

Effects of Foliar Application of Nano-Se On Photosynthetic Characteristics and Se Accumulation in *Paeonia Ostii*

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Abstract

Background

Selenium is an essential micronutrient in human metabolism. However, the Se level in foods is far below the standards due to the fact that it is deficient in two thirds of arable soils. Therefore, consuming Se-enriched plant products which convert inorganic Se into organic Se might be a safe and effective way to supplement Se for the human body. *Paeonia ostii* is a unique medicinal and edible plant in China, and also a new special woody oil crop. It serves as a perfect mediator for Se biofortification. In this report the effects of nano-Se foliar application on photosynthetic parameters, physiological characteristics and Se-enrichment effect in various plant organs of *P. ostii* cultivar Feng Dan were investigated in randomized complete block design experiments with different doses of spray in Se-deficient soils.

Results

By contrast to the control, nano-Se sprays enhanced net photosynthetic rate, transpiration rate, stomatal conductance, intercellular CO₂ concentration, and chlorophyll content of Feng Dan. The content of soluble sugar, soluble protein, proline and activities of superoxide dismutase and peroxidase were increased while malondialdehyde content was significantly reduced. The stimulatory effect at concentrations of 6.00 and 8.25 g·hm⁻² was the best in this study. nano-Se application significantly increased the Se content in all organs of Fengdan except the root compared to the control, and Se contents in various organs were increased paralleled with the increase of concentrations applied, and ordered as follows under suitable concentration, Testa > leaf > kernel > stem > root.

Conclusions

The above results show that nano-Se sprays at concentrations of 6.00-8.25 g·hm⁻² stimulated the growth of Feng Dan and achieved the best Se-enrichment effect in this study. It also proved that the Se biofortification effect depends on its dosage applied and types of plant organs. These results provide guidance on Se enrichment of horticultural crops.

Background

As an essential microelement of animals, selenium (Se) has important physiological functions and extensive pharmacological properties, such as maintaining normal reproductive function, anti-virus and anti-oxidation functions, regulating immune function, and preventing several diseases (Shalini and Bansal 2005; Ansar 2016). Adequate supplementation of Se can enhance the organism immune ability and delay senescence, while Se deficiency can directly or indirectly cause diseases such as Keshan and Kaschin-Beck (Mehdawi and Pilon-Smits 2012; Fordyce et al. 2013). Therefore, Se nutrition research has received more attention over the past few decades. However, a large number of people may have inadequate Se intake worldwide (Combs 2001). China is one of the most Se-deficient countries, with Se-

deficient soil area accounting for about 72% of the country's land area (Han et al. 2013), which is simply not enough to allow dependence on natural foods to meet organic Se needs (Buber et al. 1995).

Plants are a critical vector in the natural Se ecological cycle. They are also the main and most effective source of Se for animals (Germ et al. 2007; Hou et al. 2018). Therefore, to increase human Se intake, biofortification technology has been proposed to effectively increase plant Se content in Se-deficient area. In recent years, studies have assessed the Se-enrichment capacity of species or varieties (Bañuelos et al. 1997; Wu et al. 2003; Zahedi et al. 2009; Lee et al. 2011); absorption, distribution characteristics, and metabolic mechanism of Se in plants (Xu and Hu, 2004; Mehdawi and Pilon-Smits, 2012; Ghader, 2013), and influence of environmental factors on plants Se absorption and aggregation (Liu et al. 2017; Li et al. 2008; Hajiboland et al. 2015; Sattar et al. 2019; Mandana et al. 2019). However, existing research has mainly focused on crops, vegetables, fruits, tea, or other plants (Xu and Hu 2004; Zhao et al. 2005; Ghader 2013; Maseko et al. 2013; Han et al. 2013; Hassan et al. 2014; Maryam et al. 2016; Li et al. 2018).

The absorption of Se by plants and its biological efficacy are closely related to the method of exogenous Se application, the state of Se fertilizer, and plant species (Wang and Xu 2008; Lee et al. 2011; Hassan et al. 2014; Nawaz et al. 2015). Currently, Se content can be increased in plants by soil fertilization, foliar applications, hydroponics, or aeroponic cultivation in a nutrient solution containing Se, and soaking seeds in Se solution before sowing (Germ et al. 2007; Hassan et al. 2014), and the main application methods of Se fertilizer are soil fertilizer and foliar spray application. Se foliar applications can be quickly absorbed by leaves and transported, obviously increasing the contents of Se and essential amino acids content in plants, and can decrease the influence of soil factors and greatly reduce the quantity of Se fertilizer (Johnsson 1991). However, as a nutrient element, the window between Se deficiency and toxicity to animals is extremely narrow (Mehdawi and Pilon-Smits 2012; Fordyce et al. 2013).

