https://doi.org/10.17221/168/2022-PSE

Cerium improves plant growth and fruit quality of strawberry plants under salt stress by changing the antioxidant capacity and water physiology

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Citation: Zhao X.L., Zhang X.Q., Gao S., Shan C.J. (2022): Cerium improves plant growth and fruit quality of strawberry plants under salt stress by changing antioxidant capacity and water physiology. Plant Soil Environ., 68: 499–509.

Abstract: This study investigated the effects of cerium (Ce) on the growth and fruit quality of strawberries under salt stress. The findings revealed that salt stress markedly enhanced the activities of antioxidant enzymes and increased the contents of malonaldehyde (MDA) and hydrogen peroxide (H_2O_2) in leaves and the contents of anthocyanins, phenolic compounds, vitamin C (Vc), soluble sugar (SS) and titratable acid (TA) in fruits. Ce markedly improved the activities of ascorbate peroxidase, superoxide dismutase, peroxidase and catalase in leaves and the contents of anthocyanins, phenolic compounds, Vc and SS in fruits, but significantly decreased MDA and H_2O_2 levels in leaves and TA content in fruits under salt stress. However, salt stress significantly decreased the contents of chlorophyll (*Chl*) and carotenoids (Car), photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (g_s), relative water content (RWC), plant height and biomass, and fruit weight and sugar-acid ratio (SAR). Compared with salt stress alone, Ce obviously increased *Chl* and Car contents, P_n, T_r, g_s, RWC, plant height and biomass, as well as fruit weight and SAR. The above results suggested that Ce showed beneficial effects on the growth and fruit quality of strawberries under salt stress.

Keywords: salt tolerance; rare earth element; gas exchange parameters; abiotic stress; *Fragaria* × *ananassa* Duch.

Strawberry (*Fragaria* × *ananassa* Duch.) is famous for the higher nutritional value of fruits. However, salt stress-induced adverse effects on the growth of strawberries (Zahedi et al. 2019). Increasing evidence showed that many exogenous chemicals improved the salt tolerance of plants, such as hydrogen sulfide and rare earth elements (REEs) (Chen and Shan 2019, Li et al. 2020). Among REEs, scandium (Sc), lanthanum (La) and cerium (Ce) have been shown to enhance the salt tolerance of plants (Huang and Shan 2018, Chen and Shan 2019, Elbasan et al. 2020). For Ce, its role in improving salt tolerance has been studied on many crops, including food crop maize, cash crop cotton and fruit crop grapevine, etc. (Gohari et al. 2021, Liu et al. 2021, 2022). The above previous studies showed that Ce was effective to alleviate salt stress, and the application of REEs in improving the salt tolerance of plants was focused on Ce rather than others. Meanwhile, increasing evidence indicated that Ce also showed benefits in fighting against various abiotic stresses except for salt stress, including drought, light, heat and chilling stresses (Wu et al. 2017, Salgado et al. 2020). Therefore, the application of Ce plays a very important role in improving plant adaptations to the changing environment by mitigating the negative effects of abiotic stresses on plants. However, the effect of Ce on the salt tolerance of strawberries was still unclear. So, we preferred

Supported by the Key Scientific and Technological Research Projects in Henan Province, Project No. 192102110130.

https://doi.org/10.17221/168/2022-PSE

the application of Ce in improving the salt tolerance of strawberries. Besides, many studies showed that Ce played an important role in improving salt tolerance through an antioxidant defence system (Hou et al. 2018, Chen and Shan 2019). Whereas there is no report on the effect of Ce on the antioxidant defence system of strawberries under salt stress. Thus, this work will provide the theoretical basis for Ce application in enhancing the salt tolerance of strawberries in production.

Plant growth is related to water physiology, including photosynthetic performance and water conditions (Zhang et al. 2019). Liu et al. (2022) showed that Ce improved the growth and yield of maize by enhancing photosynthetic efficiency under salt stress (Liu et al. 2022). Gohari et al. (2021) reported that Ce significantly ameliorated chlorophyll (*Chl*) damage under salt stress. Liu et al. (2021) found that Ce improved cotton tolerance to salinity by increasing chlorophyll content, biomass and photosynthetic performance. Rico et al. (2015) showed that Ce improved *Chl* content and water content in barley. However, it is unclear for the effects of Ce on the photosynthetic performance and water conditions of strawberries under salt stress. Thus, it is necessary to investigate the effects of Ce on the photosynthetic performance and water conditions of strawberries under salt stress.

Increasing evidence showed that salt stress affected fruit weight and quality traits (Ferreira et al. 2019, Perin et al. 2019, Zahedi et al. 2019, Khan et al. 2022). For fruit weight, many studies all agreed that the effects of salt stress on the fruit weight of strawberries were related to the levels of salt stress and the strawberry cultivars (Ferreira et al. 2019, Perin et al. 2019, Yaghubi et al. 2019, Zahedi et al. 2019). Previous studies showed that the higher the degree of salt stress, the greater the reduction of strawberry fruit weight. Previous studies also showed that the more sensitive strawberry cultivars are to salt stress, the greater the reduction of fruit weight. For fruit quality, Crizel et al. (2020) and Perin et al. (2019) revealed that low levels and high levels of salt stress all increased the contents of vitamin C (Vc) and phenolic compounds of strawberry fruits. However, Yaghubi et al. (2019) showed that salt stress decreased the sugar-acid ratio of strawberry fruits, which further reduced taste quality. For the application of Ce in improving crop quality, such as oil crop soybean (Ren et al. 2019). However, there is still no report on the effects of Ce on the fruit quality of strawberries under salt stress. Therefore, it will be important to study the effects of Ce on the fruit quality of strawberries under salt stress, which will further provide a theoretical basis for its use in the production of strawberries.

