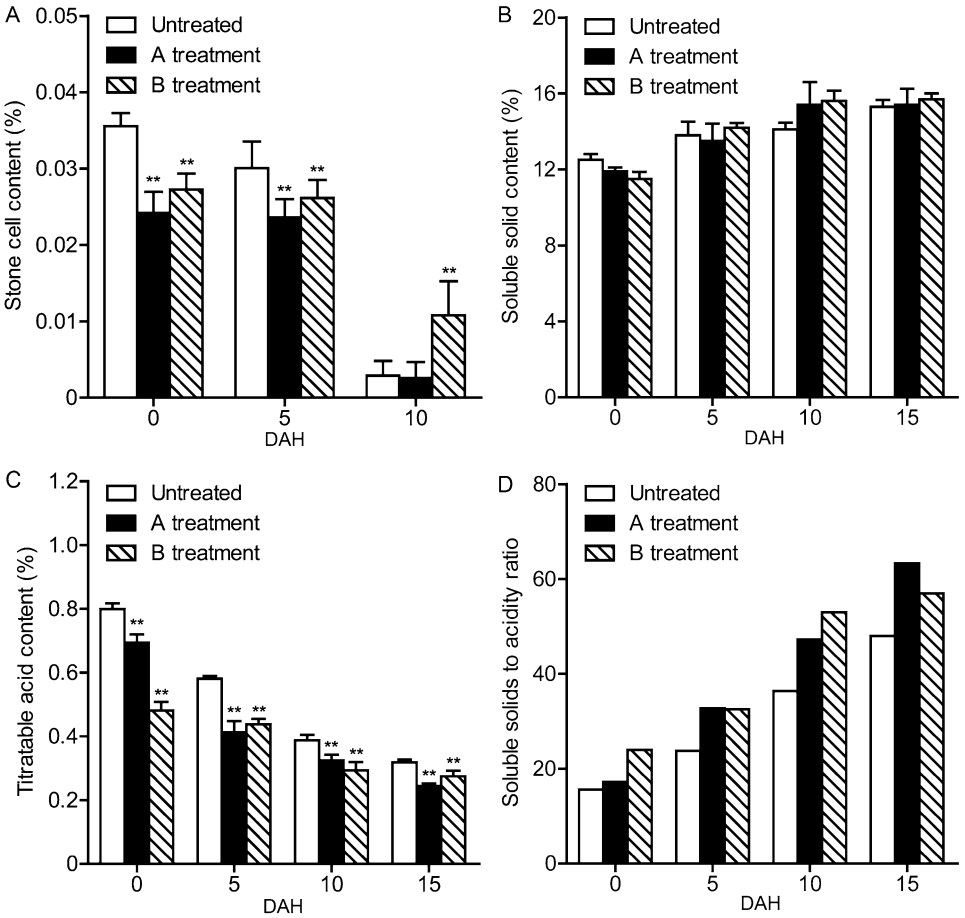

Fig. 3 The influencing of Se treatment on Nanhong pear fruits sensory quality during storage. The stone cell content (**A**), soluble acid content (**B**) and titratable acid content (**C**) were measured. Solidity-acid ratio was the ratio of soluble solid to acid (**D**). DAH (days after harvest). **Significant differences ($p < 0.01$, Student's t-test). Error bars indicate the standard deviation (SD) of three biological replicates

dietary allowance is 55–75 µg/day (National Academy of Sciences 2000), whereas a toxic critical concentration is 400 µg/day (Combs 2001). Through Se treatment, the Se concentration in 'Nanhong' pear fruit was approximately 40–60 µg/kg (Fig. 1B), and the average weight of 'Nanhong' pear fruit used in this research was about 100 g, indicating approximately 4–6 µg Se in each treated fruit. Therefore, our method used here to produce Se-biofortified pear fruit is available and safe for humans.