Within the safe range, Se fertilization can significantly increase photosynthetic and transpiration rate in plants, improve total soluble sugar and free amino acid accumulation, enhance root activity and redox capacity, improve root: shoot ratio, promote seedling growth, biomass accumulation, and conversion of organic Se and protein Se, increasing Se content in plants to different degrees, and improving plant cell penetration protection ability, antioxidant system activity, and ultraviolet resistance. Se fertilization can also increase plant resistance to stresses, slow down the aging process, and play a significant role in promoting vegetative growth and reproductive growth of plants (Germ et al. 2007; Zhang M et al. 2014; Nawaz et al. 2015; Deng et al. 2017; Li et al. 2018; Zhang et al. 2019; Alam et al. 2019). However, high concentrations of exogenous Se may lead to poor growth, slow growth, and reduced yield and quality (Germ et al. 2007; Garousi et al. 2015). As it is difficult to control the application amount, Se fertilizer products with high efficiency, low toxicity, and no pollution are always emphatically studied. In recent years, different Se forms, have been widely used in plant nutrition fertilization studies, including organic and some salts such as selenite and selenite. Furthermore, nanoparticles of elemental Se have gained attention as a possible source of this beneficial element. Nano-Se is a kind of nano-elemental Se with protein as a dispersant, and has different absorption and metabolism patterns in the organism than those of traditional Se sources, since the unique and subtle spatial structure and the nanometer scale of

nano-Se is the length scale possessed by most of the body's natural materials, and studies have shown that nano-Se has comparable efficacy to organic, selenite, and selenite in biological activities, and lower toxicity among various Se forms (Jani et al. 1992; Florence 1998; Tran and Webster 2008; Hassan et al. 2014; Song et al. 2017). Therefore, owing to its high bioavailability and low environmental pollution, nano-Se has become a popular material in Se nutrition research (Zhang et al. 2008; Haghghi et al. 2014; Li et al. 2018).

Tree peony (*Paeonia suffruticosa* Andr.) is a perennial deciduous shrub belonging to Sect. *Moutan* DC. of *Paeonia* L. (Paeoniaceae). It is indigenous to China and has been cultivated and used for 2,000 years as garden flowers (peonies) and medicinal plants (cortex moutan) (Jin et al. 2015; Li et al. 2015). Recent studies have found that, peony seed oil contains several unsaturated fatty acids such as linolenic, oleic, and linoleic acid, VE, stilbenes, flavonoids, and other nutritional and pharmacological components. Peony seed oil has high nutritional value and medical and health care functions, e.g. anti-tumor, anti-inflammatory, improvement of cardiovascular, and immune. Therefore, peony is also an excellent medicinal and edible homologous plant (Li et al. 2015; Han et al. 2018). In 2011, peony seed oil was approved as a woody edible oil in China by the Minister of Health of China. Currently, woody oil development has become the main channel and trend to solve the shortage of edible oil, as some Western European countries have basically realized the woody edible oil, the self-sufficiency rate of edible vegetable oil in China is only about 40%, and mostly comes from herbal oil plants (Wang 2020). Thus, developing and utilizing peony seed oil is of great significance. However, Se-related research is rarely reported on peony, as a new oil plant.

wild *Paeonia ostii* T. Hong et J. X. Zhang is a rare species of peony and the one of the most famous medicines in China, with high seeding rate and seed oil content. Feng Dan is a cultivar of *P. ostii*, which is mainly distributed in the area of Fenghuang Mountain and Nanling Western Hills in Tongling, Anhui Province, where it came from (Hong and Pan 1999; Li et al. 2007). Feng Dan has been planted in a large area in China with strong growth adaptability and high seed yield (Li et al. 2015), In recent years, studies have focused on cultivation and extraction technology, oil accumulation, variety selection, and gene sequencing of Feng Dan (Wang and Staden 2002; Li et al. 2007; Qin et al. 2009; Jin et al. 2015; Li et al. 2015; Han et al. 2018). However, the effects of Se fertilizer nutrition on Se enrichment, photosynthesis, and physiological characteristics on Feng Dan have not been reported.

In this study, the effect of different foliar application concentrations of nano-Se solutions on Feng Dan photosynthetic characteristics, osmotic cell protection ability, activity of antioxidant system, and Se-enrichment effect on different organs were explored to provide a theoretical basis for the scientific production of Feng Dan. The aims of this study were (i) to study the effects of nano-Se on photosynthetic and physiological characteristics in *P. ostia*, (ii) investigate the Se content of *P. ostii*'Feng Dan' after the foliar application of different nano-Se concentrations, and (iii) determine the optimum foliar application concentration that could not only promote Feng Dan photosynthesis and physiological activity, but also increase its Se content, providing theoretical basis for the cultivation and management of the crop.

Materials And Methods

Site characteristics

The study was conducted in the experimental field of Heifeng Village, Taigu district, Jinzhong, Shanxi Province (112°64'E, 37°34'N), located in the east margin of the Loess Plateau in the west of North China. The area is characterized by a temperate, semi-arid continental, and monsoonal climate, with an average annual temperature of 8–10°C. The mean temperature in August is 27–29 °C, with minimum and maximum monthly temperatures of 9 °C and 38 °C. The average frost-free period is 175 d, with an average annual precipitation of 600 mm, most of which falls in summer, between June and September.

The study soil type is carbonate brown soil, pH value ranges from 6.2 to 8.1, with average organic matter, total nitrogen, and available phosphorus content of 17.45, 0.86 and 18.37 g·kg⁻¹, respectively, available potassium and total Se content of 196.88 and 0.27 mg·kg⁻¹, belonging to the Se-deficient area.

Experimental treatments

The tested materials were 5-year-old 'Feng Dan' with strong and consistent growth, and the planting density was 45 000 plants·hm⁻². Nano-Se fertilizer was provided by Shanxi University and its particle size was 91.28-531.2nm. Se foliar application was performed at five experimental treatments levels, i.e. 0, 1.50, 3.75, 6.00 and 8.25g·hm⁻² (CK, S1, S2, S3 and S4, respectively) by drone. The experiment had a completely random block design and three replications.

Nano-Se foliar application was carried out for the first time at the end of the flowering stage of 'Feng Dan' in mid-June 2018 and 2019 which is the early stage of kernel formation. The spraying interval was 15 d, and application was supplemented in case of rain.