According to the above effects of Ce on various stress tolerance and crop quality of different plant species, our opinion was that Ce application in the production practice of different plant species was feasible. In the current study, we hypothesised that the application of Ce could improve plant growth and fruit quality of strawberries under salt stress by changing antioxidant capacity and water physiology. To test the above hypothesis, we investigated the effects of Ce on antioxidant capacity, water physiology and the growth and fruit quality of strawberry plants under salt stress. The purpose of this study was to clarify the regulation of salt tolerance of strawberries by Ce, which will provide a theoretical basis for the application of Ce in the salt-resistant cultivation of strawberries.

MATERIAL AND METHODS

Plant material and treatment. In two years (2018 and 2019), seedlings of strawberry cvs. Sweet Charlie and Hongyan with four fully expanded leaves were used as experimental materials and cultivated in plastic boxes containing 500 mL full Hoagland's solution in an artificial climatic chamber. Seedlings were grown in the following conditions: 25 ± 5 °C day temperature, 20 ± 5 °C night temperature, 500 μmol/m^2/s photosynthetic active radiation, 70 ± 10% relative humidity and 10 h photoperiod. After the full expansion of the fifth leaves, seedlings with similar growth status were selected for the whole experiment.

The suitable NaCl concentration (50 mmol/L) was selected from 20, 50, 80 and 110 mmol/L NaCl. After 3 days of treatment, 80 and 110 mmol/L NaCl induced an obvious wilting phenomenon in strawberry seedlings, 20 mmol/L NaCl induced no obvious wilting phenomenon, and 50 mmol/L NaCl induced a slight wilting phenomenon. Thus, 50 mmol/L NaCl was selected as the suitable concentration for this study. Seedlings were treated with 50 mmol/L NaCl for 7 days by placing their roots in plastic boxes containing 500 mL, 50 mmol/L NaCl. To study the effects of Ce, three groups of plants were respectively treated with 15, 30 and 60 μmol/L cerium nitrate ($Ce(NO_3)_3$) for 24 h and then treated by 50 mmol/L NaCl for 7 days. 50 mmol/L NaCl and different concentrations of $Ce(NO_3)_3$ were prepared by dissolving corresponding chemicals in the full Hoagland solution. Full Hoagland's solution only

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treated control seedlings. The above solutions were exchanged every day. To ensure the normal growth of roots, the oxygen pump was used to provide enough oxygen in solutions. Each treatment was repeated 4 times with two seedlings per time. After 3 days of treatment, the fifth leaves of seedlings under different treatments were sampled and immediately frozen in liquid N_2. The above samples were then kept at –80 °C until the analyses of antioxidant enzymes. Fresh fifth leaves were sampled and immediately used to determine RWC and the contents of chlorophyll (*Chl*), carotenoids (Car), malonaldehyde (MDA) and hydrogen peroxide (H_2O_2). Meanwhile, we determined photosynthetic rate (P_n), transpiration rate (T_r) and stomatal conductance (g_s) under different treatments by Licor6400 photosynthetic instrument (Lincoln, USA).

To determine the effects of Ce on the growth and fruit quality of strawberries, 15, 30 and 60 μmol/L $Ce(NO_3)_3$ were applied to plants through foliar spraying under 50 mmol/L NaCl every 9 days from the seedling stage to the mature period. For salt stress alone, seedlings were only treated by 50 mmol/L NaCl. Hoagland's solution only treated control seedlings. At the mature period of strawberry fruit, we determine plant height and biomass, fruit weight and quality, as well as Ce contents in leaves and fruits.

Assays of ascorbate peroxidase, superoxide dismutase, peroxidase and catalase. Each sample of leaves (0.5 g) was homogenised in 10 mL ice-cold 50 mmol/L potassium phosphate buffer (pH 7.0) containing 1 mmol/L EDTA and 0.1% (*w*/*v*) CHAPSO. The homogenates were centrifugated at 12 000 × *g* for 10 min at 4 °C. Then the supernatant was used to analyse the activities of antioxidant enzymes. The activities of ascorbate peroxidase (APX) (EC 1.11.1.11), superoxide dismutase (SOD) (EC 1.15.1.1), peroxidase (POD) (EC 1.11.1.7) and catalase (CAT) (EC 1.11.1.6) were analysed according to Zheng and Guo (2018). Their specific activities were expressed as U/mg protein. Protein concentration was determined according to Bradford (1976). Four repetitions were done for each treatment.

Assays of chlorophyll and carotenoids. Chlorophyll and carotenoids contents were determined according to Song et al. (2016) with some modifications. Leaf samples were homogenised in 80% acetone and then filtered through filter paper. The absorption value of the above filtrate was measured by spectrophotometer at 665, 649 and 470 nm. Four repetitions were done for each treatment.

Assays of relative water content, photosynthetic rate, transpiration rate and stomatal conductance. Relative water content (RWC) was measured according to Hou et al. (2018). RWC was calculated as below. RWC = [(fresh weight (FW) – dry weight (DW))/(saturated weight (TW) – DW)] × 100. Photosynthetic rate, transpiration rate and stomatal conductance were determined through a photosynthesis system (Licor-6400, Lincoln, USA). The conditions in the leaf chamber were set as the light intensity of 1 000 μmol(photon)/m^2/s, relative humidity of 60% and leaf temperature of 25.0 °C. The fifth leaves were first equilibrated, then steady-state gas exchange values of P_n, T_r and g_s were recorded. Four repetitions were done for each treatment.

