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Foliar Application of Chelated Selenium Modulated the Chlorophyll Metabolism, Antioxidant Capacity, and Yield of Rice under Salt Stress

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Abstract

Exogenous application of chelated selenium (Se) has shown potential in alleviating salt stress in crops, yet its specific effects on the yield and rice remain elusive. This study investigated the impact of foliar application of different concentrations of chelated Se *i.e.*, 0 (CK), 5, 10, and 15 mg L^{-1} denoted as T1, T2, and T3, respectively on morpho-physio-biochemical and yield attributes of two rice varieties *i.e.*, Meixiangzhan 2 (MXZ2) and Liangxiangyou 868 (LXY868) under salt stress (0.1%). The results demonstrated that the Se application at 10 mg/L treatment exhibited the highest yield for both rice varieties among all treatments. Physiological analyses revealed that the 10 mg L^{-1} treatment elevated chlorophyll content and 5-aminolevulinic acid (ALA) levels during the grain-filling stage while inhibiting the activities of chlorophyll degradation enzymes *i.e.*, chlorophyllase and pheophorbide an oxygenase). Moreover, Se application also modulated the net photosynthetic rates and leaf area index at grain filling stage and dry matter accumulation at maturity stage by 17.25 - 21.52%, 13.77 - 22.18%, and 14.95 - 19.01%, respectively. Furthermore, Se application at 10 mg L^{-1} treatment markedly improved antioxidant enzyme activities and reduced malondialdehyde (MDA) content, effectively mitigating salt stress-induced membrane damage. In conclusion, foliar application of Se at 10 mg L^{-1} proved to be the optimal dose for enhancing rice growth and yield under salt stress conditions.

Keywords

Antioxidant Enzymes, Chelated Selenium, Photosynthesis, Rice Yield, Salt Stress

1. Introduction

Soil salinization is becoming a critical environmental issue due to global climate change and irrational irrigation practices, severely affecting crop growth, development, and yield, particularly in arid, semiarid, and coastal regions [1]. Rice (*Oryza sativa* L.), as one of the world's major food crops, is highly sensitive to salinity, that inhibits its growth, photosynthesis, dry matter accumulation, and ultimately reduces yield and quality [2]. Under salt stress, rice plants experience ionic imbalance owing to excessive accumulation of sodium ions (Na^+) that affects normal physiological and metabolic metabolism [3] [4]. Therefore, developing effective strategies to enhance rice salt tolerance is crucial for ensuring successful rice production under saline conditions.

Selenium (Se), an essential trace element for humans and animals, has gained attention for its potential to improve plant stress resistance and yield [5]. Previous studies have shown that Se application can enhance crop growth, yield, and quality by regulating photosynthesis, antioxidant enzyme activities, and nutrient uptake [6]. Chelated selenium, in particular, has been demonstrated to be more effective than inorganic selenium in improving plant physiological functions due to its higher bioavailability and lower toxicity [7]. Recent research has highlighted the role of chelated Se in alleviating salt stress in various crops, such as improving photosynthetic efficiency, enhancing antioxidant capacity, and promoting biomass accumulation [8] [9]. For example, a study on safflower found that Se application in soil substantially improved the photosynthetic pigments and reduced oxidative damage under salt stress [10]. Moreover, Se application improved antioxidant enzyme activities, photosynthetic efficiency and enhanced the slat tolerance in wheat [11] [12]. Overall, chelated selenium (Se) has proven to be an effective strategy for enhancing crop performance under saline conditions. At the molecular level, Se application can influence the expression of genes related to stress tolerance. For instance, studies have shown that Se can upregulate the expression of antioxidant-related genes like superoxide dismutase (SOD) and catalase (CAT), as well as salt tolerance genes such as SOS1 and NHX, thereby reinforcing the plant's intrinsic stress defense mechanisms [13] [14].

Although the effects of Se on other crops under salt stress conditions are widely reported, the effects of chelated Se on rice growth, yield, and physiological traits under salt stress remain elusive. The present study was therefore conducted to explore the impact of foliar application of chelated Se on the performance of rice under saline conditions.