Se treatment decreased the biosynthetic rate of ethylene in red tomato fruit (Pezzarossa et al. 2014) and increased the fruit firmness in peach and pear (Pezzarossa et al. 2012). This study showed that Se treatment inhibited ethylene production during the pear storage period (Fig. 2B), which was consistent with the results mentioned above. Based on previous studies, ACS (ACC synthase) is the rate-limiting enzyme in ethylene biosynthesis (Kende 1993). *PuACS1* and *PuACS4* are the main *ACS* genes controlling ethylene production in 'Nanguo' pear, which is similar to 'Nanhong' pear (Yuan et al. 2020). Here, for the first time, we showed that Se could inhibit the expression of *PuACS1* and *PuACS4* in pear (Fig. 5A and B), leading to ethylene reduction. This is consistent with a previous study in which *ACS2* and *ACS4* of tomato fruit were inhibited by Se treatment (Zhu et al. 2017). As ERF (ethylene response factor) is a key transcription factor in the ethylene signaling pathway (Stepanova and Alonso 2009), it could regulate the transcription of ethylene-responsive genes, including *ACS* genes. The expression of *PuERF2* was induced by ethephon treatment and was considered to play an important role in 'Nanguo' pear fruit ripening (Yue et al. 2019). In addition, Se treatment also inhibited the expression of *PuERF2* (Fig. 5C), with a similar expression pattern to *PuACS1* and *PuACS4* (Fig. 5). Therefore, we speculated that PuERF2 could control ethylene production by regulating the expression of *PuACS2* and *PuACS4*, and Se could effectively inhibit the expression of *PuERF2*, finally leading to a decrease in ethylene. However, further research may be needed to determine how Se treatment regulates *PuERF2* expression.

The stone cell content is very important for pear fruit and can influence the pear fruit quality, such as flesh hardness and chewiness (Zhang et al. 2017). Therefore, it is very important to lower the stone cell content in pear. $CaCl_2$ treatment (0.50%) reduced the stone cell distribution density in pear (Tao et al. 2009). In addition, ethephon reduced the stone cell content in 'Korla fragrant pear' (Chen et al. 2020). In the present study, we found that Se treatment reduced the stone cell content in pear fruit (Fig. 3A), but the fruit

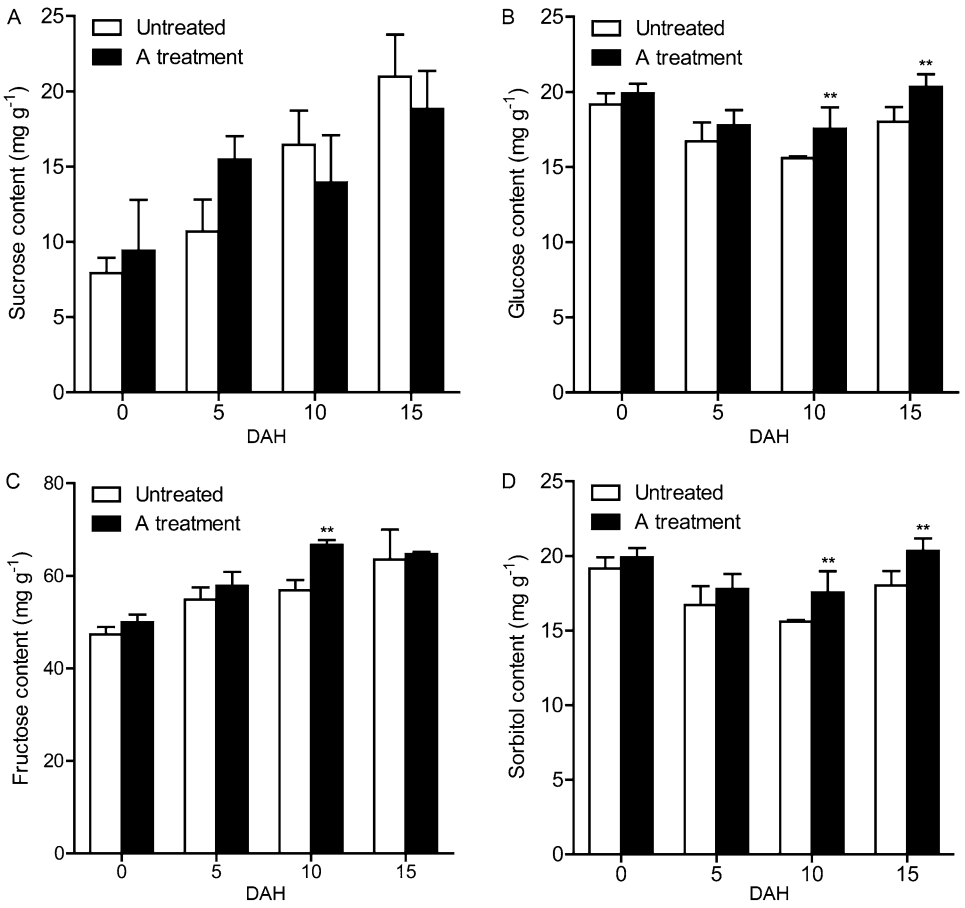

Fig. 4 Sugar content of Se treatment of Nanhong pear fruits during storage. Sucrose (**A**), glucose (**B**), fructose (**C**) and sorbitol (**D**) content were measured using high-performance liquid chromatography (HPLC) of Nanhong fruits. Commercial harvest day was 134 DAH (days after harvest). **Significant differences ($p < 0.01$, Student's *t* test). Error bars indicate the standard deviation (SD) of three biological replicates

