

<https://doi.org/10.17221/406/2023-PSE>

## Effects of foliar application of amino acid-chelated selenite on photosynthetic characteristics of peanut (*Arachis hypogaea* L.) leaves at the podding stage

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**Citation:** Wang Y., Zhu Q., Wang Z.W., Wang J.P., Wang Z., Yu F.Y., Zhang L.H. (2024): Effects of foliar application of amino acid-chelated selenite on photosynthetic characteristics of peanut (*Arachis hypogaea* L.) leaves at the podding stage. Plant Soil Environ., 70: 17–25.

**Abstract:** Foliar application of selenium (Se) is an effective measure to increase Se concentrations in peanut pods. However, how the foliar application of amino acid-chelated selenite affects the photosynthetic characteristics of peanut leaves at the podding stage is still unclear. Here, the effects of Se on the activities of antioxidant enzymes, the concentrations of chlorophyll, soluble protein, soluble sugar, and reduced glutathione (GSH), photosynthetic parameters, and Se concentration of peanut leaves were investigated by spraying selenite, L-lysine-chelated selenite, and amino acid-chelated selenite solutions, respectively. The results indicated that foliar application of Se could significantly increase leaf Se concentration. The net photosynthetic rate ( $P_n$ ), stomatal conductance ( $g_s$ ), and transpiration rate ( $T_r$ ) of leaves were significantly higher than those in the control. However, peanut leaves' intercellular CO<sub>2</sub> concentration ( $c_i$ ) decreased significantly. Further study found that the concentrations of chlorophyll, soluble protein, soluble sugar, and GSH in peanut leaves increased significantly, and the activities of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) in peanut leaves were significantly higher than those in control. However, there were no significant differences between the foliar application of selenite, L-lysine-chelated selenite, and amino acid-chelated selenite. Thus, foliar application of selenite, L-lysine-chelated selenite, and amino acid-chelated selenite could effectively enhance the photosynthetic functions of peanut leaves, which was closely associated with the improvement of antioxidant enzyme activities and the concentrations of soluble sugar, soluble protein, and GSH, resulting in inhibiting chlorophyll degradation and improving the photosynthetic functions of peanut leaves.

**Keywords:** chelated selenium; beneficial element; foliage spray; oil crop; physiological parameters

Selenium (Se) is an essential micronutrient for humans and animals, which has multiple biological functions such as anti-oxidation, scavenging free radicals, enhancing immune function, and preventing the division and growth of cancer cells (Rayman 2000, Combs 2001). Its functions on human health should be attributed to its presence within at least

25 selenoproteins (Kryukov et al. 2003). Sufficient Se in the human body benefits the full expression of selenoproteins and plays its multiple functions. Se required by the human body is predominantly from dietary intake. Increasing Se concentrations in plant foods is an effective strategy for enhancing Se intake and Se levels in the human body.

Supported by the National Natural Science Foundation of China-Henan Joint Fund, Grant No. U1904114.

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The Se concentration of crops can be improved by applying Se in soil or foliar spray of Se. Selenate and selenite are the main inorganic selenium available to plants, readily losing water or fixed by iron oxides when applied to soil (Rovira et al. 2008). In addition, most of the Se was retained in the roots, and only a small part of the Se was transported to the shoots after the plant took up selenite (Arvy 1993). By contrast, foliar spray of Se can be directly taken up by leaves, thus avoiding fixation by soil particles and water loss in the soil. Previous studies on wheat, rice and corn indicated that foliar application of Se could effectively increase grain Se concentrations, suggesting being a more effective measure to increase Se concentrations in the edible part of the plant (Li et al. 2022, Yi et al. 2022, Wang et al. 2022).