Assays of malondialdehyde and hydrogen peroxide. Malondialdehyde content was analysed according to Wang et al. (2018) using the thiobarbituric acid (TBA) method. Hydrogen peroxide content was analysed according to Brennan and Frenkel (1977) by measuring the absorption of titanium-hydroperoxide at 415 nm by spectrophotometer and calculated from the standardised curve of H_2O_2. Four repetitions were done for each treatment.

Assays of plant height and biomass. Plant height was determined by the ruler. Plant biomass was determined by using the oven to dry fresh samples of whole strawberry plants at 80 °C for 72 h. Then dry weights of different treatments were recorded. Four repetitions were done for each treatment.

Assays of fruit average weight and quality. Mature fruits were sampled and weighted by electronic balance. And then average fruit weight was calculated. Vitamin C (Vc) was determined according to Shan et al. (2018). Titratable acids (TA) were measured according to Li (1994). Soluble sugar (SS) was analysed according to Wei (2009). Sugar-acid ratio (SAR) was expressed as the ratio of SS content to TA content. Total phenolic content was analysed according to Swain and Hillis (1959) and presented as grams of gallic acid equivalents per kilogram of fruit (g GAE/kg FW). Total anthocyanins content was analysed according to Zhang et al. (2004) and presented as grams of elargonidin equivalents per kilogram of fruit (g PE/kg FW). Four repetitions were done for each treatment.

Determination of Ce content. Ce contents in leaves and fruits were analysed according to Yan et al. (2008) by using flame atomic absorbance spectrometry (Hitachi 180-80, Tokyo, Japan). Ce's standard curve was prepared using a series of diluted solutions of its commercially available standards. Four repetitions were done for each treatment.

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Data analysis. The data in Figures 1–5 was the mean of four replications. Means were compared by one-way analysis of variance and Duncan's multiple range test at the 5% significance level.

RESULTS

Effect of Ce on the antioxidant capacity of strawberries under salt stress. Salt stress enhanced the activities of APX, SOD, CAT and POD and increased MDA and H_2O_2 levels in leaves of strawberry cvs. Sweet Charlie and Hongyan, compared with control (Figure 1). Furthermore, the application of $Ce(NO_3)_3$ to salt-stressed plants significantly enhanced above antioxidant enzymes of two cultivars, especially for 30 µmol/L $Ce(NO_3)_3$. For cv. Sweet Charlie in 2019, 30 µmol/L $Ce(NO_3)_3$ respectively improved the activities of APX, SOD, CAT and POD by 66.1, 46.7, 77.7 and 86.6% under salt stress, compared with salt stress alone. For cv. Hongyan in 2019, 30 µmol/L $Ce(NO_3)_3$ respectively improved the activities of APX, SOD, CAT and POD by 75.9, 38.2, 66.8 and 47.2% under salt stress, compared with salt stress alone. Meanwhile, the application of $Ce(NO_3)_3$ to salt-stressed plants significantly decreased the contents of MDA and H_2O_2, especially for 30 µmol/L $Ce(NO_3)_3$. For cv. Sweet

