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The effect of selenium biological enhancement on cucumber growth and powdery mildew control under greenhouse conditions

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In this study, we clarified the effects of selenium fertilizer application on the growth of cucumber, explored the impact of exogenous selenium on the control of powdery mildew and its pathogens. Selenium-enriched ionic fertilizer and cucumber were selected as the test materials. A one-way, randomized design was adopted to set up four selenium solutions with concentrations of 0 mg/L, 3 mg/L, 6 mg/L, and 12 mg/L to investigate the effects of biofortification with different amounts of selenium concentrations on the growth of cucumber and the occurrence of powdery mildew in greenhouses. A leaf inoculation test was conducted by setting up three groups of treatments: water and fungicide (seedling fungicide) as the control groups, and 6 mg/L selenium-enriched ionic fertilizer as the treatment group. These treatments were selected to investigate the effect of selenium on the control of powdery mildew in greenhouse-grown cucumbers as well as the effect of selenium on the germination of powdery mildew pathogen spores. The results demonstrated that both the 6 mg/L and 12 mg/L selenium-enriched ionic fertilizer solutions had growth-promoting and yield-increasing effects on cucumber and that the difference in the growth-promoting effects of these treatments was insignificant. The 3 mg/L, 6 mg/L, and 12 mg/L treatments improved the nutritional quality of cucumber fruits, reducing the total acidity of the fruits and increasing the content of soluble proteins in the fruits; the 6 mg/L and 12 mg/L treatments increased the content of selenium in the fruits, and the difference in selenium enrichment between the two treatments was not significant. The 6 mg/L selenium solution had the greatest effectiveness in alleviating leaf photosynthesis inhibition by the powdery mildew fungus, in mitigating powdery mildew damage and in reducing the plant disease index. The results of the leaf inoculation trials revealed that at a concentration of 6 mg/L, the effects of the selenium-enriched ionic fertilizer were comparable to those of pharmaceutical treatments for powdery mildew disease. The activities of superoxide dismutase and peroxidase in all treatments tended to increase but then decreased within 72 h after pathogen inoculation. Nevertheless, selenium fertilizer treatment inhibited the germination of powdery mildew pathogen conidia, the number of conidial germination shoot tubes and mycelium formation.

Selenium is a nonmetallic trace element that has been proven to be essential for maintaining vital life activities signs in humans and animals[1–3], and is a key elements for plant growth[4]. Selenium deficiency in the body can result in various diseases, such as cardiovascular disease, Keshan disease and Kashin–Beck syndrome (macroglossia)[5]. Selenium deficiency is prevalent in China, with 51% of the people in the country experiencing selenium deficiency or showing a low selenium status[6]. Numerous studies have demonstrated that plant-derived foods are the primary source of selenium to supplement in diet of humans[1,7]. Currently, selenium biofortification has become a hotspot for research in the fields of plant science, agronomy, and food science[8], and selenium biofortification of plants is achieved mainly through agronomic measures (e.g., soil or foliar selenium fertilizer application) as well as modern molecular biotechnological approaches (breeding)[9,10]. Currently, foliar spraying of Se fertilizer is the most extensively used method of Se application[11], and studies have shown that the soil application of Se reduces the timely administration and utilization rate of Se. In comparison, the foliar spraying of selenium results in more robust targeting and high efficiency[12,13]. In addition, selenium biofortification is the most common and effective means of increasing plant selenium content, and the application of selenium

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fertilizers to increase crop selenium content has more reliable health benefits and results in greater resource use efficiency than the use of selenium supplements[14]. In previous studies on plant selenium biofortification, selenium fertilizer spraying promoted the growth of maize, increased selenium accumulation in maize kernels[15], and improved the development of pear tree leaves[16]. Foliar selenium nutrient biofortification positively affects the high-quality yield increase of lettuce, potato, and rye oats[17–19]. Exogenous selenium treatment during apple fruit development can effectively enhance antioxidant capacity and improve apple quality[20]; selenium fertilizer application can also promote antagonistic reactions or nutrient fixation after plant fertilization and increase selenium utilization[11,21].