Parameter measurement

From the middle to the end of August, 2018 and 2019, the photosynthetic parameters of 'Feng Dan' leaves under different nano-Se foliar application treatments were measured using LI-6400 (Li-COR, USA). In this study, photosynthetic parameters included net photosynthetic rate, transpiration rate, intercellular CO₂ concentration, and stomatal conductance.

Leaf samples were collected at 9:00 to 10:00. Healthy leaves were sampled in the middle and upper part of the plant, washed with clean water, and dried to determine chlorophyll content and other physiological indices. Chlorophyll content was determined by the 80% acetone extraction method (Pirzad et al. 2011), soluble protein, soluble sugar, and proline content were determined by G-250 Coomassie brilliant blue, anthrone colorimetry, and ninhydrin colorimetry method (Drabik et al. 2016; Sinay and Kruwal 2014, KOÇ et al. 2010), respectively. Superoxide dismutase (SOD), peroxidase activity (POD), and malondialdehyde (MDA) content were determined by NBT illumination, Guaiacol assay, and thiobarbituric acid method (Xue et al. 2001; Cakmak and Marschner 1992; Hu et al. 2013), respectively.

Different organ samples such as the root, stem, leaves, testa, and kernel, were collected for Se content determination at the maturity stage of Feng Dan seeds. The samples were washed and dried in an oven at 80 °C for 24 h, and then crushed into powder. Then, Se content was determined by atomic fluorescence spectrometry.

Data analysis

All data were statistically analyzed using SPSS 12.0 software, and the mean values of each treatment group were subjected to multiple comparisons analysis using least significant difference (LSD) test and a significance level of $p < 0.05$.

Results

Effects of Se on the photosynthetic parameters and chlorophyll content of Feng Dan

Diurnal variations in photosynthetic characteristics of Feng Dan leaves under different Se foliar application were plotted (Fig. 1), and compared through LSD test (Table 1), and their chlorophyll content was compared with ANOVA and LSD test (Fig. 2).

Table 1
Effect of Se application on photosynthetic characteristics of Feng Dan

Treatment	Net photosynthetic rate $/\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$		Transpiration rate $/\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$		Internal carbon dioxide concentration $/\mu\text{mol CO}_2\cdot\text{mol}^{-1}$		Stomatal conductance $/\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	
CK	8.47±0.55	a	2.18±0.09	a	171.38±7.35	a	0.14±0.02	a
S1	11.48±0.67	bc	2.82±0.13	b	211.94±11.82	b	0.16±0.02	ab
S2	11.71±0.73	bc	2.94±0.17	bc	196.94±8.63	ab	0.16±0.03	ab
S3	12.26±1.03	c	3.36±0.21	c	214.92±11.42	b	0.21±0.02	b
S4	9.74±0.73	ab	2.96±0.18	bc	191.99±6.73	ab	0.17±0.02	ab
F	4.320		6.829		3.448		1.599	
P	0.003		<0.001		0.012		0.182	

The data in the table are mean value \pm standard error, and lowercase letters indicate the significant difference between the treatments based on the LSD-test ($p < 0.05$).

According to Fig. 1a, the net photosynthetic rate of Feng Dan leaves under Se foliar application treatments was higher than that in CK, and its diurnal variation trend was generally a "bimodal" curve, with the first peak value at 10:00, when the net photosynthetic rate of reached the highest value, an obvious photosynthetic midday depression at 14:00, and a second relatively smaller peak at 16:00. The

net photosynthetic rate of Feng Dan leaves under Se foliar application treatments was higher than that of CK (Table 1), and significantly different between S3, S2 and S1 treatments, and CK ($p < 0.05$). According to daily mean value of net photosynthetic rate, treatments were ordered as S3 > S2 > S1 > S4 > CK.

The diurnal transpiration rate variation of Feng Dan leaves under Se foliar application treatments was similar to a "unimodal" curve (Fig. 1b), with transpiration rate rising from 8:00, peaking at 12:00, and then falling rapidly, while that of CK leaves reached its peak value at 10:00, which was significantly lower than that of treatments, S2, S3, and S4 ($p < 0.05$). The transpiration rate of Feng Dan leaves after Se foliar application was significantly higher than that of CK ($p < 0.05$, Table 1), and according to daily average transpiration rate, treatments were ordered as S3 > S2 > S4 > S1 > CK.

The diurnal variation of intercellular CO₂ concentration in leaves of Feng Dan generally showed a 'U' shaped curve. With the increase of environmental temperature from 8:00, the intercellular CO₂ concentration decreased, and were maintained at a low level from 10:00 to 16:00 (Fig. 1c). At 16:00, the intercellular CO₂ concentration under Se treatment was significantly higher than that of CK ($p < 0.05$). The intercellular CO₂ concentration of Feng Dan leaves under Se foliar application were higher than that of CK, with statistical significance for S1 and S3 treatment ($p < 0.05$, Table 1). According to the daily intercellular CO₂ concentration mean value, treatments were ordered as S3 > S1 > S2 > S4 > CK.

The diurnal variation of stomatal conductance in Feng Dan leaves initially increased, then decreased, and finally increased (Fig. 1d). The stomatal conductance of Feng Dan under Se foliar application was significantly higher than that of CK from 8:00 to 10:00. At 10:00, the stomatal conductance of Feng Dan reached its peak value, and then decreased with increasing environmental temperature. During the time period from 12:00 to 16:00, the values were maintained at a low level under different Se treatments, and then increased. At 10:00, stomatal conductance of leaves under Se treatments was significantly higher than that of CK ($p < 0.05$), and those in S2 and S3 treatments were significantly higher than those under S1 and S4 ($p < 0.05$). The stomatal conductance of Feng Dan leaves under Se foliar application was higher than that of CK, being significantly different between S3 and CK ($p < 0.05$, Table 1). According to mean stomatal conductance, treatments were ordered as S3 > S4 > S2 > S1 > CK.