2. Materials and Methods

2.1. Experimental Location and Materials

The pot experiment was conducted in the Experimental Farm, Fettes College (113.57˚ E, 23.16˚ N), China in 2024. The region has a maritime subtropical monsoon climate, with a mean annual temperature of 23.1˚C, mean annual precipitation of 2342 mm, relative humidity of 70 - 85%. Two rice varieties *i.e.*, Meixiangzhan 2 (MXZ2) and Liangxiangyou 868 (LXY868), were selected for the study. The experimental soil was loam, with an organic matter content of 20.1 g kg^{-1}, available nitrogen 100.2 mg kg^{-1}, and a total nitrogen content of 2.14 g kg^{-1}.

2.2. Experimental Treatments

Seedlings of both rice varieties were transplanted at the three-leaf stage, with two seedlings per hill and three hills per pot. The experiment included four levels of chelated Se (selenium ethylenediamine tetraacetate, EDTA-Se) *i.e.*, 0 (CK), 5, 10, and 15 mg L^{-1} denoted as T1, T2, and T3, with each treatment applied at heading stage. The treatments were arranged in a completely randomized design and all treatments were subjected to 0.1% (w/w) salt content to simulate salt stress. The dosage of Q/ZLY type rapid—dissolving sea salt crystals (produced by Zhejiang Lanhongxing Salt Products Factory, with the main components being sodium chloride 94.5%, potassium 0.11%, magnesium 0.13%, calcium 0.06%, and sulfate 3.7%) was calculated based on the soil mass to prepare soil with a salinity of 0.1% (1 g kg^{-1}). The pot was filled with 12 kg of sieved soil. Fresh water was used for irrigation during the whole growth period, and irrigation was stopped one week prior to harvest. To maintain the salt stress throughout the experiment, the soil salinity was monitored weekly using a portable soil salinity meter (Model SS-31, Soiltest Co., USA). If the salinity dropped below 0.1%, additional salt solution was added to each pot to maintain the target salinity level. This ensured consistent salt stress conditions throughout the experiment. The specific fertilization conditions were as follows: nitrogen fertilizer was applied at 180 kg N/ha, divided into a ratio of 1:1:1 for basal, tillering, and panicle fertilizer. Phosphatic fertilizer was applied at 60 kg P/ha as a one-time basal application, and potash fertilizer was applied at 100 kg K/ha, divided at a ratio of 1:1 for basal and panicle fertilizer.

2.3. Sampling and Measurements

2.3.1. Growth and Yield Related Attributes

To record the total aboveground biomass, rice yield and harvest index, three pots were harvested at maturity, sun-dried, and weighed to obtain the grain yield, with the grain moisture content adjusted to 13.5%. Three hills were randomly selected from each treatment, washed, separated into stems, leaves, and panicles, and oven-dried at 105˚C for 30 mins and then at 60˚C till constant weight. The harvest index was calculated by dividing the grain yield by the total aboveground dry matter accumulation.

2.3.2. Determination of Chlorophyll Content and Antioxidants

Fresh leaves were sampled at grain filling stage and extracted with acetone to determine the chlorophyll content [15]. Moreover, 15 - 20 flag leaves were collected from each pot and kept at −80˚C for biochemical analyses. The contents of 5-aminolevulinic acid (ALA) as well as the activities of chlorophyllase (CHL) and pheophorbide an oxygenase (PAO) were determined by readymade kits (Jiangsu Jingmei Biotechnology Co., LTD., Jiangsu, China).

The activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), as well as the content of malondialdehyde (MDA) were estimated according to Chen *et al.* [16].

Moreover, net photosynthetic rates and leaf area index were measured at grain filling stage according to Gu *et al.* [17].

2.4. Statistical Analysis

Data were analyzed using DPS 9.50 for analysis of variance (ANOVA), and Origin Pro 2022 (Origin Lab Corporation, USA) was used for graph plotting to ensure the results were analyzed in a systematic and scientifically rigorous manner.