Cucumber (*Cucumis sativus* L.) is one of the most important vegetable crops in China. Powdery mildew is the most common fungal disease in the production process of cucumber in greenhouses, it spreads very fast and mainly harms the leaves, forming white filaments on the surface of the leaves, inhibiting plant photosynthesis and resulting in a decrease in yield and related economic benefits[22,23]. To date, the application of selenium fertilizer in cucumber production has rarely been reported. The effect of exogenous selenium fertilizer on the growth of cucumber seedlings and antioxidant indexes were studied, and the results confirmed that the spraying of selenium fertilizer during production produced vigorous cucumber seedlings[24]; In another study on the effect of selenium fertilizer on cucumber seedling growth and physiological characteristics, selenium foliar fertilizers promoted the development of cucumber seedlings, and improved the quality of the seedlings[25]. A few studies have been conducted on the prevention and control of cucumber diseases by selenium fertilizers under disease stress; most of these studies have been focused on heavy metals or other stressors, and it has been reported that selenium fertilizers can effectively alleviate the effects of environmental stressors on cucumber or other vegetables[26–29].

For this reason, selenium-enriched ionic fertilizer was taken as the test material, cucumber as the test crop, and a combination of lab test as well as leaf inoculation test were done to study the effect of selenium biofortification on the growth of cucumber and the occurrence of powdery mildew, to provide the theoretical basis for the application of selenium fertilizer on cucumber grown in controlled facilities and in the field production.

Materials and methods

Test materials

The cucumber variety "Dongnong 808," was sourced from the College of Horticulture and Landscape Architecture of Northeast Agricultural University. Selenium-enriched ionic fertilizer containing 6 g/L selenium, produced by Harbin Yao Yuan Modern Agricultural Science and Technology Service Co., China, was used in this study.

Experimental design

Effects of biofortification with different selenium concentrations on cucumber growth and powdery mildew incidence

This experiment was conducted in a cucumber greenhouse at the Changling Lake Experimental Base of Northeast Agricultural University (45° 48′ N, 126° 40′ E). The variety Dongnong "808" was planted on September 10, 2023, in the cucumber greenhouse, with an indoor ridge length of 3 m and a width of 0.5 m. Selenium-enriched ionic fertilizer solutions of four concentrations were used: 0 mg/L (CK), 3 mg/L, 6 mg/L, and 12 mg/L (concentrations in terms of the selenium content). Four treatments were set up according to the selenium fertilizer concentration for testing, with 22 cucumbers planted in each row, two rows of cucumbers in each treatment, and three replications. After planting and seedling growth, we carried out routine water, fertilization and foliar selenium spray treatment during the early growth, early flowering, and early fruiting stages, totaling three rounds of Se spraying, with a dosage of 1 L for each row. The plant growth potential was determined after 14 days of treatment, and the cucumber plant height, stem thickness, chlorophyll concentration, fruit nutritional quality, yield and powdery mildew incidence were measured.

Effects of selenium biofortification on cucumber powdery mildew disease and its pathogens

A leaf inoculation test was conducted to investigate the efficacy of selenium biofortification on the control of powdery mildew in cucumber and to observe the microstructure of the pathogen. These studies were conducted from November to December 2023 in the greenhouse of the Physiology and Ecology Subject Group, College of Horticulture and Landscape Architecture, Northeastern University. The test included water, seedling fungicide (11 mg/L), and 6 mg/L selenium-enriched ionic fertilizer (concentrations in terms of selenium content).

(1) Effect on the growth of cucumber seedlings

Four treatments were set up: water, seedling fungicide (11 mg/L), and 6 mg/L selenium-enriched ionic fertilizer, corresponding to CK, MJ, and XX, respectively, and each treatment was repeated three times, with each replicate involving nine seedlings. After the seedlings reached the two leaves and one heart stage, selenium fertilizer was sprayed every 7 days, with a dosage of 10 mL for each plant, for a total of three spraying event, and the growth indices of the seedlings were measured.

(2) Effect of the treatments on powdery mildew in cucumber

Four treatments were set up as described in (1), treatment was started 7 days after inoculation, the disease index was determined before treatment, and the plants were sprayed every 7 days with a dosage of 10 mL for each plant, for a total of three times. The disease index was measured 7 days after the treatment was stopped, and the effect of the treatment was determined.

(3) Effect on the treatments on powdery mildew prevention in cucumber

Four treatments were set up as described in (1); each treatment was repeated three times, with nine seedlings in each replicate. After 24 h of treatment, inoculation was performed, and the selenium solution was sprayed once every 7 days, with a dosage of 10 mL for each plant. Selenium was sprayed twice in total. The disease index was calculated by determining the disease index 7 days after the treatment was stopped.

(5) Changes in enzyme activity during cucumber powdery mildew infection

Four treatments were set up, as in (1). Nine replicates were performed. Each plant was dosed with 10 mL solution, and inoculation was performed 24 h after treatment. Under infection by the powdery mildew pathogen, samples were taken at 0 h, 6 h, 12 h, 24 h, 48 h, and 72 h to measure changes in the activities of relevant enzymes in the leaves during different periods.