Figure 2 showed that foliar Se application increased the chlorophyll content of Feng Dan leaves. Compared with that of CK, chlorophyll content increased by 23.26%, 9.30%, 29.07%, and 13.95% under treatments S1–S4, respectively. Among them, the chlorophyll content in S3 was the highest, and those under S3 and S1 were significantly higher than that of CK ($p < 0.05$).

Effects of Se on Feng Dan physiological parameters

The soluble protein content, soluble sugar content, proline content, SOD and POD activity, and MDA content of Feng Dan leaves were compared using ANOVA and LSD test among different nano-Se foliar application (Fig. 3).

Se foliar application improved the soluble protein, soluble sugar, and proline content of Feng Dan leaves (Fig. 3a-c). Compared with those in CK, soluble protein content increased by 15.48%, 9.68%, 21.29%, and 33.55%, soluble sugar content increased by 39.17%, 35.30%, 41.21%, and 57.48%, and proline content increased by 14.38%, 25.86%, 24.71%, and 24.14% under S1-S4 treatment, respectively. Among them, the soluble protein content under S4 treatment was significantly higher than that of CK ($p < 0.05$). The soluble sugar content under Se treatment was significantly higher than in CK ($p < 0.05$), and treatment S4 had the highest soluble sugar content. Meanwhile, the proline content of under treatment S2 was significantly higher than that of CK ($p < 0.05$).

Se foliar application increased SOD and POD activities in Feng Dan leaves, and significantly reduced MDA content (Fig. 3d-f). Compared with those in CK, SOD activity increased by 8.17%, 21.37%, 12.59%, and 12.97%, POD activity increased by 21.21%, 31.14%, 56.85%, and 34.46%, and MDA content decreased by 32.26%, 33.40%, 33.52%, and 38.71%, in Feng Dan leaves under treatments S1-S4, respectively. Among them, both SOD and POD activities under treatments S2-S4 were significantly higher than those of CK ($p < 0.05$), S2 treatment had the highest SOD activity, S3 treatment had the highest POD activity, and MDA content under treatments S1-S4 was significantly lower than that of CK ($p < 0.05$), while treatment S4 had the lowest MDA content.

Effects of Se on the Se content indifferent organs of Feng Dan

Se contents in the root, stem, leaf, testa, and kernel of Feng Dan under different Se treatments were compared by ANOVA and LSD test (Fig. 4).

Se content in the root, stem, leaves, testa, and kernel of Feng Dan increased with the concentration of Se foliar application (Fig. 4).

In the root, Se content was 1.12, 1.16, 1.22, and 1.24 times higher than that of the control under S1-S4 treatment, respectively, but there was no significant difference in Se content between treatments ($p > 0.05$). Se content in root was $0.01-0.02\text{mg}\cdot\text{kg}^{-1}$.

In the stem, Se content was within the range of $0.01-0.35\text{mg}\cdot\text{kg}^{-1}$, and Se foliar application significantly increased the Se content of Feng Dan ($p < 0.05$). Se content in the stem under S2-S4 treatment was significantly higher than that under treatment S1 and CK ($p < 0.05$), and that under S1-S4 treatment was 6.00, 8.89, 8.88, and 10.01 times that of the control, respectively.

In the leaves, Se content ranged from 0.05 to $2.50\text{mg}\cdot\text{kg}^{-1}$, and it was significantly higher under treatment S2-S4 than under S1 and CK ($p < 0.05$), being 1.44, 14.90, 19.63, and 22.07 times that of the control under treatment S1-S4, respectively.

In the testa, Se content was $0.005-2.500\text{mg}\cdot\text{kg}^{-1}$, and was significantly increased by foliar application compared to that of CK ($p < 0.05$), being significantly higher in treatment S3 and S4 than under S1 and S2

($p < 0.05$); Se content in testa was 12.71, 23.09, 253.80, and 255.41 times that of the control under S1–S4, respectively.

In the kernel, Se content was $0.005\text{--}1.200\text{mg}\cdot\text{kg}^{-1}$, being significantly higher under treatment S1–S4 than that in the control group ($p < 0.05$). Se content in the kernel under the treatment S3 and S4 was significantly higher than that under S1 and S2 ($p < 0.05$), being 17.34, 21.64, 58.14, and 61.93 times that of CK under S1–S4, respectively.

Discussion

Photosynthetic characteristics and chlorophyll content

In this study, both net photosynthetic rate and stomatal conductance of 'Feng Dan' leaves peaked at 10:00, with transpiration rate also increasing significantly. Then, net photosynthetic rate gradually decreased with increasing temperature, reaching an obvious photosynthetic midday depression at 14:00, which indicated that high temperature, high light, and low humidity in summer lead to high leaf surface temperature and water metabolism disorder, which inhibits the activity of enzymes involved in the photosynthetic process. Meanwhile, leaves stomatal closure and intercellular CO_2 concentration decreased rapidly, decreasing net photosynthetic rate, which was consistent with previous research results (Zhang Z-H et al. 2014).