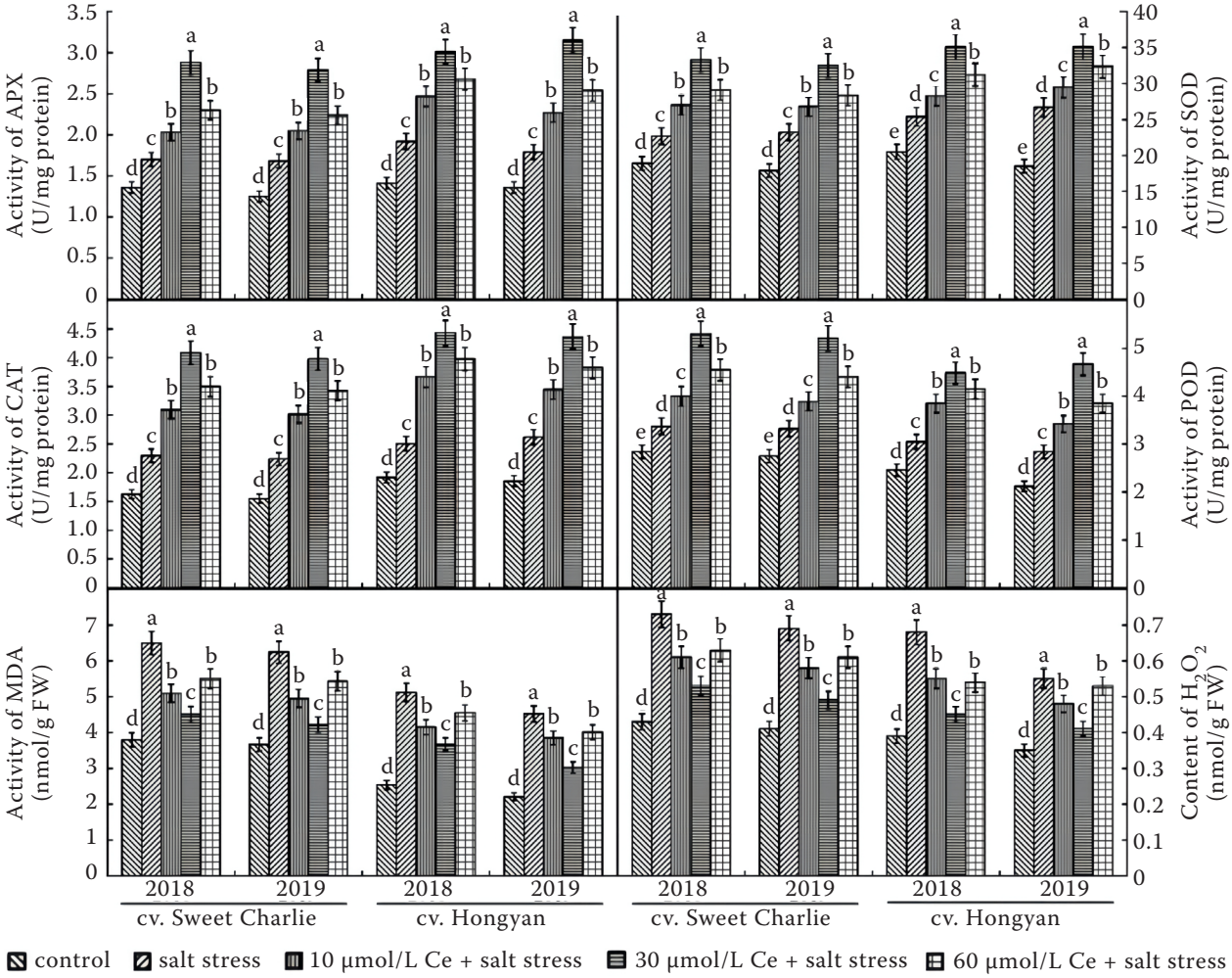

Figure 1. Effects of cerium (Ce) on the activities of antioxidant enzymes and the contents of malonaldehyde (MDA) and hydrogen peroxide (H_2O_2) in leaves of strawberry plants under salt stress. The plants were treated as follows: control – full Hoagland's solution; salt stress – 50 mmol/L NaCl; 10 µmol/L Ce + salt stress, spray application of 10 µmol/L Ce to strawberry plants under 50 mmol/L NaCl; 30 µmol/L Ce + salt stress, spray application of 30 µmol/L Ce to strawberry plants under 50 mmol/L NaCl; 60 µmol/L Ce + salt stress, spray application of 60 µmol/L Ce to strawberry plants under 50 mmol/L NaCl; APX – ascorbate peroxidase; CAT – catalase; SOD – superoxide dismutase; POD – peroxidase; FW – fresh weight

https://doi.org/10.17221/168/2022-PSE

Charlie in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively decreased the contents of MDA and H_2O_2 by 32.4% and 27.4% under salt stress, compared with salt stress alone. For cv. Hongyan in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively decreased the contents of MDA and H_2O_2 by 33.0% and 33.8% under salt stress. The above results suggested that Ce improved salt tolerance by enhancing the antioxidant capacity of strawberries.

Effects of Ce on P_n and the contents of *Chl* and Car of strawberry under salt stress. Salt stress decreased P_n and the contents of *Chl* and Car of cvs. Sweet Charlie and Hongyan, compared with control (Figure 2). Application of $Ce(NO_3)_3$ to salt-stressed plants significantly improved the above indicators, especially for 30 μmol/L $Ce(NO_3)_3$. For cv. Sweet Charlie in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively improved P_n and the contents of *Chl* and Car by 35.1, 23.7 and 39.0% under salt stress, compared with salt stress alone. For cv. Hongyan in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively improved P_n and the contents of *Chl* and Car by 26.4, 19.4 and 30.8% under salt stress. The above results suggested that Ce improved salt tolerance by increasing the contents of photosynthetic pigments, which further enhanced the P_n of strawberries.

Effects of Ce on T_r, g_s and RWC of strawberry under salt stress. Salt stress decreased T_r, g_s and RWC of