3. Results

3.1. Aboveground Biomass, Yield and Harvest Index

The application of chelated Se significantly improved the aboveground biomass and yield of rice. Specifically, compared with CK, the aboveground biomass of both rice varieties under T1, T2, and T3 treatments increased by 9.61 - 11.64%, 14.95 - 19.01%, and 13.62 - 14.81%, respectively. Compared with CK, the yield was the highest under T2 treatment, which increased by 35.16% and 26.46% in MXZ2 and LXY868, respectively. In addition, in MXZ2, the yield of T2 was substantially higher than that of T1 and T3 whereas all the chelated Se treatments remained statistically similar for LXY868 (**Figure 1**).

Different concentrations of chelated Se substantially affected the harvest index of both rice varieties. For MXZ2, there was no significant difference in the harvest index among T1, T2, and T3, however, it increased significantly by 15.56%, 17.31%, and 10.00%, compared with CK, respectively. For LXY868, the harvest index of T2 was the highest among all treatments, with an increase of 14.58%, compared with CK (**Figure 2**).

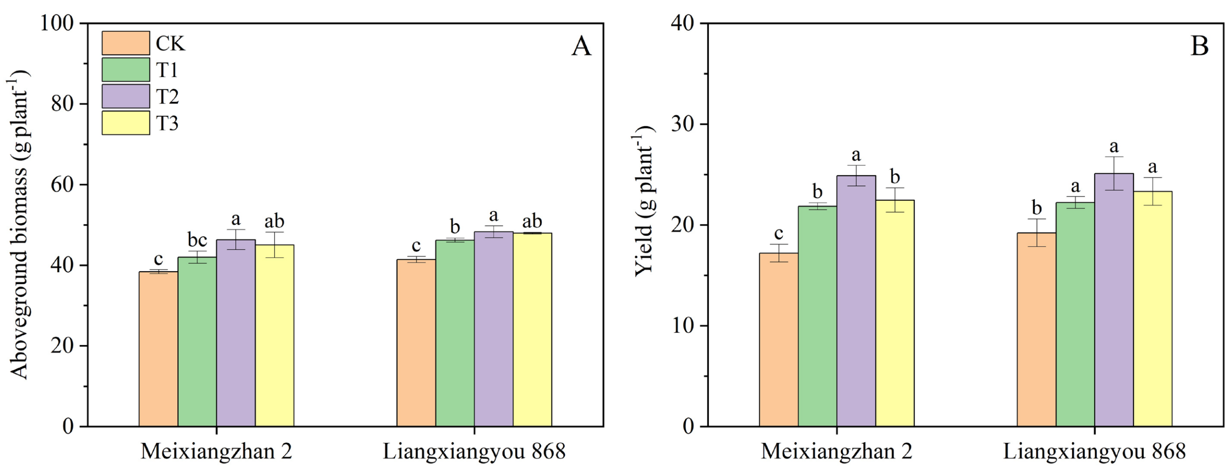


Figure 1. Effects of different concentrations of chelated Se on aboveground biomass (A) and yield (B) during maturity stage under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated Se concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.

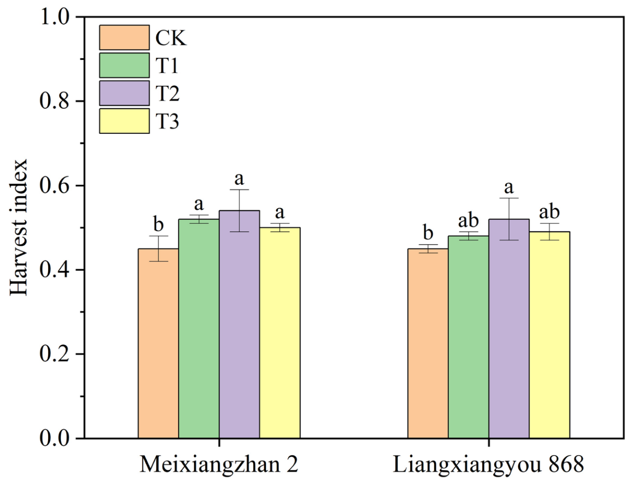


Figure 2. Effects of different concentrations of chelated Se on harvest index under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated selenium concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.