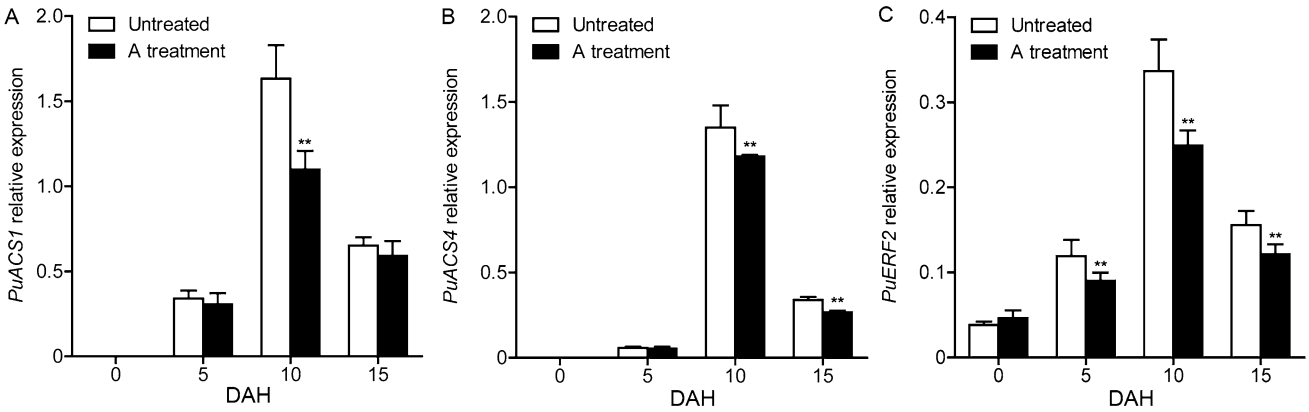

Fig. 5 Se treatment suppressed the expression of ethylene biosynthesis and signal transduction genes. The expression of ethylene biosynthesis genes *PuACS1* (**A**) and *PuACS4* (**B**) were investigated in Nanhong pear fruits. Ethylene signal transduction gene *PuERF2* was investigated in Nanhong pear fruits (**C**). DAH (days after harvest). **Significant differences ($p < 0.01$, Student's *t* test). Error bars indicate the standard deviation (SD) of three biological replicates

firmness was promoted by Se treatment (Fig. 2A). We speculate that pear fruit softening was mainly due to the degradation of polysaccharides, such as pectin and hemicellulose (Fischer and Bennett 1991). Lignin is the main component of stone cells in pears (Zhang et al. 2020). Lignin biosynthesis is controlled by enzymes that participate in lignin monomer transport and polymerization (Li et al. 2020a), and COMT, CAD and C4H are key enzyme of lignin biosynthesis. Here, the expression of *PuCOMT* declined during fruit storage in the untreated fruit (Fig. 6A), showing a same tendency with