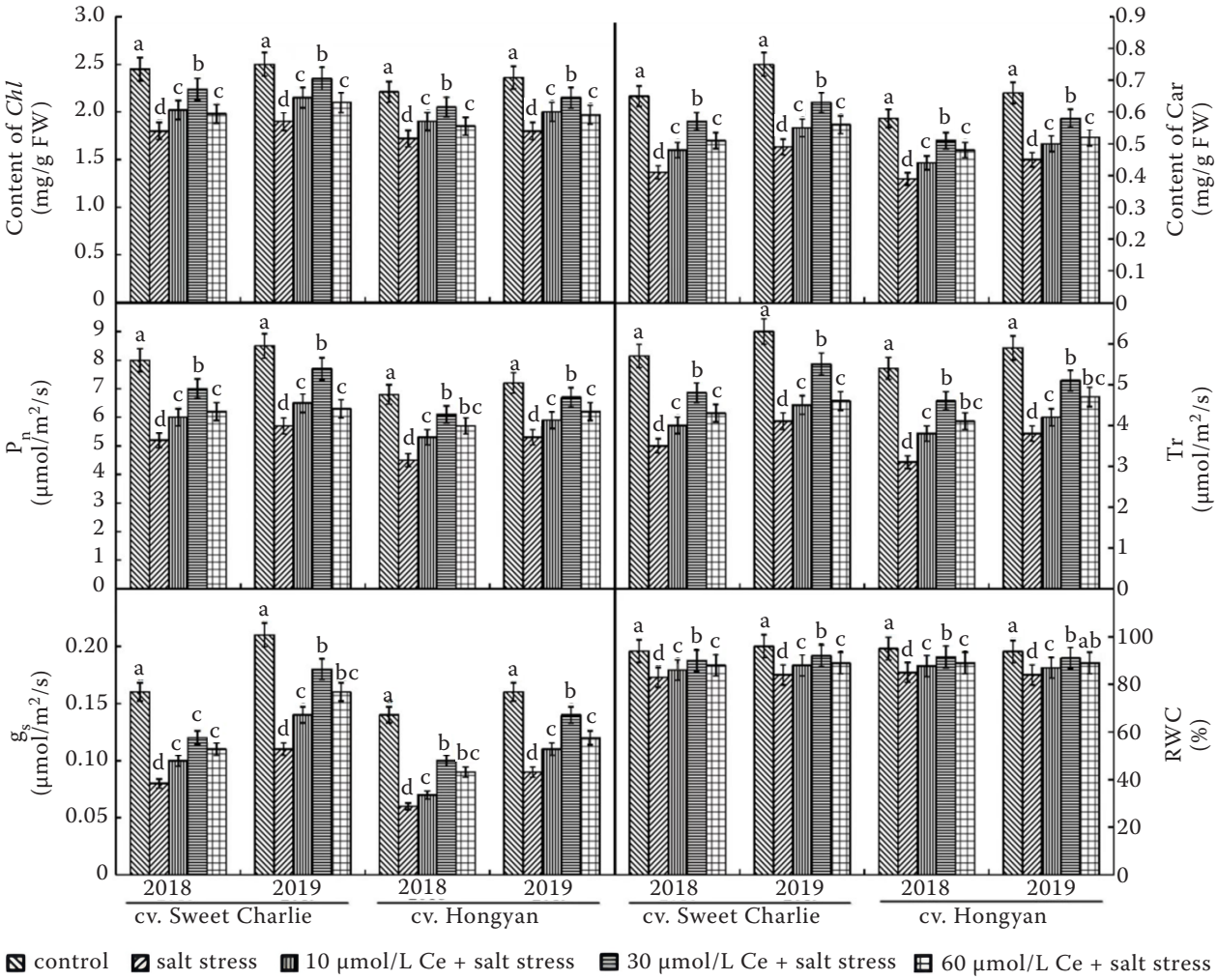

Figure 2. Effects of cerium (Ce) on photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (g_s), relative water content (RWC) and the contents of chlorophyll (*Chl*) and carotenoids (Car) in leaves of strawberry plants under salt stress. The plants were treated as follows: control – full Hoagland's solution; salt stress – 50 mmol/L NaCl; 10 μmol/L Ce + salt stress, spray application of 10 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 30 μmol/L Ce + salt stress, spray application of 30 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 60 μmol/L Ce + salt stress, spray application of 60 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; FW – fresh weight

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cvs. Sweet Charlie and Hongyan, compared with control (Figure 2). Application of $Ce(NO_3)_3$ to salt-stressed plants significantly increased the above indicators, especially for 30 μmol/L $Ce(NO_3)_3$. For cv. Sweet Charlie in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively improved T_r, g_s and RWC by 37.1, 63.6 and 8.4% under salt stress, compared with salt stress alone. For cv. Hongyan in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively improved T_r, g_s and RWC by 48.4, 55.5 and 7.7% under salt stress. The above results suggested that Ce improved salt tolerance by maintaining the water balance of the strawberry.

Effects of Ce on fruit quality of strawberry under salt stress. Salt stress increased the contents of anthocyanins, phenolic compounds, Vc, SS and TA in the fruits of cvs. Sweet Charlie and Hongyan (Figure 3), compared with control. However, salt stress decreased SAR (Figure 3). Applying $Ce(NO_3)_3$ to salt-stressed plants significantly increased SAR and the contents of anthocyanins, phenolic compounds, Vc and SS but obviously decreased TA content, especially for 30 μmol/L $Ce(NO_3)_3$. For cv. Sweet Charlie in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively improved SAR and the contents of total anthocyanins, total phenolic compounds, Vc and SS by 62.1, 36.0, 26.4, 30.0 and 23.1% under salt stress, compared with salt stress alone. Meanwhile, 30 μmol/L $Ce(NO_3)_3$