3.2. Leaf Area Index, Chlorophyll Content and Net Photosynthesis

The application of chelated Se significantly increased the leaf area index of the rice during grain filling stage. Specifically, the leaf area index of the T2 treatment in the MXZ2 and LXY868 was the highest among all treatments, which significantly increased by 17.04% and 19.06% compared with CK, respectively. There was no significant difference in the leaf area index between the T2 and T3 in LXY868, however, in the MXZ2, the T2 was significantly higher than the T3 (Figure 3).

The concentration of chelated Se substantially affected the chlorophyll content and net photosynthetic rate of rice during grain filling stage. The chlorophyll content in T2 was the highest, with no significant difference compared to the T3, but both were increased by 23.17 - 29.74% and 16.92 - 21.38% compared with CK for both MXZ2 and LXY868, respectively (Figure 4(A)). For net photosynthesis, compared with CK, the T1, T2, and T3 in both rice varieties were significantly increased by 15.03 - 17.22%, 17.25 - 21.52%, and 12.99 - 13.18%, respectively. Among all treatments, the T2 was significantly higher than T1 and T3 in the MXZ2, while there was no significant difference among the T1, T2, and T3 for LXY868 (Figure 4(B)).

3.3. ALA Content, PAO, and CHL Activity

The application of chelated Se regulated the leaf ALA contents and the activities of PAO, and CHL of the rice during grain filling stage. Specifically, the leaf ALA content of the T2 was the highest among all treatments, and it significantly increased by 18.52 - 21.10%, 9.55 - 16.03%, and 5.77 - 7.55% compared with CK, T1, and T3, respectively for both rice varieties. Compared with CK, the leaf PAO activity of both rice varieties were reduced by 24.59 - 25.80%, 31.09 - 35.04%, and 38.52 - 39.91% under T1, T2, and T3 treatments, respectively. Similarly, compared with CK, the leaf CHL activity of both rice varieties were reduced by 11.81 - 12.12%, 16.61 - 24.65%, and 21.73 - 25.09% under T1, T2, and T3 treatments, respectively.

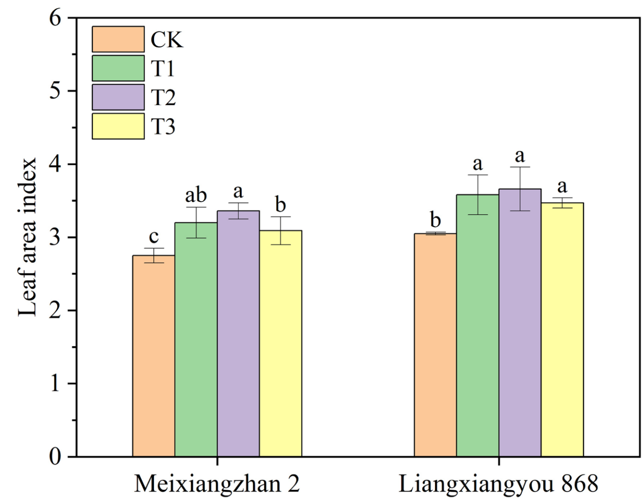


Figure 3. Effects of different concentrations of chelated Se on leaf area index during grain filling stage under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated selenium concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.