Se is a beneficial trace element for higher plants. It could improve the antioxidant capacity of plants by regulating the formation of antioxidants in plants, such as reduced glutathione (GSH) and ascorbic acid (AsA), and increase the activity of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and glutathione peroxidase (GSH-Px) (Feng et al. 2013). Additionally, applying optimal Se could increase rice's photosynthetic rate ( $P_n$ ), ETR photosynthesis index, and chlorophyll fluorescence parameters (Zhang et al. 2014). Se could stimulate plant growth by improving photosynthetic capability (Jiang et al. 2017). Applying appropriate Se could improve crops' yield and quality while improving the Se concentration of crops (Xiang et al. 2022). The increase in crop yield by Se was related to the increase in the concentration of chlorophyll and photosynthetic characteristics of crops, thus improving the dry matter accumulation and transport of crops (Zhang et al. 2014). The mechanism by which Se works on photosynthesis may be associated with the antioxidant system. Se affects photosynthesis by directly or indirectly inhibiting or inducing the accumulation of ROS and enzyme activity in plants (Feng et al. 2013). In addition, Se could repair Cd-induced chloroplast membrane structural damage and promote thylakoid and mechanical structural reorganisation and membrane fluidity (Filek et al. 2010).

Peanut (*Arachis hypogaea* L.) is an important oil crop in China with high nutritional value and health functions. It is widely planted in China's Huang-Huai-Hai River Basin, the southeast coast, and the Yangtze River Basin. Peanut has high nutritional value and can be utilised as a raw material for developing

high-value-added functional products. Se application could significantly increase peanuts' Se concentration. Foliar application of Se could more effectively promote the biotransformation of inorganic Se to organic Se in peanut plants, and the Se concentration increased in a dose-dependent (Broadley et al. 2010, Deng et al. 2017, Luo et al. 2021). The research on peanuts mainly focused on the effects of selenate or selenite on the Se concentration, yield, and quality of peanuts. Amino acid-chelated selenite is one form of Se sprayed on leaves to increase the concentration of the edible part of the plant. However, there are few reports on the effects of chelated selenite on peanut photosynthetic performance. In this study, the effects of selenite, L-lysine-chelated selenite, and amino acid-chelated selenite on enzyme activity and photosynthetic characteristics of peanut leaves were investigated, which provided a theoretical basis for the production of Se-enriched peanut.

## MATERIAL AND METHODS

**Plant materials and growth conditions.** The experiment was performed on the farm of Henan University of Science and Technology (34°36'23"N, 112°25'20"E). The peanut cultivar was Yuhua 22. The physical and chemical properties of the soil in the experimental field were as follows: the concentrations of alkali-hydrolysable nitrogen, available phosphorus, and exchangeable potassium were 61.34 mg/kg, 11.37 mg/kg, and 193.46 mg/kg, respectively. The concentration of organic carbon was 11.9 mg/kg. The pH is 7.8. Before ploughing, 450 kg of diammonium phosphate and 150 kg of potassium chloride were applied per hectare of soil. Peanuts were sown at the end of May, and the growth period of these plants was from May till the end of September. The average temperature in the growth period was 27 °C (27 °C in June, 28 °C in July, 27 °C in August, and 27 °C in September), and the average maximum temperature was 31 °C (33 °C in June, 32 °C in July, 31 °C in August, and 27 °C in September). Average precipitation was 96 mm (66 mm in June, 137 mm in July, 101 mm in August, and 79 mm in September). Average rainfall days were 5 days (5 days in June, 9 days in July, 6 days in August, and 5 days in September). The measurements were performed on the 3<sup>rd</sup> fully expanded compound leaf from the top during the podding formation stage (the 7<sup>th</sup> day after the Se application) in the middle of August. The field experiment was performed in a randomised block design with three

<https://doi.org/10.17221/406/2023-PSE>

replications, and four treatments were set up, including no selenite (CK), selenite (T1), L-lysine-chelated selenite (T2), and amino acid-chelated selenite (T3). The concentration of selenite application was 150 g/ha (containing pure Se 68.50 g/ha). The area of each plot was 50 m<sup>2</sup>. The first spray of Se was performed on the 7<sup>th</sup> day of pod formation, the second on the 14<sup>th</sup>, and the third on the 21<sup>st</sup>.