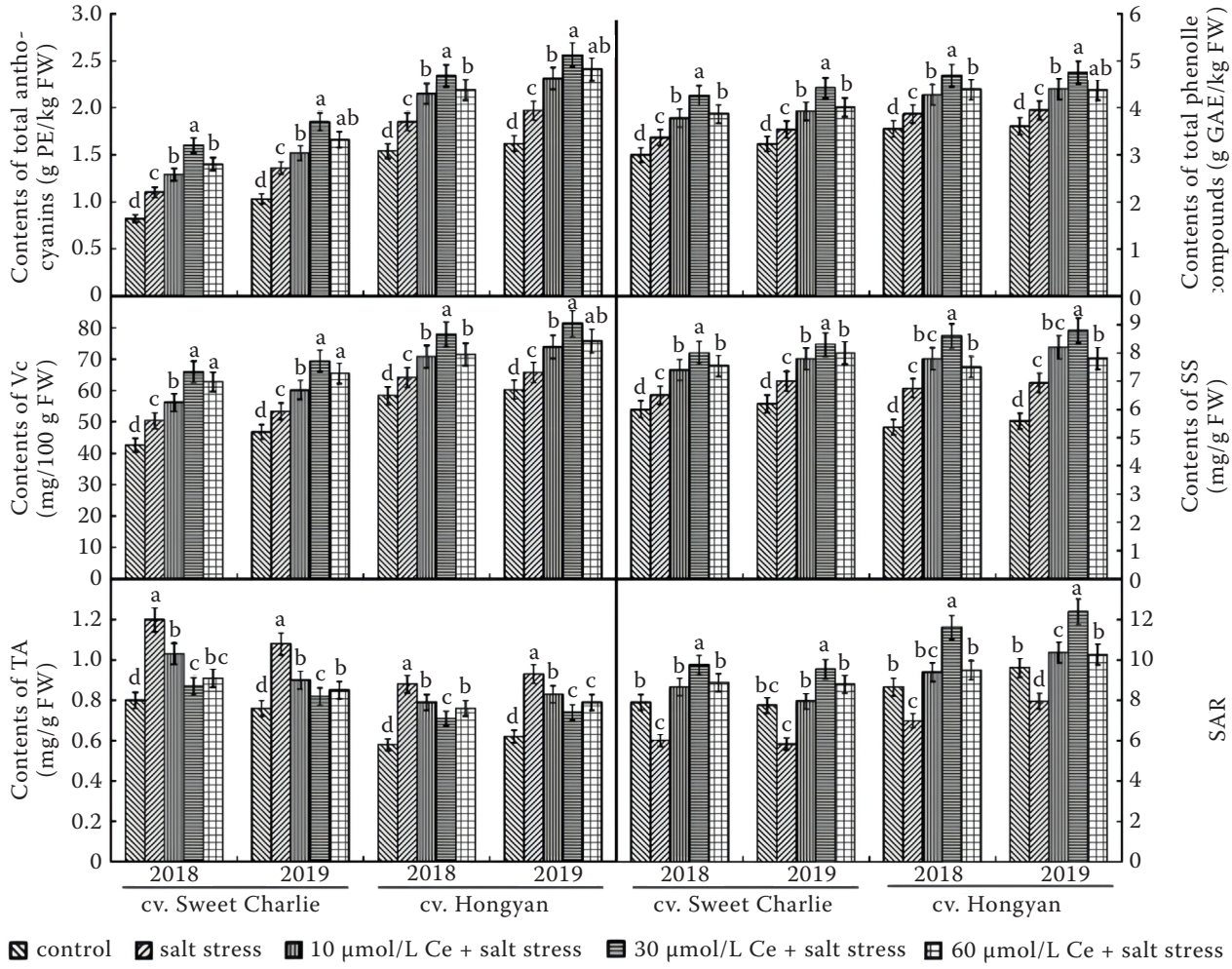

Figure 3. Effects of cerium (Ce) on the fruit qualities of strawberry plants under salt stress. The plants were treated as follows: control – full Hoagland's solution; salt stress – 50 mmol/L NaCl; 10 μmol/L Ce + salt stress, spray application of 10 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 30 μmol/L Ce + salt stress, spray application of 30 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 60 μmol/L Ce + salt stress, spray application of 60 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; PE – pelargonidin equivalent; Vc – vitamin C; TA – titratable acid; GAE – gallic acid equivalent; SS – soluble sugar; SAR – fruit weight and sugar-acid ratio; FW – fresh weight

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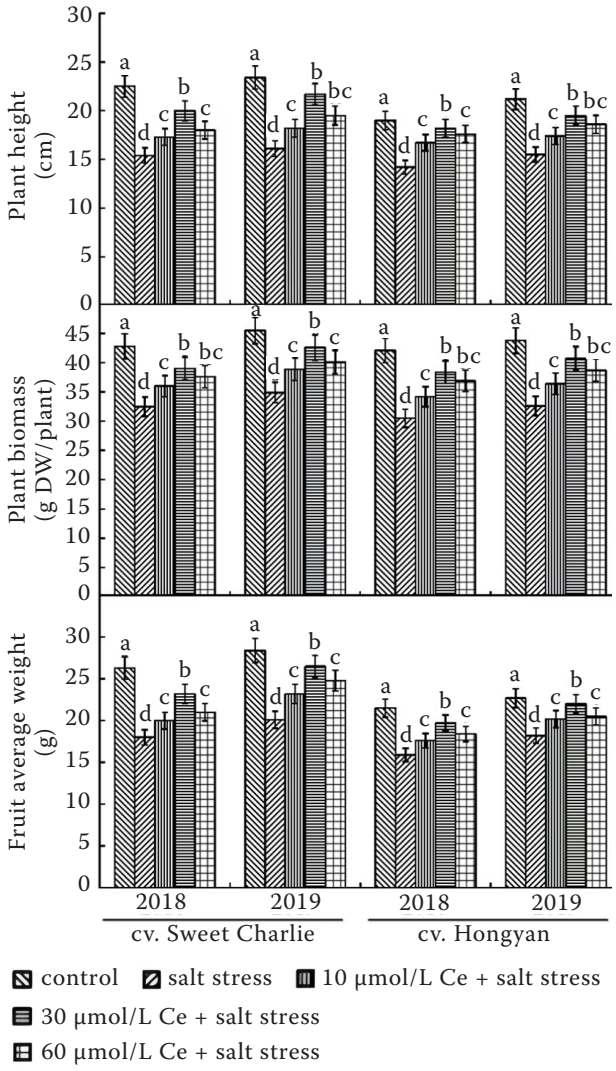

Figure 4. Effects of cerium (Ce) on plant height, plant biomass and fruit weight of strawberry plants under salt stress. The plants were treated as follows: control – full Hoagland's solution; salt stress – 50 mmol/L NaCl; 10 μmol/L Ce + salt stress, spray application of 10 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 30 μmol/L Ce + salt stress, spray application of 30 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 60 μmol/L Ce + salt stress, spray application of 60 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; DW – dry weight

decreased TA content by 24.1% under salt stress. For cv. Hongyan in 2019, 15, 30 and 60 μmol Ce respectively improved SAR and the contents of total anthocyanins, total phenolic compounds, Vc and SS by 66.3, 29.9, 21.2, 23.9 and 27.4% under salt stress. Meanwhile, 30 μmol/L $Ce(NO_3)_3$ decreased TA content by 20.4% under salt stress. The above results suggested that Ce improved the fruit quality of strawberries under salt stress.