Se foliar application improved the net photosynthetic rate, transpiration rate, and stomatal conductance of leaves and had a significant effect on plant photosynthesis. Even in the period of high temperature and high light from 12:00 to 16:00, Feng Dan net photosynthetic and transpiration rates were still relatively high under Se treatment. At 16:00, Feng Dan net photosynthetic rate showed a small second peak under treatment S1, S2, and S3, while transpiration and net photosynthetic rate of CK were at a lower level, which showed that within a certain concentration range, appropriate Se supplementation can increase Feng Dan leaves stomatal conductance, improve photosynthetic and transpiration rate, and thus effectively improve growth and development of vegetative organs. Increasing intercellular CO_2 concentration will affect the net photosynthetic rate of plants. After Se treatments, daily mean intercellular CO_2 concentration of Feng Dan leaves was significantly higher than that of CK, maybe owing to Se application increasing the size of intercellular spaces in the mesophyll, resulting in the increase of leaf thickness and dry mass. This indicated that Se improved the net photosynthetic rate of leaves by increasing intercellular CO_2 concentration, which is consistent with the results of Alves on tomatoes (Alves et al. 2020).

Chlorophyll content is closely related to photosynthesis, and the increase in chlorophyll helps plants to increase light energy capture. Padmaja believed that Se could adjust the interaction of sulfhydryl-containing enzymes 5-aminolevulinic acid dehydratase and porphobilinogen deaminase, and then regulate the chlorophyll synthesis (Padmaja et al. 1990). Moreover, Pezzarossa found that Se also inhibited chlorophyll degradation in a study of hydroponic tomatoes (2014). In this study, Se foliar

application significantly increased the chlorophyll content of Feng Dan leaves, and chlorophyll content increased with increasing Se concentration, which was consistent with the previous research results (Moldovan et al. 2009; Sharma et al. 2014; Naim et al. 2017). It was proved that under natural conditions, in the summer high temperature season, high light intensity and long light duration would inhibit chlorophyll synthesis to some extent (Aarti et al. 2007; Sun et al. 2008), and appropriately applying Se could promote the increase of chlorophyll content and net photosynthetic rate.

Physiological and biochemical index

Soluble protein, soluble sugar, and proline are important nutrient and osmotic regulating substances in plants. In this study, Se foliar application significantly increased the soluble protein and soluble sugar content of Feng Dan, both increasing with increasing Se concentration, which was similar to the results of Turakainen's study (2004). In plants, soluble protein has strong water retention and may act as a protective agent for dehydration; therefore, its content increase in dry environments can play a positive and effective role in the protection of Feng Dan. Soluble proteins contain various enzymes that regulate metabolism, e.g. RuBP carboxylase accounts for more than 50% of the soluble protein content (Kung and Holder 1984), it plays an important role in photosynthesis, and its content increase may also enable Feng Dan to maintain a high photosynthetic rate. Changes in soluble sugar content are an important indicator of carbohydrate metabolism in plants, and can also reflect the carbohydrates synthesis and transport, which could reflect the environmental influence the plants growth and development. The increase in soluble sugar content can be considered as an adaptive defense response of plants by regulating specific enzyme metabolism or osmotic balance (Seppänen et al. 2003; Kuznetsov et al. 2003). Proline can promote protein hydration in the plant, increase the protein gel water area and soluble protein, participate in chlorophyll synthesis, reduce cell osmotic potential to maintain pressure, stabilize macromolecular material, and maintain the normal function of the cell membrane. Therefore, the increase in proline content can enhance plant resistance to adversity (Szabados and Saviouré 2010). In this study, Se application significantly increased the proline content of Feng Dan, and enhanced their ability to resist adversity, which was consistent with the research results of Khan et al. (Khan et al. 2015).

In plants, as important protective enzymes, SOD and POD are considered free radical scavengers, and changes in their activity reflect the metabolism of free radicals in organisms to a certain extent. MDA is a highly active lipid peroxide, which affects the fluidity of cytomembrane and the binding force of proteins on the membrane with enzymes. It is an important parameter to reflect the potential antioxidant capacity of organisms, and an important index of plant aging and resistance physiology. Thus, to assess the extent of damage to the plasma membrane system peroxidation and resistance of plants, the degree of membrane lipid peroxidation can be determined by measuring MDA content (La et al. 2011; Ebrahimi et al. 2016). In this study, compared with those in CK, Se treatment significantly increased SOD and POD activity of Feng Dan, and significantly reduced MDA content, maybe owing to Se directly participating in the enzymatic or non-enzymatic antioxidant process of organisms as a component of glutathione peroxidase (GSH-Px) system. In Feng Dan, Se improves the GSH-Px activity and promotes the toxic peroxide reduction into non-toxic hydroxyl compounds. Meanwhile, it promotes H_2O_2 decomposition,

improves the cell antioxidant ability and membrane stability, balance of free radicals in plants, and reduces cell membrane permeability, protecting the cell membrane structure and function from interference and damage of oxide (Hartikainen et al. 2000). Results were consistent with those of Xue (Xue et al. 2001) and Alyemeni (Alyemeni et al. 2018).

It can be concluded that, in the summer, high temperature and high light conditions may induce plants to produce a large number of reactive oxygen species (ROS) through various pathways, and the scavenging capacity of ROS decreased, leading to accumulation of active oxygen free radicals, which can cause damage to cells and affect the growth and biomass accumulation of Feng Dan. However, appropriate Se application can reduce the environmental damage on the plant cell, retarding cell senescence.