**Chelation of lysine or amino acid with selenite.** 4% L-lysine or amino acid and 0.5 mol/mL selenite solution were prepared by dissolving them in distilled water. L-lysine and selenite solution were mixed thoroughly following the volume ratio 2:1 (pH 8.0), and the chelation was performed by heating and stirring in a water bath at 60 °C for 120 min. The samples were concentrated to 1/5 volume under vacuum, and five times the volume of 95% ethanol was added. The samples were then refrigerated at 4 °C for 12 h, centrifuged at 8 000 r/min for 5 min, the supernatant was removed, and the precipitate was vacuum freeze-dried to obtain L-lysine- or amino acid-chelated Se product (Chen et al. 2020).

**Determination of chlorophyll concentration.** Fresh leaves were removed from the veins and cut into 2 mm pieces. About 0.5 g of chopped leaf tissue was put into a test tube with a plug, and 10 mL of pure acetone and absolute ethanol (1:1) mixture were added and soaked in the dark for 24–36 h. The chopped leaf tissue became completely white and removed, and chlorophyll concentration (including *Chl a* and *Chl b*) was measured at wavelengths 663 nm and 646 nm with an ultraviolet spectrophotometer (Beijing Purkinje General Instrument Co., Ltd., T6 New Century, Beijing, China) (Ahmad et al. 2022).

**Determination of soluble protein, soluble sugar, and GSH concentration.** After the fresh leaves were ground with phosphate buffer, the supernatant was taken, 5 mL Coomassie Brilliant Blue G-250 solution was added, and the soluble protein concentration was measured at a wavelength of 595 nm with a spectrophotometer. About 0.5 g of chopped leaf tissue and 15 mL of distilled water were put into a test tube and boiled in a boiling water bath for 20 min. After filtration, 1 mL of extract and 5 mL of anthrone reagent were mixed and boiled in a water bath for 10 min. After cooling, soluble sugar concentration was determined at a wavelength of 620 nm. About 0.2 g of chopped leaves were ground to a pulp with 2.0 mL of trichloroacetic acid (TCA) and centrifuged at 8 000 r/min for 20 min. 0.25 mL of the supernatant, 2.6 mL of phosphate buffer (150 mmol/L,

pH 7.7), and 0.15 mL of 5'5'-dithiol-2-nitrobenzoic acid (DTNB) were mixed. The mixture was incubated at 30 °C for 5 min, after which an ultraviolet spectrophotometer measured GSH concentration at a wavelength of 412 nm (Li et al. 2021).

**Determination of SOD, CAT, and POD activity.** About 0.5 g of chopped leaf tissue was ground into pulp with 1.8 mL phosphate buffer (50 mmol/L, pH 7.8) pre-cooled at 4 °C and centrifuged at 10 000 r/min for 20 min at 4 °C. 0.05 mL of the supernatant, 1.5 mL of phosphate buffer, 0.3 mL of 130 mmol/L Met, 0.3 mL of 20 µmol/L riboflavin, 0.3 mL of 0.1 mmol/L EDTA-Na<sub>2</sub>, and 0.75 mmol/L nitro-blue tetrazolium (NBT) were put into a centrifuge tube, respectively. After mixing thoroughly, the reaction was performed under 4 000 LX-ray for 20 min. SOD activity was measured at 560 nm with an ultraviolet spectrophotometer (Ahmad et al. 2022). 0.05 mL of the enzyme extract solution and 1.95 mL of phosphate buffer were put into a centrifuge tube and preheated in a water bath at 25 °C for 3 min, then 1 mL of 0.3% H<sub>2</sub>O<sub>2</sub> was added and rapidly mixed. CAT activity was measured at a wavelength of 240 nm every 30 s for 3 min (Ahmad et al. 2022). 2.0 mL of phosphate buffer (pH 5.5), 1 mL of 2% H<sub>2</sub>O<sub>2</sub>, and 1 mL of 50 mmol guaiacol were put into a centrifuge tube, then 0.1 mL of enzyme extract solution was added and immediately placed in a water bath at 37 °C for 15 min. POD activity was determined by calculating the increase in absorbance at 470 nm over 3 min with an ultraviolet spectrophotometer (Ahmad et al. 2022).