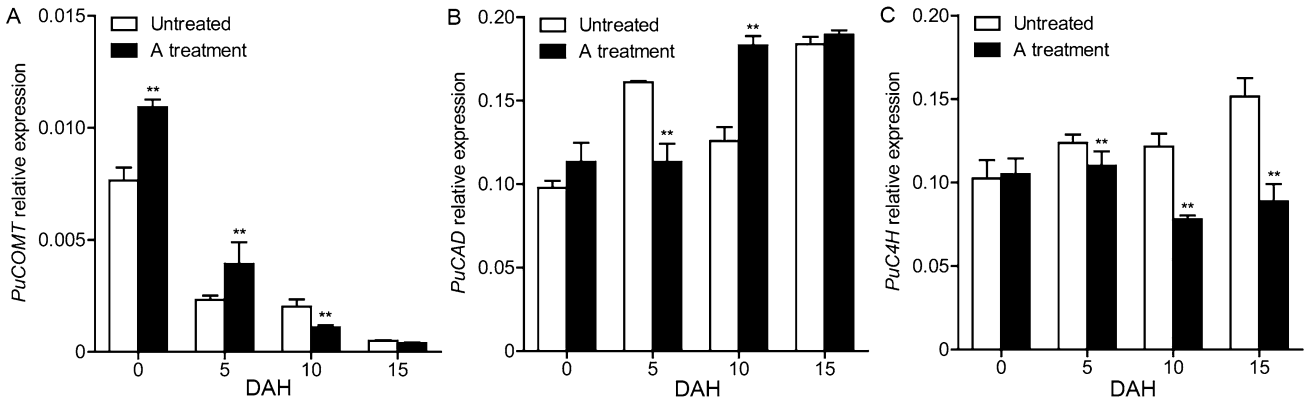

Fig. 6 The influence of Se treatment on lignin synthesis genes of Nanhong pear fruits. On-tree Nanhong fruits were treated with Se treatment at on 60, 75 and 95 days after flower, respectively, and harvested at 139 DAH (days after harvest). The expression of *PuCOMT* (A), *PuCAD* (B) and *PuC4H* (**C**) were investigated by qRT-PCR in untreated and A treatment fruits. **Significant differences ($p < 0.01$, Student's t test). Error bars indicate the standard deviation (SD) of three biological replicates

stone cell content (Fig. 3A). But under Se treatment, the expression pattern of *PuCOMT* was not in consistent with stone cell content, which means that the inhibition of lignin biosynthesis by Se treatment is independent of *PuCOMT* expression. Overexpression of *PbC4H1* and *PbC4H3* increased the lignin content of xylem cells in *Arabidopsis* (Li et al. 2020a). When *C4H* expression is inhibited, the total lignin content is significantly reduced (Sykes et al. 2015). The expression level of *GbC4H* was correlated with the lignin content in different tissues (Cheng et al. 2018). The expression of *C4H* can be regulated by certain abiotic stresses and hormonal treatments. The *C4H* gene in kenaf was induced by ABA treatment (Kim et al. 2013), similar to the result for *GbC4H* (Cheng et al. 2018). Low temperature can also induce the expression of *C4H* genes, such as *Rhododendron catawbiense RcC3H* and *Hibiscus cannabinus HcC4H* (Wei et al. 2006; Janská et al. 2011). Here for the first time, we showed that Se treatment inhibited the expression of *PuC4H* in pear (Fig. 6C). These results indicate that in addition to abiotic stresses and hormonal treatments, Se can also influence the expression of *C4H*. Therefore, we speculate that Se may reduce the stone cell content by inhibiting the expression of *PuC4H*.

Se application influences TA and soluble solid content (SSC). Studies showed that one and 1.5 mg/l Se could increase the TA content in 'Starking Delicious' apple, but 0.5 mg/l Se treatment had no significant effect on TA content (Babalar et al. 2019), which was in agreement with the results reported in peach (Wu and Tian 2009). But Se treatment did not affect the TA and SSC content in tomato fruit (Pezzarossa et al. 2014). Nevertheless, the finding that Se could decrease the pear TA content in this study is just the opposite. The discrepancy might be due to the difference in sensitivity to Se among pear, tomato and apple. Another explanation might be related to the Se concentration. The SSC was not affected in apple (Babalar et al. 2019), pear-jujube (Zhao et al. 2013) and other plants (Pezzarossa et al. 2012, 2014). Here, the SSC also showed no differences between control and treated fruits. The SSC includes sugar, TA and other components. During fruit ripening, organic acid is used as respiratory substrates and carbon skeleton for the synthesis of new compounds (Stanley 1991). Meanwhile, starch converts to soluble sugars. These may lead to TA content decrease, while SSC increase during fruit ripening.

In conclusion, Se treatment increased the Se content in pear fruit. In addition, Se decreased ethylene production and the stone cell content. Moreover, the key genes for ethylene production (*PuACSs* and *PuERF2*) and lignin biosynthesis (*PuC4H*) were also inhibited by Se treatment. This provides a practical method for fruit quality improvement and is beneficial for prolonging shelf life.

Author contribution statement AW: conceived this project. CY: performed most of the experiments. JZ, JL and GW: treated the sample. HB and HY: wrote the manuscript. All the authors have read and agreed to the published version of the manuscript.

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Data availability The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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