Se content in different organs of Se enrichment Feng Dan

Se absorption by plants is similar to that of other nutrient elements. Within a certain range, the absorption of elements in edible parts of plants increases with the application dosage, which is the theoretical basis of applying exogenous Se to Se-enrich plants (Liu et al. 2016; Hou et al. 2018). Se absorption varies among plant species; the growth of non-Se-enriched plants will be inhibited in high-Se environment, even suffering Se-poisoning. However, Se-enriched plants in the same environment do not suffer from Se-poisoning, and can grow normally even at Se concentrations exceeding $400 \text{ mg}\cdot\text{kg}^{-1}$ (Shrift 1969). In this study, compared with those in CK, Se foliar application significantly increased Se content in various organs such as the root, stems, leaves, testa, and kernel of Feng Dan, with increasing Se content in various organs of Feng Dan with increasing Se concentration, which was the same conclusion as that of Zhang's study on rice (Zhang M et al. 2014). After nano-Se is absorbed by the leaves, nano-Se may be transported to various organs within a certain period of time and transformed into organic Se, or converted into organic Se in the leaves and transported to other organs, and most Se eventually accumulate in this form. In this study, the highest Se concentration treatment had no significant toxic effect on Feng Dan, which implies that Feng Dan has a strong Se-enrichment ability.

Meanwhile, Se movement and distribution in plants also depend on the location of Se absorption by plants. For example, with soil Se application, most Se stays in the root, while only a small portion is transported to the stem and leaves (Zhang M et al. 2014), while foliar application with selenite significantly increased Se content in the leaves (Hu et al. 2003). In this study, under relatively high concentrations treatments S3 and S4, Se content was the highest in the testa, being significantly higher than that in other organs ($p < 0.05$), followed by that in leaves, kernel, stems, and roots. Therefore, it can be inferred that after Se foliar application, plant leaves would absorb and transform Se first, which then was continuously transported to organs such as the testa and kernel together with other nutrients during the organ forming stage. Finally, most Se accumulated in the product organs as organic Se, which conforms to the general transfer route of nutrient elements in plants after foliar application (Boynton 1954; Germ et al. 2007).

In this study, the collection and determination of Se content of different organs, such as Feng Dan roots, were performed only for seeds in the mature stage. Thus, the dynamic monitoring of Se content in different organs at different stages of seed growth, such as the early seed formation, rapid growth, and inclusions enrichment stages, would be an area of valuable future research. Furthermore, the application concentration of nano-Se was 1.50- 8.25 g· hm⁻² in this study, the highest concentration that significantly inhibit the photosynthesis, physiological properties and Se enrichment of Feng Dan was not be detected, therefore, the subsequent experiments can be carried out by increasing the spraying concentration of nano-Se on the basis of this research for the better Se enrichment effect of Feng Dan. On the other hand, leaves and testae had the highest Se content in this study (Fig. 4), therefore, determining how to promote leaf Se conversion and increase Se content in the kernel is of great significance for production practices and needs further study. In production practice, Feng Dan was introduced as a drought-resistant plant in the medium-altitude, semi-arid area, and the irrigation conditions in the mountainous planting areas were lacking, as the normal growth was only dependent on natural rainfall, Se soil fertilization was difficult to implement, thus the comparative experiments between soil fertilizer and foliar spray application and their interactions could not be conducted, which was the limitation of this study.

Conclusions

In this study, Se foliar application improved the photosynthetic capacity of Feng Dan leaves, and to a certain extent, promoted osmotic regulation and reactive oxygen radical scavenging, delayed the senescence of photosynthetic organs, effectively improved the growth and development of vegetative organs, and promoted the enrichment of Se content in Feng Dan. Considering the photosynthetic characteristic index, chlorophyll content, various physiological and biochemical indices, and Se content accumulation of Feng Dan, Se application dosage of 6.00 and 8.25g· hm⁻² (treatment S3 and S4) provided a better Se-biofortification effect. These results have practical significance for the commercial production of Feng Dan.

Abbreviations

CK: Control check (control group with no Selenium fertilizer applied in the experimental field)

Feng Dan: Cultivar of *Paeonia ostii* T. Hong et J. X. Zhang

MDA: Malondialdehyde

nano-Se: Nanoparticles of elemental Selenium

P. ostia: *Paeonia ostii* T. Hong et J. X. Zhang

POD: Peroxidase activity

S1-S4: Se foliar application was performed at five experimental treatments levels (experimental group with 1.50, 3.75, 6.00 and 8.25g·hm⁻² applied in the experimental field, respectively)

Se: Selenium

SOD: Superoxide dismutase

Declarations

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Contributions

JHL and YBN conceived the idea and designed the experiments, HW, CLZ, MN, DC, JXC, and SJW executed the experiments and collected the data. HW, CLZ and JHL drafted the manuscript which all authors agreed. HW and CLZ contributed equally to this work.