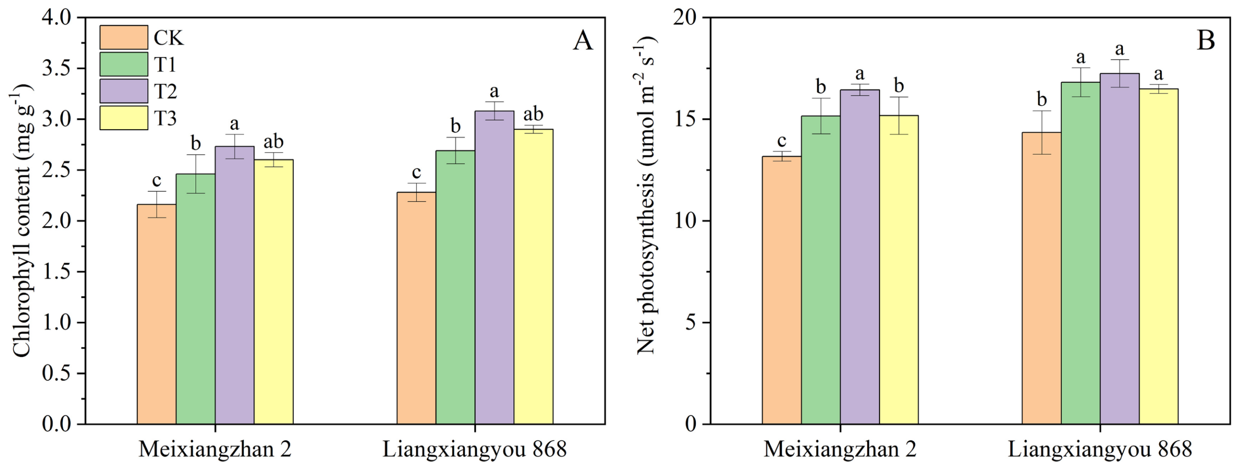


Figure 4. Effects of different concentrations of chelated selenium on chlorophyll content and net photosynthesis during grain filling stage under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated Se concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.

3.4. Antioxidant Enzyme Activity and MDA Content

Foliar application of chelated Se at different concentrations significantly regulated the antioxidant enzyme activities in the leaf. In MXZ2, compared with the CK, the leaf SOD activity of T1, T2, and T3 increased by 17.31%, 19.20%, and 13.41%, respectively. In LXY868, leaf SOD activity increased by 9.15%, 17.30%, and 11.88% in the T1, T2, and T3 treatments, respectively, compared to the control. In MXZ2, leaf POD activity was highest in the T2 treatment, while no significant difference was observed between T1 and T3. However, both T1 and T3 showed a significant increase of 15.19% in POD activity compared with the control. In

LXY868, significant differences in leaf POD activity were observed among all treatments, with T2 showing the highest activity. The leaf CAT activity of both rice varieties showed a consistent trend among all treatments with the following trend: T2 > T3 > T1 > CK (Figure 5 and Figure 6).