**Determination of photosynthetic physiological parameters.** During the podding formation stage (the 7<sup>th</sup> day after the Se application), a portable photosynthesis system (LI-6400, LI-COR, Nebraska, USA) was used to determine the photosynthetic parameters at 09:00–11:30 a.m. with the following settings: the photosynthetically active radiation at the leaf surface was between 1 100 and 1 200 µmol/m<sup>2</sup>/s, ambient CO<sub>2</sub> concentration was between 385.0 and 400.0 µmol/mol, and the air temperature was 31.5 ± 0.5 °C with 60–80% relative humidity. After the leaf was placed in the chamber for about 2 min until the readings became stable, net photosynthetic rate ( $P_n$ ), stomatal conductance ( $g_s$ ), intercellular CO<sub>2</sub> concentration ( $c_i$ ), and transpiration rate ( $T_r$ ) were measured.

**Assay of Se concentration.** Peanut leaves were sampled and dried at the mature stage. Dried samples were weighed and placed into 100 mL digestion

Table 1. Effects of selenium (Se) on chlorophyll concentration, soluble protein, and soluble sugar in peanut leaves

Treatment	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Total chlorophyll	Soluble protein	Soluble sugar
	(mg/g)				(%)
CK	1.17 ± 0.07 <sup>b</sup>	0.23 ± 0.01 <sup>b</sup>	1.40 ± 0.07 <sup>b</sup>	19.02 ± 1.30 <sup>b</sup>	0.88 ± 0.04 <sup>b</sup>
T1	1.28 ± 0.02 <sup>a</sup>	0.26 ± 0.01 <sup>a</sup>	1.55 ± 0.04 <sup>a</sup>	23.46 ± 1.12 <sup>a</sup>	1.05 ± 0.07 <sup>a</sup>
T2	1.31 ± 0.03 <sup>a</sup>	0.27 ± 0.02 <sup>a</sup>	1.58 ± 0.04 <sup>a</sup>	24.19 ± 1.34 <sup>a</sup>	1.08 ± 0.04 <sup>a</sup>
T3	1.32 ± 0.04 <sup>a</sup>	0.28 ± 0.01 <sup>a</sup>	1.60 ± 0.03 <sup>a</sup>	24.69 ± 1.07 <sup>a</sup>	1.10 ± 0.03 <sup>a</sup>

Values are the means of three replicates. Error bars represent ± standard deviation ( $n = 3$ ). Different letters of a, b, and c indicate differences among different treatments in the same treatment ( $P < 0.05$ ). CK – no selenite; T1 – selenite; T2 – L-lysine-chelated selenite; T3 – amino acid-chelated selenite

tubes, and a 5 mL acid mixture ( $\text{HNO}_3:\text{HClO}_4$ ; 4:1, v/v) was added. The samples were digested at room temperature overnight and then completely digested at 150–165 °C in a digestion oven. After cooling, a 2.5 mL 6 mol/L HCl was added to reduce  $\text{SeO}_4^{2-}$  to  $\text{SeO}_3^{2-}$  at 100 °C. The digests were diluted with millipore water to a final volume of 25 mL. Se concentrations were determined by atomic fluorescence spectrometry (Beijing Purkinje General Instrument Co., Ltd., PF32, Beijing 2017). Standard tea material (GSV-4, 0.072 mg Se/kg, GBW07605) and a blank were simultaneously digested with the test samples for quality control (Li et al. 2022).

**Statistical analysis.** One-way analysis of variance (ANOVA) was performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA) to determine the significant differences ( $P < 0.05$ ) between control and treatments. Statistical differences were assessed by Student's *t*-test.