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Ethics declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

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

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Figures

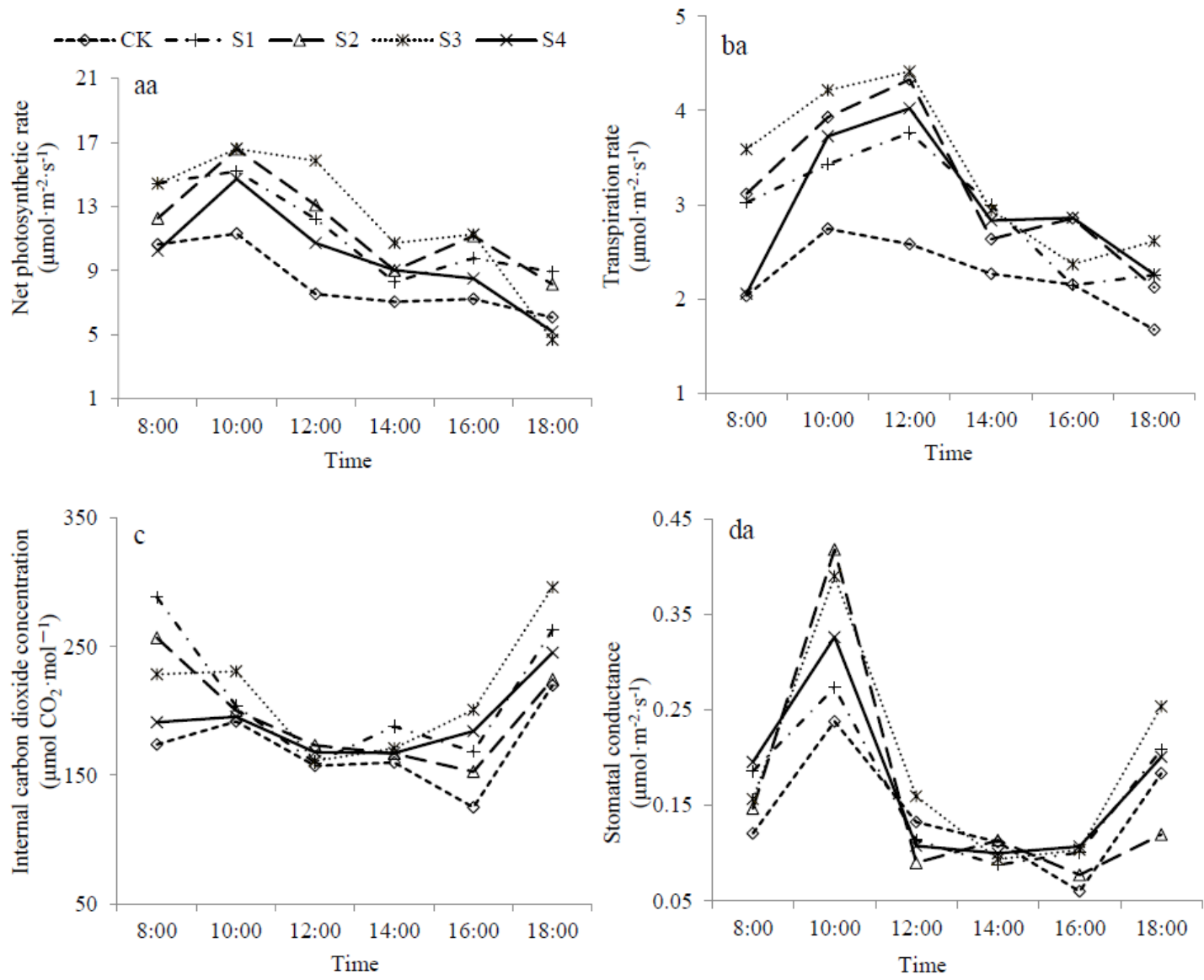


Figure 1

Diurnal photosynthetic parameters variation of Feng Dan leaves under different Se applications

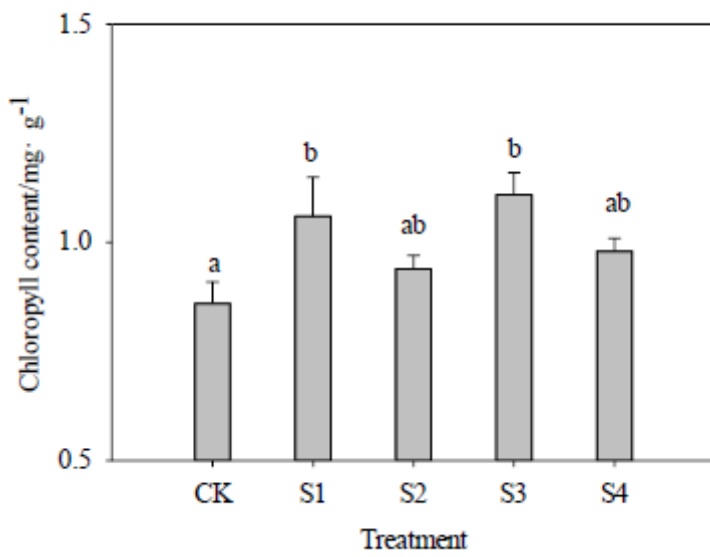


Figure 2

Effect of Se application on Feng Dan chlorophyll content. The bars indicate the standard error of the mean, and lowercase letters indicate the significant difference between the treatments ($p < 0.05$), the same as the following Figs.