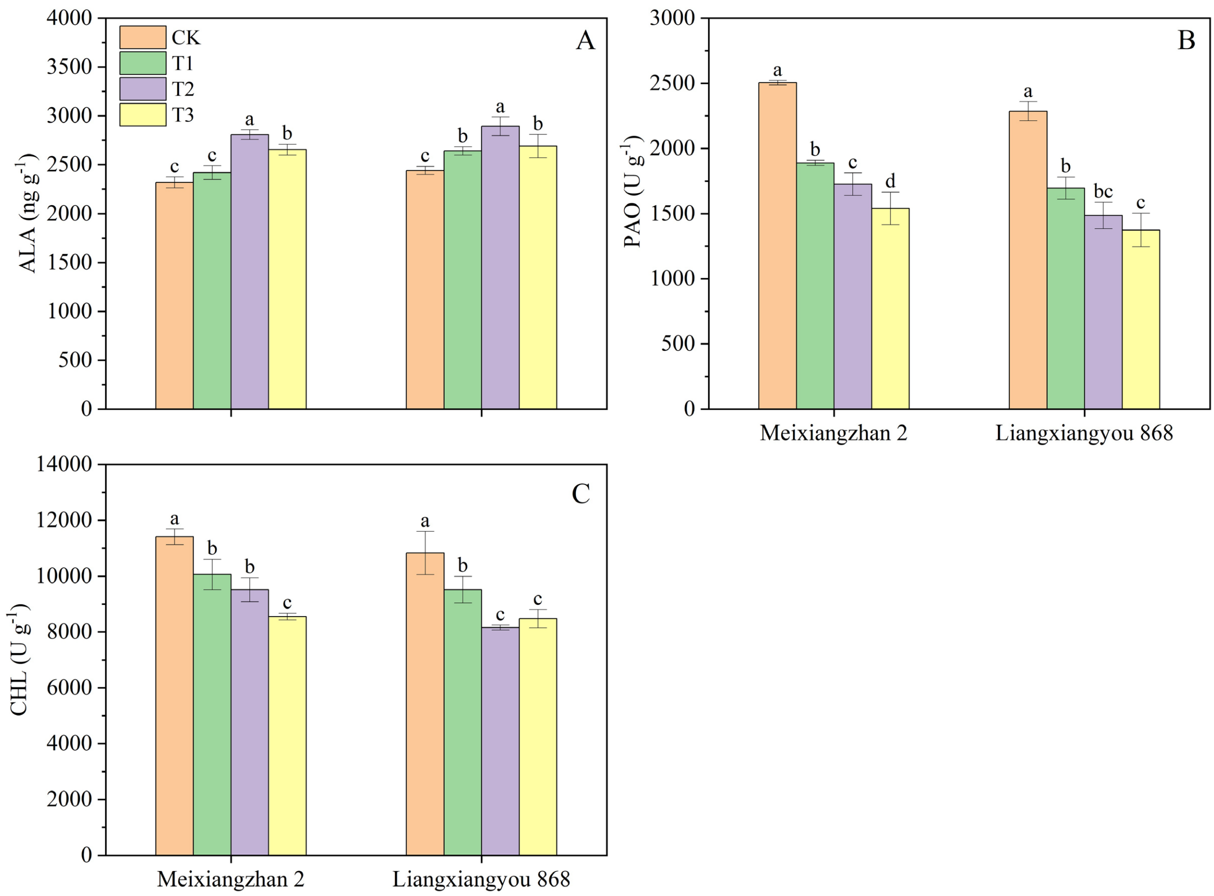
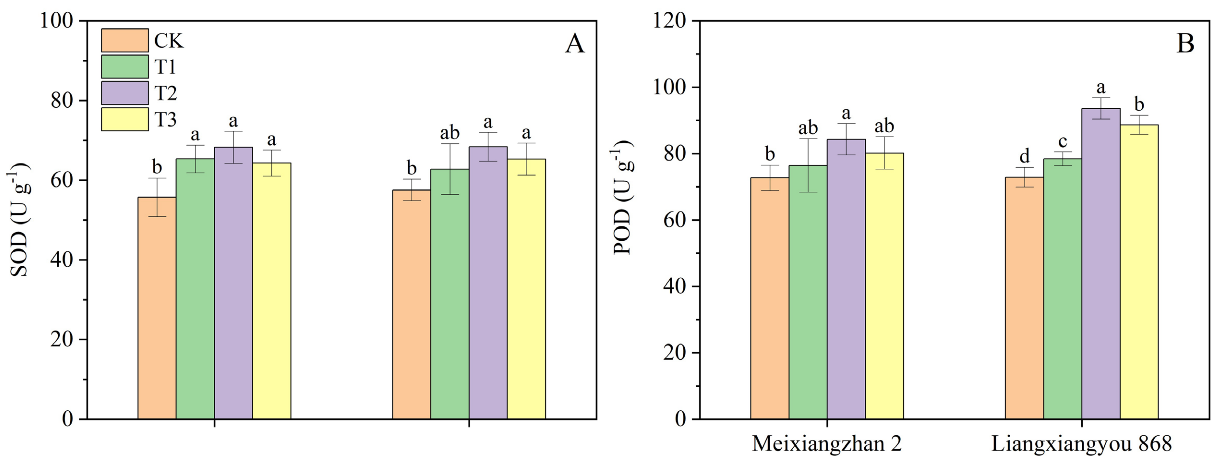


Figure 5. Effects of different concentrations of chelated selenium on leaf 5-aminolevulinic acid (ALA), chlorophyllase (CHL) and pheophorbide a oxygenase (PAO) during grain filling stage under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated selenium concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.



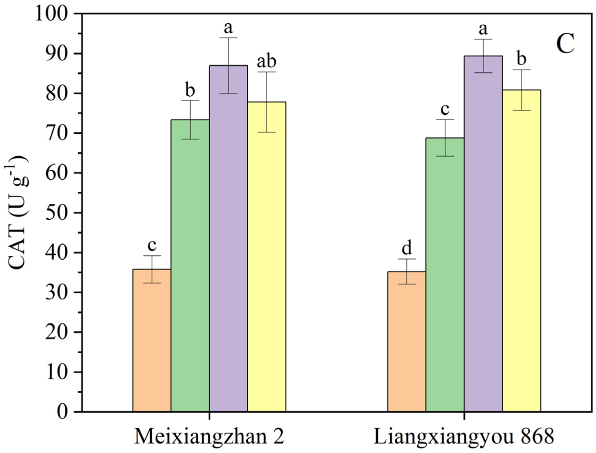


Figure 6. Effects of different concentrations of chelated Se on leaf antioxidant enzyme activity during grain filling stage under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated selenium concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.