Effects of Ce on the growth and fruit average weight of strawberry under salt stress. Salt stress decreased plant height, plant biomass and average fruit weight of cvs. Sweet Charlie and Hongyan, compared with control (Figure 4). Application of $Ce(NO_3)_3$ to salt-stressed plants significantly improved the above indicators, especially for 30 μmol/L $Ce(NO_3)_3$. For cv. Sweet Charlie in 2019, 30 μmol/L $Ce(NO_3)_3$ respectively improved plant height, plant biomass and average fruit weight by 34.8, 22.1 and 31.8% under salt stress, compared with salt stress alone. For cv. Hongyan in 2019, 15, 30 μmol/L $Ce(NO_3)_3$ respectively improved plant height, plant biomass and average fruit weight by 25.8, 24.8 and 20.9%

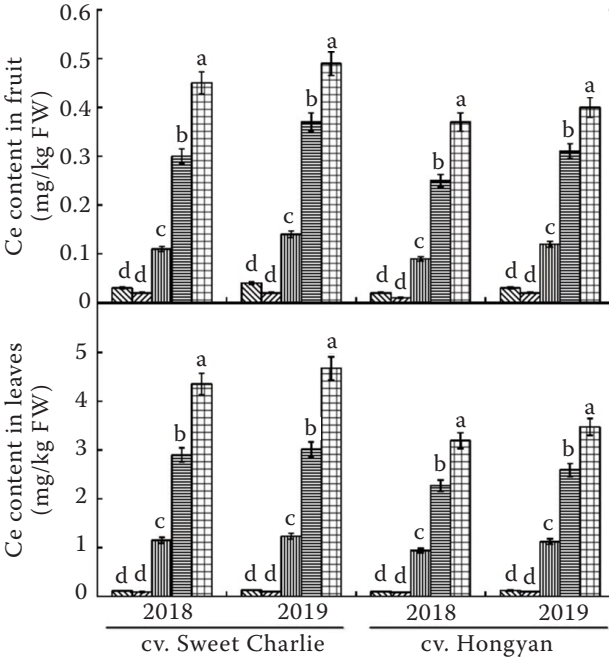

Figure 5. Effects of cerium (Ce) on the contents of Ce in fruits and leaves of strawberry plants under salt stress. The plants were treated as follows: control – full Hoagland's solution; salt stress – 50 mmol/L NaCl; 10 μmol/L Ce + salt stress, spray application of 10 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 30 μmol/L Ce + salt stress, spray application of 30 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; 60 μmol/L Ce + salt stress, spray application of 60 μmol/L Ce to strawberry plants under 50 mmol/L NaCl; FW – fresh weight

https://doi.org/10.17221/168/2022-PSE

under salt stress. The above results suggested that Ce improved salt tolerance by improving the growth of strawberry plants and fruits.

Effects of Ce on Ce contents in leaves and fruits of strawberry under salt stress. Salt stress had no obvious effects on Ce contents in leaves and fruits of cvs. Sweet Charlie and Hongyan, compared with control (Figure 5). Applying $Ce(NO_3)_3$ to salt-stressed plants significantly increased Ce contents in leaves and fruits. For cv. Sweet Charlie in 2019, 15, 30 and 60 μmol/L $Ce(NO_3)_3$ respectively increased Ce contents in fruits by 6.0, 17.5 and 23.5 fold under salt stress, compared with salt stress alone. 15, 30 and 60 μmol Ce increased Ce contents in leaves by 11.3, 29.1 and 45.7 fold under salt stress, respectively. For cv. Hongyan in 2019, 15, 30, and 60 μmol Ce respectively increased Ce contents in fruits by 5.0, 14.5 and 19.0 fold under salt stress. 15, 30 and 60 μmol Ce increased Ce contents in leaves by 10.2, 24.9 and 33.7 fold under salt stress, respectively. The above results suggested that Ce improved Ce contents in leaves and fruits.

DISCUSSION

Salt stress causes oxidative damage to many plants by increasing MDA levels (Samadi et al. 2019, Zhang et al. 2020). In this study, we observed enhanced levels of MDA and H_2O_2 in strawberry leaves under salt stress, indicating that salt stress also induced oxidative damage to strawberries. Increasing evidence showed that many crops could fight against salt stress by enhancing the activities of antioxidant enzymes such as bitter melon, tomato and faba bean (Zhang et al. 2020, Latef et al. 2021, Javeed et al. 2021, Sheikhalipour et al. 2021). For strawberries, Zahedi et al. (2019) reported that strawberries improved salt tolerance by enhancing the activities of SOD and POD. Lamnai et al. (2021) showed that strawberries improved salt tolerance by enhancing the activities of CAT, SOD and POD. In this study, we showed that salt stress also enhanced the activities of SOD, POD and CAT, which was identical to previous studies. In addition, we found that salt stress also enhanced APX activity in strawberry leaves. Some studies have shown Ce relieved the oxidative damage induced by salt stress in plants (Hong et al. 2017, Hu and Shan 2018, Liu et al. 2021, Dong et al. 2022). Hong et al. (2017) showed that Ce alleviated oxidative damage in maize by enhancing the activities of SOD, APX, CAT and POD under salt stress. Liu et al. (2021) reported that Ce alleviated oxidative damage in cotton by enhancing the activities of SOD, CAT and POD under salt stress. However, there is still no knowledge about the effects of Ce on the activities of antioxidant enzymes in strawberries under salt stress. Current findings showed that Ce increased the activities of SOD, APX, CAT and POD in strawberry leaves under salt stress. By this way, the application of $Ce(NO_3)_3$ further reduced MDA and H_2O_2 levels under salt stress. Our results indicated that Ce could be considered as a regulator to enhance the salt tolerance of strawberries by enhancing the activities of antioxidant enzymes, which further improved the growth of strawberry plants and fruits.