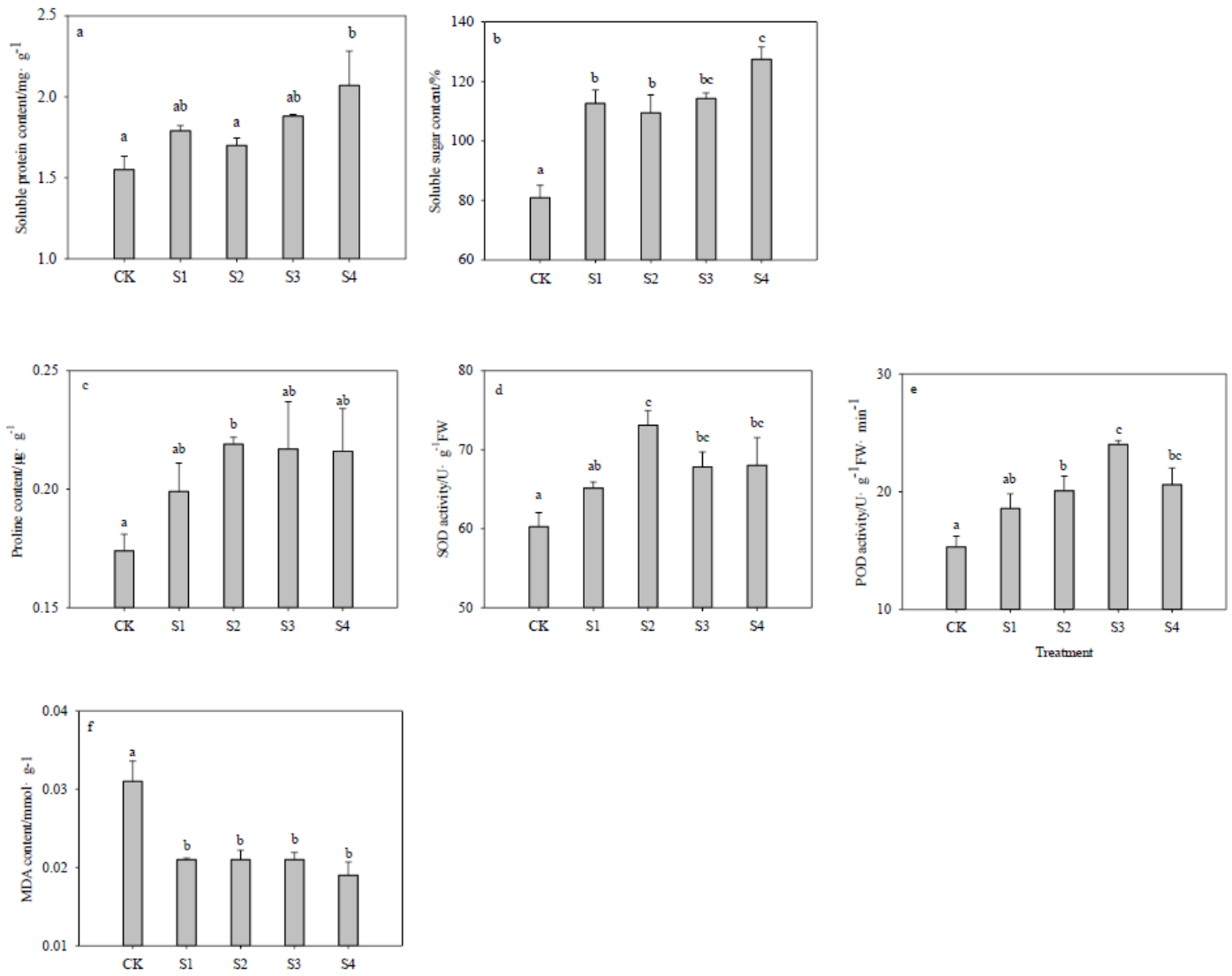


Figure 3

Effect of Se application on Feng Dan physiological parameters

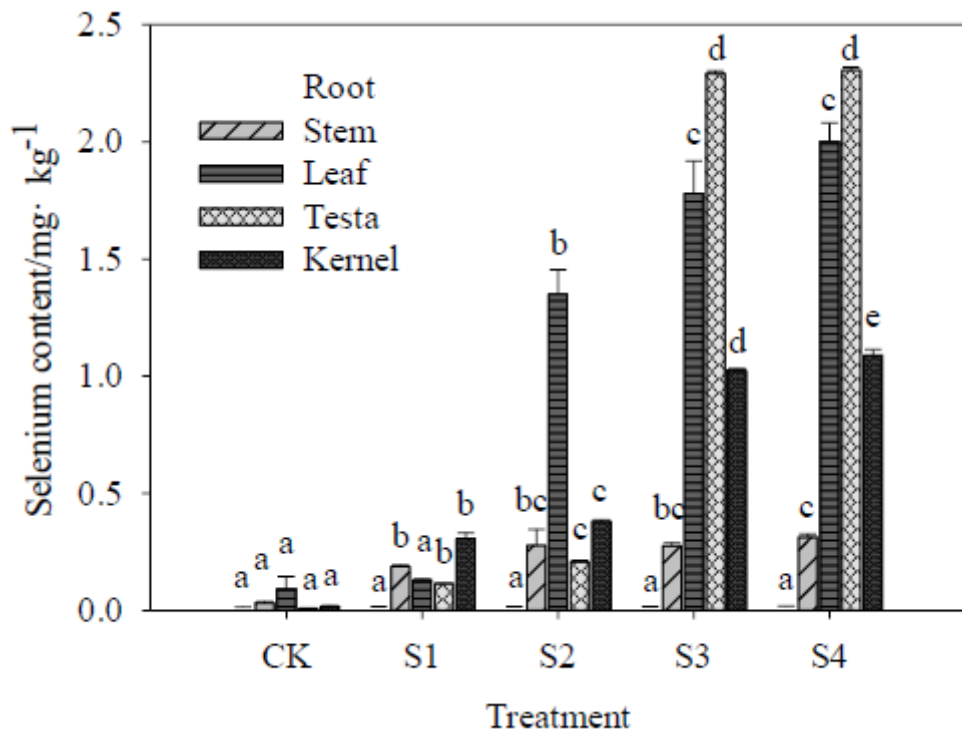


Figure 4

Effect of Se foliar application on Se content in different organs of Feng Dan