The application of chelated Se at different concentrations significantly reduced the MDA content in the leaf. Compared with CK, the leaf MDA content of T1, T2, and T3 treatments in both rice varieties decreased by 10.00 - 10.89%, 13.57 - 24.31%, and 14.34 - 23.19%, respectively. In addition, in MXZ2, the leaf MDA content of T2 and T3 was significantly lower than that of T1, while there was no significant difference among T1, T2, and T3 treatments for LXY868 (Figure 7).

4. Discussion

It was found that foliar application of chelated Se significantly improved the growth and yield of rice under salt stress (Figure 1). Compared with CK, the

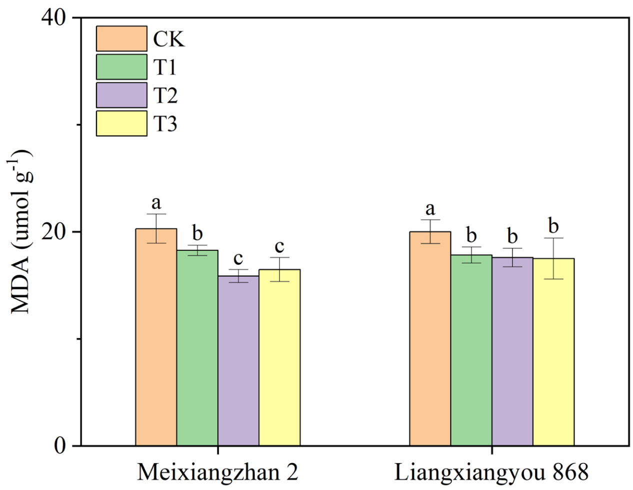


Figure 7. Effects of different concentrations of chelated Se on leaf MDA content during grain filling stage under salt stress. According to the LSD (0.05) test, different lowercase letters represent significant differences between different treatments of the same variety. CK, T1, T2, and T3 represent chelated selenium concentrations of 0, 5, 10, and 15 mg L^{-1}, respectively.

application of chelated Se increased the dry matter accumulation at maturity, promoted the translocation of nutrients to the grains, and increased the harvest index (**Figure 2**). This finding is consistent with Zhang *et al.* [18], who found that nano-selenium application significantly increased the dry matter accumulation and yield of rice. In addition, Gu *et al.* [17] also showed that the application of bio-nano-selenium significantly increased the yield and dry matter accumulation of rice which indicates that Se alleviated the negative effects of salt stress on rice by improving the photosynthesis and antioxidant activities in plants. It was found that chelated Se substantially improved the net photosynthetic rate and leaf area index of rice (**Figure 3** and **Figure 4**) during the grain-filling period, which is consistent with the results of Zhang *et al.* [18]. The study of Gu *et al.* [17] further showed that bio-nano-selenium increased the dry matter accumulation of rice by delaying leaf senescence and improving photosynthetic capacity. Luo *et al.* [7] found that the application of chelated selenium significantly increased the net photosynthetic rate and leaf area index of fragrant rice, improved the seed setting rate and grain weight, and increased grain yield. Our results suggest that selenium may improve the photosynthetic performance of rice by promoting the photosynthetic pigments and enhancing the efficiency of photosynthetic electron transport in chloroplast.