## RESULTS

**Effects of Se on chlorophyll concentration, soluble protein, and soluble sugar in peanut leaves.** Chlorophyll is a lipid-containing pigment in the

thylakoid membrane. It plays a central role in light absorption. In this study, chlorophyll *a*, *b*, and total chlorophyll concentration in peanut leaves increased significantly after Se application compared with the control (Table 1). Soluble proteins in plants are important osmotic adjustment substances and nutrients, most of which are enzymes involved in various metabolism. The soluble protein concentration in peanut leaves increased significantly after Se application compared with the control (Table 1). Soluble sugar can counteract oxidative challenges during abiotic stress in plants and serve multiple roles as osmoregulators, cryoprotectants, signalling molecules, and scavengers of reactive oxygen species. Soluble sugar concentration in peanut leaves increased significantly after Se application compared with the control (Table 1). However, there was no difference in the concentration of chlorophyll, soluble protein, and soluble sugar among T1, T2, and T3 treatments.

**Effects of Se on enzyme activities in peanut leaves after foliar application of Se.** Superoxide dismutase, catalase, and peroxidase are important protective enzymes in the enzymatic defence system. After Se application, SOD, CAT, and POD activity

Table 2. Effects of selenium (Se) on enzyme activities and glutathione (GSH) concentration in peanut leaves after foliar application of Se

Treatment	SOD (U/g FW/min)	CAT (U/g FW/min)	POD (U/g FW/min)	GSH (μmol/g FW)
CK	228.49 ± 8.95 <sup>c</sup>	206.51 ± 11.01 <sup>b</sup>	28.46 ± 1.33 <sup>b</sup>	2.41 ± 0.09 <sup>b</sup>
T1	257.24 ± 3.01 <sup>b</sup>	269.58 ± 17.56 <sup>a</sup>	34.17 ± 1.85 <sup>a</sup>	2.99 ± 0.13 <sup>a</sup>
T2	262.62 ± 2.23 <sup>ab</sup>	274.16 ± 8.73 <sup>a</sup>	34.73 ± 2.25 <sup>a</sup>	3.01 ± 0.11 <sup>a</sup>
T3	271.01 ± 3.57 <sup>a</sup>	278.01 ± 10.78 <sup>a</sup>	35.83 ± 2.73 <sup>a</sup>	3.11 ± 0.12 <sup>a</sup>

Values are the means of three replicates. Error bars represent ± standard deviation ( $n = 3$ ). Different letters of a, b, and c indicate differences among different treatments in the same treatment ( $P < 0.05$ ). SOD – superoxide dismutase; CAT – catalase; POD – peroxidase; CK – no selenite; T1 – selenite; T2 – L-lysine-chelated selenite; T3 – amino acid-chelated selenite; FW – fresh weight



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in peanut leaves in T1, T2, and T3 treatment was significantly higher than that in control (Table 2). There was no significant difference in the activity of POD and CAT among T1, T2, and T3 treatments. However, SOD activity in the T3 treatment was significantly higher than that in the T1 treatment, while there was no significant difference between T2 and T3 treatments. Reduced glutathione is an important antioxidant in the non-enzymatic defence system. After Se application, the GSH concentration of peanut leaves in T1, T2, and T3 treatment was significantly higher than that in the control (Table 2), but there was no significant difference among T1, T2, and T3 treatments.

**Effects of Se on photosynthetic physiological parameters in peanut leaves after foliar application of Se.** The photosynthetic parameters can indicate the capability of peanut leaves to produce carbohydrates through photosynthesis. The net photosynthetic rate, stomatal conductance, and transpiration rate of peanut leaves after Se application in T1, T2, and T3 treatment were significantly higher than those without Se application (CK) regardless of the first, second, and third spray (Figure 1), but intercellular  $\text{CO}_2$  concentration was significantly lower in the T1,

T2, and T3 treatment than that in control. There was no significant difference in the photosynthetic physiological parameters among T1, T2, and T3 treatments.

**Differences of Se concentration in peanut leaves after foliar application of Se.** After foliar application of Se, the Se concentration of peanut leaves at the maturity stage increased significantly with the increase of spraying times. However, there was no significant difference among T1, T2, and T3 simultaneously (Figure 2). The Se concentration of peanut leaves under different treatments was 59–122 times higher than that of CK.