Many studies also showed that salt stress had significant effects on plant water physiology (Li et al. 2019, Abdelaal et al. 2020). Zahedi et al. (2019) and Avestan et al. (2019) showed that salt stress significantly decreased *Chl* and Car contents in strawberry leaves. Faghih et al. (2017) showed that salt stress significantly reduced water physiological parameters P_n and g_s of strawberries. Yang and Lu (2005) reported that salt stress resulted in a decrease in growth, RWC, P_n, g_s and T_r in maize leaves. For this study, we found that salt stress significantly reduced *Chl* and Car contents, P_n, T_r, g_s and RWC of strawberry leaves, which was consistent with previous studies (Yang and Lu 2005, Faghih et al. 2017, Avestan et al. 2019, Zahedi et al. 2019). Chen and Shan (2019) have reported that Ce increased *Chl* and Car contents, as well as water physiological parameters P_n in wheat leaves under salt stress. However, there is still no report on the effects of Ce on water physiological parameters of strawberries under salt stress. For this study, we found that Ce increased *Chl* and Car contents, as well as water physiological parameters P_n, T_r, g_s and RWC of strawberries under salt stress. Besides, we found that Ce increased the growth of strawberries, indicated by plant height and biomass and fruit weight under salt stress. Thus, current results also indicated that Ce could be considered as a regulator to enhance the salt tolerance of strawberries by regulating water physiology, which further improved the growth of strawberry plants and fruits.

To fight against the reduction in RWC induced by salt stress, plants usually enhance their ability to keep water balance by increasing the contents of osmotic adjustment substances, including soluble sugars, soluble protein and proline, etc. (Latef et al. 2021, Javeed et al. 2021, Sheikhalipour et al. 2021). However, we did not investigate the contents of osmotic adjustment substances in the current study.

https://doi.org/10.17221/168/2022-PSE

Therefore, the effects of salt stress and salt stress plus Ce on the contents of osmotic adjustment substances in strawberry leaves are needed in the future study. Besides, it has been reported that cross-talk between signal molecules H_2O_2, NO and Ca^{2+} induced salt tolerance by regulating the contents of osmotic adjustment substances soluble sugars, protein and amino acid contents in *Chenopodium quinoa* C.L. Willdenow (Willd.) (Hajihashemi et al. 2020). Thus, the roles of H_2O_2, NO and Ca^{2+} in Ce-regulated osmotic adjustment are also needed in the future study. The above two work parts can explain why Ce improved the RWC of strawberry leaves under salt stress. Previous studies also showed that salt stress induced ion imbalances by changing the optimum ratios of K^+/Na^+ and ion levels of Na^+ and Cl^- (Latef et al. 2021). This part of the work is also lack in the current study. Thus, the effects of salt stress and salt stress plus Ce on the optimum ratios of K^+/Na^+ and ion levels of Na^+ and Cl^- in strawberry leaves are needed in the future study. This part of the work can explain more physiological mechanisms for improving salt tolerance by Ce in strawberries.

Increasing evidence showed that salt stress affected the fruit quality of strawberries (Galli et al. 2016, Perin et al. 2019, Yaghubi et al. 2019). Galli et al. (2016) and Perin et al. (2019) showed that salt stress improved the contents of anthocyanins and phenolic compounds in strawberry fruits. Besides, Perin et al. (2019) showed that salt stress improved Vc content in strawberry fruits. For this study, we also found that salt stress improved the above indicators in strawberry fruits. However, Yaghubi et al. (2019) showed that salt stress decreased fruit quality by reducing the sugar-acid ratio. In this study, we found that salt stress improved sugar and organic acids contents but reduced SAR. Thus, the results of present and previous studies all agreed that salt stress decreased the sugar-acid ratio. However, there is still no report on the effects of Ce on the fruit quality of strawberries. The current study found that Ce increased SAR and the contents of SS, Vc, anthocyanins and phenolic compounds but reduced TA content in strawberry fruits under salt stress. For the sugar-acid ratio, our results indicated that Ce could improve it by increasing sugar content and reducing TA content. Thus, current results indicated that applying Ce to salt-stressed strawberries is an effective strategy to increase the fruit quality of strawberries.

According to the National Standard for Contaminant Limit in Food of China (GB 2762-2005), the safe content of Ce in fruits is less than 0.7 mg/kg. We found that Ce contents in fruits of $Ce(NO_3)_3$-treated strawberries were all less than 0.7 mg/kg. Therefore, applying 10–60 μmol/L $Ce(NO_3)_3$ to salt-stressed strawberries is a safe and effective strategy to improve the fruit quality of strawberries under salt stress, especially for 30 μmol/L $Ce(NO_3)_3$.

In conclusion, the current study clearly showed that Ce improved the growth and fruit quality of strawberries under salt stress by enhancing antioxidant capacity, photosynthetic capacity and water balance. Our results also indicated that applying low concentrations of Ce is a safe and effective strategy to improve salt tolerance and fruit quality of strawberries under salt stress. In the future study, the effects of Ce on ions homeostasis and the contents of osmotic adjustment substances, as well as the roles of H_2O_2, NO and Ca^{2+} in Ce-regulated osmotic adjustment in strawberries under salt stress, are needed. These future studies will explain more physiological mechanisms for the improvement of salt tolerance by Ce in strawberries.

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Received: May 6, 2022
Accepted: October 10, 2022
Published online: October 19, 2022