Salt stress usually triggers the production of reactive oxygen species (ROS) in plants. While ROS play essential roles as signaling molecules under normal physiological conditions, whilst excessive salt stress can cause their overproduction, surpassing the cellular threshold. This imbalance leads to oxidative stress, resulting in significant damage to organic molecules such as lipids, proteins, and nucleic acids, as well as the disruption of cellular membranes, which often leads to significant reductions in plant growth and productivity. It was further noticed that application of chelated Se improved the activities of SOD, POD, and CAT in rice leaves, while reducing the content of malondialdehyde (MDA) (**Figure 6** and **Figure 7**). This indicates that Se alleviated oxidative damage caused by salt stress by enhancing antioxidant enzyme activity. Previous studies have also reported that the application of exogenous Se can improve the antioxidant defense system, reduce ROS accumulation, and improve osmotic stress conditions [19] [20]. Our findings are consistent with Gu *et al.* [17], who found that bio-nano-selenium significantly increased the antioxidant capacity of rice, thereby alleviating oxidative stress. In addition, Zhang *et al.* [18] also reported that nano-selenium protected the photosynthetic system of rice leaves by increasing antioxidant enzyme activity. Similarly, the application of selenium enhances antioxidant defense system to cleanse ROS in chloroplasts by regulating the ascorbate-glutathione cycle and the thioredoxin mechanism in tomatoes and corn plants [14] [21]. In addition, plants applied with sodium selenite solution can improve plant growth and increase salt tolerance by modulating the activities of SOD and POD under salt stress conditions [22]. Regarding antioxidant activity, Se can upregulate the expression of antioxidant enzyme-related genes, such as SOD, CAT, thereby enhancing the activity of antioxidant enzymes and improving the plant's antioxidant capacity [23].

Additionally, Se can influence the synthesis of secondary metabolites by regulating the transcription of key enzymes and transcription factors in secondary metabolic pathways [24]. For instance, Se can promote the expression of phenylalanine ammonia lyase (PAL), a key gene in the phenylpropanoid metabolic pathway, thereby enhancing the accumulation of flavonoids and other antioxidants. These antioxidants can scavenge ROS, alleviate oxidative stress, and protect cellular membranes and other biomolecules from damage [25] [26].

Our results further showed that the application of chelated Se can reduce the activity of enzymes related to chlorophyll degradation while improving ALA content, the substrate for chlorophyll synthesis (**Figure 4** and **Figure 5**). The application of Se enhances the integrity of chloroplast membranes in plant leaf and maintained leaf chlorophyll content. For example, the application of sodium selenite improved the size of the chloroplasts and improved the chloroplast ultrastructure in rapeseed leaves [27]. Lan *et al.* [28] showed that seedlings treated with sodium selenite exhibited more stable chlorophyll fluorescence parameters and lower degradation of photosynthetic pigments (including total chlorophyll and carotenoids) under salt stress conditions. Liang *et al.* [29] found that melatonin treatment significantly reduced chlorophyll degradation, inhibited the transcription of senescence-related genes, delayed leaf senescence, and enhanced salt tolerance. Therefore, mitigating chlorophyll degradation through exogenous selenium application helps delay leaf senescence, consequently extending the photosynthetic period and ultimately contributing to increased rice yield.

5. Conclusion

In summary, the foliar application of chelated Se at 10 mg L^{-1} during the heading stage significantly improved the yield in both rice varieties under salt stress conditions. These improvements were attributed to the significant enhancement of chlorophyll content and the accumulation of the chlorophyll synthesis substrate *i.e.*, ALA, coupled with a reduction in the activity of chlorophyll degradation-related enzymes (chlorophyllase and PAO). Additionally, the application of chelated Se markedly increased the net photosynthetic rate and aboveground dry matter accumulation and improved the antioxidant enzyme activities (SOD, POD, and CAT) while lowering MDA content under salt stress conditions. These findings collectively suggest that the appropriate application of chelated Se serves as an effective strategy to boost rice yield and quality under salt stress, indicating its practical application in crop improvement strategies.

Availability of Data and Materials

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Authors' Contributions

Chuling Deng and Na Jin designed the study; Chuling Deng, Yien Liang, Jiaoyu

Liao, Jingsen Lan, Miwa Saito, Yixuan Chen, Xiujie Zhan, Na Jin collected and analyzed the data; Xiujie Zhan and Na Jin wrote the manuscript; and all authors revised the manuscript.

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Conflicts of Interest

The authors declare that they have no competing interests.

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