## DISCUSSION

Chlorophyll is the basis of plant photosynthesis and carbon assimilation, and chlorophyll concentration reflects the intensity of plant photosynthesis to a certain extent. Previous studies indicated that Se could significantly increase the chlorophyll concentration in peanut leaves (Sali et al. 2018, He et al. 2019, Cunha et al. 2022). The reason might attribute that Se could promote the uptake of elements related to chlorophyll syntheses, such as iron, manganese,

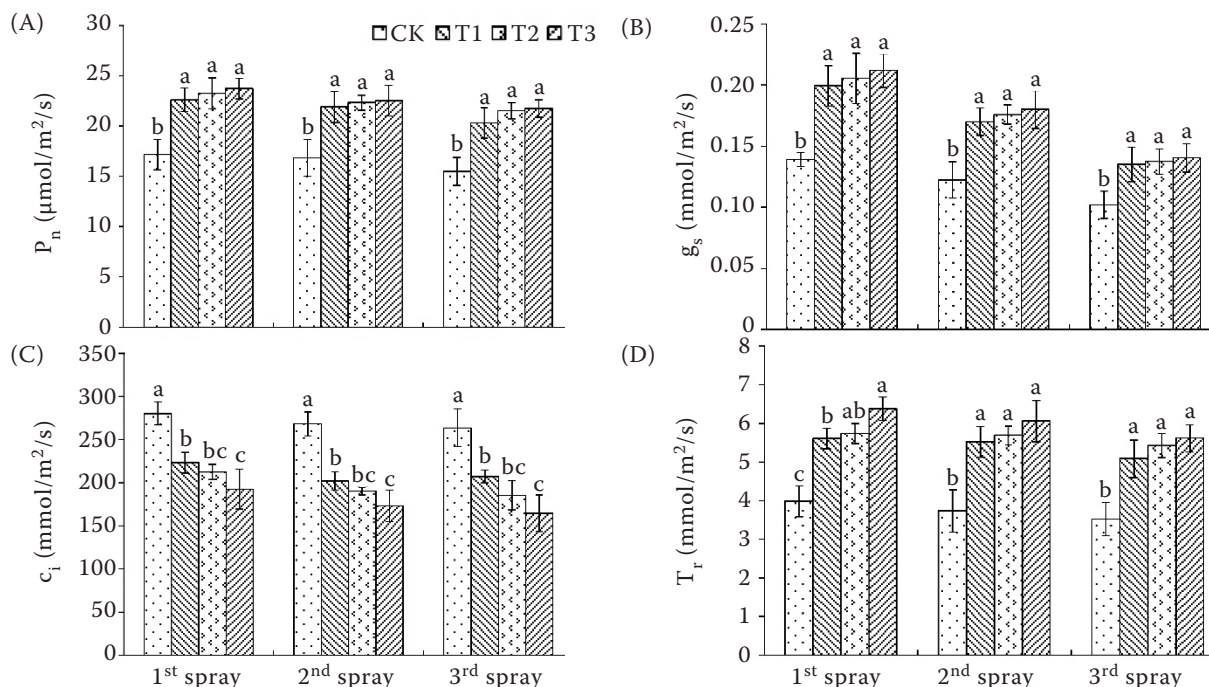


Figure 1. Effects of selenium (Se) on photosynthetic physiological parameters in peanut leaves after foliar application of Se. Values are the means of three replicates. Error bars represent  $\pm$  standard deviation ( $n = 3$ ). Different letters of a, b, and c indicate differences among different treatments in the same treatment ( $P < 0.05$ ).  $P_n$  – net photosynthetic rate;  $g_s$  – stomatal conductance;  $T_r$  – transpiration rate;  $c_i$  – intercellular  $\text{CO}_2$  concentration; CK – no selenite; T1 – selenite; T2 – L-lysine-chelated selenite; T3 – amino acid-chelated selenite

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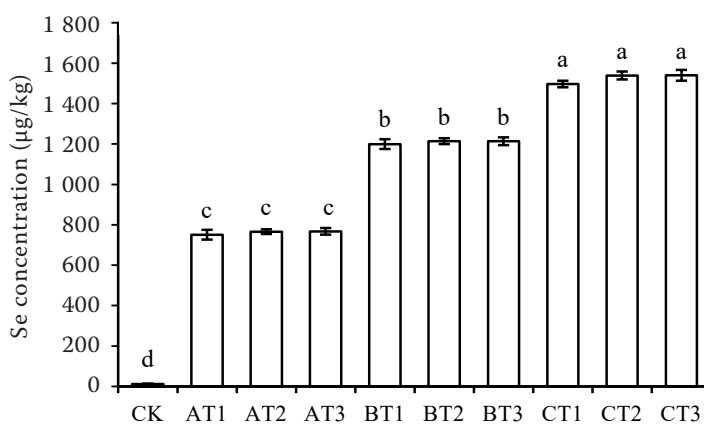


Figure 2. Effects of selenium (Se) on selenium concentration in peanut leaves after foliar application of Se. Values are the means of three replicates. Error bars represent  $\pm$  standard deviation ( $n = 3$ ). Different letters of a, b, and c indicate differences among different treatments in the same treatment ( $P < 0.05$ ). A – first spray; B – second spray; C – third spray; T1 – selenite; T2 – l-lysine-chelated selenite; T3 – amino acid-chelated selenite

copper, and zinc, thereby increasing the chlorophyll concentration of plant leaves (Wang et al. 2015, Yang et al. 2021). In this study, foliar application of Se could increase the chlorophyll concentration of peanut leaves at the podding stage, in which leaves enter senescence and chlorophyll begins to degrade. Therefore, Se's increased chlorophyll concentration should be attributed to Se's inhibition of the degradation of chlorophyll, resulting in maintaining the function of chlorophyll for a longer time. Leaf senescence results in the gradual loss of green pigments due to chlorophyll degradation. Most chlorophyll is present in protein complexes in leaves because it is critical to prevent cells from the photooxidative damages caused by the free chlorophyll molecules if disassociated from the light-harvesting chlorophyll-binding complex proteins (LHCs) of the thylakoids (Kuai et al. 2018, Lee et al. 2021). Thus, it was postulated that Se inhibited chlorophyll degradation by improving the stability of the thylakoid proteins.

When peanut leaves are in the process of senescence, the balance of production and elimination of free radicals will be destroyed, resulting in the accumulation of a large amount of active oxygen, destroying the biological macromolecules in cells, and the accumulated superoxide free radicals will cause membrane lipid peroxidation, resulting in damage to the cell membrane system. Superoxide dismutase plays a vital role in removing excess superoxide anion in plant cells; catalase is responsible for removing  $H_2O_2$  and delaying plant senescence; peroxidase is mainly involved in the process of removing active oxygen in plant stress (Laxa et al. 2019); reduced glutathione is involved in the redox reaction in the body, scavenging free radicals, and reducing the body peroxidation damage. Various abiotic stresses lead to the overproduction of ROS in plants, which are highly

reactive and toxic and cause damage to proteins, lipids, carbohydrates, and DNA, ultimately resulting in oxidative stress (Rasel et al. 2020). Stress-induced ROS accumulation is counteracted by enzymatic antioxidant systems that include a variety of scavengers, such as SOD, APX, GPX, GST, and CAT, and non-enzymatic low molecular metabolites, such as ASH, GSH,  $\alpha$ -tocopherol, carotenoids, and flavonoids (Gill and Tuteja 2010). Previous studies indicated that Se application could change the antioxidant system of peanuts (Ramos et al. 2010, Chu et al. 2010, Auobi Amirabad et al. 2020). Reactive oxygen species (ROS) accumulated during leaf senescence, contributing to chlorophyll degradation (Zhao et al. 2022). Increased ROS levels due to decreased antioxidant capacity were highly correlated with leaf senescence (Kan et al. 2021). Applying Se to plants under stress could alleviate the decline of chlorophyll (Sharifi et al. 2021). In this study, the activities of SOD, CAT, POD, and the concentration of GSH in the leaves of peanuts applied with Se were significantly higher than those in the leaves without Se application, indicating that SOD, CAT, POD, and GSH could cooperate in scavenging active oxygen, inhibit membrane lipid peroxidation, and reduce the damage of superoxide free radicals to the cell membrane, thus protecting the damage of chloroplast structure and inhibiting the decomposition of chlorophyll.

Soluble protein and soluble sugar, as important nutrients and osmotic adjustment substances in plants, play important roles in protecting the integrity of cell membrane structure and maintaining the osmotic pressure balance of cells. As essential nutrients and osmotic adjustment substances in plants, soluble sugar plays important roles in protecting the integrity of cell membrane structure and maintaining the

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osmotic pressure balance of cells (Cui et al. 2015). Previous studies indicated that Se could increase the concentration of soluble protein and sugar in tomato leaves under low temperatures and light (Li et al. 2020, Zhong et al. 2021). The soluble proteins play an important role in the growth of plants and are crucial components of numerous plant enzymes that reflect the overall plant metabolism (Kucerova et al. 2019). In this study, the foliar application of Se could significantly increase the concentration of soluble protein and soluble sugar in peanut leaves, which enhanced the stability of cell membrane structure and inhibited the decomposition of chlorophyll.

Photosynthesis is the most important physiological process of plants, and most of the carbon sources come from the product of photosynthesis. Se could improve the photosynthetic characteristics of plants, and foliar spraying of selenate at the heading stage was conducive to inducing the absorption of light energy by rice leaves, exhibiting obvious light advantage (Luo et al. 2019, Alves et al. 2020). In this study, the net photosynthetic rate, stomatal conductance, and transpiration rate of peanut leaves with Se application were significantly higher than those without Se application. The intercellular CO<sub>2</sub> concentration of peanut mesophyll cells was significantly lower than that without Se application. Thus, the decrease of *c<sub>i</sub>* while the increase of CO<sub>2</sub> assimilation was not due to stomatal limitation because of the increased stomatal conductance after foliar application of Se. Se could increase peanut leaves' net photosynthetic rate, which might be related to the increase of chlorophyll concentration by foliar spraying of Se. At the same time, Se application increased peanut leaves' stomatal conductance and transpiration rate. It decreased the intercellular CO<sub>2</sub> concentration of mesophyll cells, indicating that an appropriate amount of Se promoted photosynthesis, enhanced CO<sub>2</sub> assimilation capacity, and increased photosynthetic rate, resulting in the decreased CO<sub>2</sub> concentration of mesophyll cells (Malik et al. 2012).

In this study, foliar application of Se significantly increased Se concentration in peanut leaves and other parts of the peanut, especially in the grains at the maturity stage. However, there was no significant difference between treatments of foliar application of selenite, L-lysine-chelated selenite, and amino acid-chelated selenite. The results indicated that there was no difference in plant Se concentration by foliar application of different forms of Se under field conditions, resulting in no significant difference in

the concentration of chlorophyll, soluble sugar, and soluble protein, the enzyme activity of SOD, CAT, and POD, the photosynthetic rate in peanut leaves among the three Se treatments.

In conclusion, foliar application of Se could effectively increase the chlorophyll concentration in peanut leaves, which was related to the significant increase of enzyme activity, soluble protein, and soluble sugar concentration in peanut leaves, thus reducing the degree of membrane lipid peroxidation and enhancing the light energy utilisation efficiency of peanut leaves. However, there was no significant difference in the concentration of chlorophyll, soluble sugar, and soluble protein, the enzyme activity of SOD, CAT, and POD, the photosynthetic rate in peanut leaves by foliar application of selenite, L-lysine-chelated selenite, and amino acid-chelated selenite.

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Received: November 6, 2023

Accepted: December 1, 2023

Published online: January 15, 2024