(6) Microscopic observation of the inhibition of powdery mildew fungal conidia

Four treatments were set up as described in (1); inoculation was performed 24 h after treatment, three plants were taken from each treatment, three leaf discs were collected per plant, and nine replicates were performed. Leaf discs were punched from cucumber leaves at 24 h, 48 h, 72 h, 96 h and 120 h after inoculation with a 10 mm hole punch and stained with Taipan blue. The spore germination rate, number of shoot tubes at 24 h, and mycelium formation rate at 72 h were calculated.

Measurement methods

Vernier calipers were used to measure plant stem thickness (mm), metric rulers were used to measure plant height (cm), and electronic scales were used to measure yield (g). Inductively coupled plasma-mass spectrometry was employed to determine the selenium content; Abe's refractometer was used to measure soluble solids, and a saccharimeter was used to measure the total acidity and soluble solids content. SOD and POD enzyme activities were measured by a spectrophotometer. Taipan blue staining was performed to observe the spore germination and the number of bud tubes. A portable photosynthesis system (Li-6400, LI-COR, Lincoln, NE, USA) was used to determine the net photosynthetic rate (Pn), stomatal conductance (gs), intercellular CO_2 concentration (Ci), and transpiration rate (E)[15,17,18,24].

Powdery mildew grading standards: grade 0, no symptoms; grade 1, white powder micro-spotting, lesion area of less than 10% of the leaf area; grade 3, obvious lesions, thin spore piles, lesion area of 11–25% of the leaf area; grade 5, yellowing of the leaf blade occurs lesion area of 26% to less than 50% of the leaf area; grade 7, thick spore piles, heavier yellowing of the leaf blade lesion area of 51% to less than 75% of the leaf area; grade 9, leaf blade yellowing is severe or dry spot area is more than 75% of leaf area.

$$\text{Preventative effect } (\%) = (1 - \text{Treatment condition index/control condition index}) \times 100\%$$

$$\text{Treatment effect } (\%) = [1 - (\text{CK}_0 \text{ disease index} \times \text{Pt}_1 \text{ disease index}) / (\text{CK}_1 \text{ disease index} \times \text{Pt}_0 \text{ disease index})] \times 100\%$$

where CK_0 represents the disease index of the control before treatment; CK1 represents the disease index of the control after treatment; Pt0 represents the disease index of each treatment group before treatment; and Pt1 represents the disease index of each treatment group after treatment.

Data analysis

The raw data of the experiment were organized using Microsoft Excel 2019; ANOVA one-way analysis of variance (Tukey) was performed using IBM SPSS Statistics 25.0 ($P < 0.05$ was considered significant), and bar charts were produced using GraphPad Prism 9.0.

Results and analysis

Effects of biofortification with different selenium concentrations on cucumber growth and powdery mildew incidence

Effects of selenium at different concentrations on cucumber growth

Selenium at concentrations up to 6 mg/L promoted an increase in cucumber plant height (Fig. 1a). The plant height under the 6 mg/L treatment at the initial flowering stage was greater than that under the CK (0 mg/L) and 3 mg/L treatments by 23.53% and 22.43% ($P < 0.05$), respectively, and the differences between the plant heights under the 12 mg/L treatment and those under the CK and 3 mg/L treatments were not significant. At the early stage of fruiting, the plant height was greater in the 3 mg/L, 6 mg/L and 12 mg/L groups than in the CK group ($P < 0.05$), and the differences among the three groups were not significant. At the fruiting stage, the effect of the 6 mg/L selenium treatment was greater than that of CK by 19.16% ($P < 0.05$), and differences between the 6 mg/L treatment and the 3 mg/L and 12 mg/L treatments were negligible.

Selenium at concentrations of 6 mg/L and 12 mg/L promoted an increase in cucumber stem thickness (Fig. 1b). When the Se concentration exceeded 6 mg/L, the stem thickness of the plants no longer increased with increasing Se concentration. At the initial flowering stage, the stem thickness in the 6 mg/L and 12 mg/L treatments was greater than that in the CK treatment by 18.64% and 18.15% ($P < 0.05$), and the differences in stem thickness between the 3 mg/L treatment and the CK, 6 mg/L and 12 mg/L treatments were not significant. At the early stage of fruiting, the stem thickness in the 6 mg/L and 12 mg/L treatments was greater than that in the CK and 3 mg/L treatments ($P < 0.05$), which were 11.38% and 10.79% greater than that in the CK treatment and

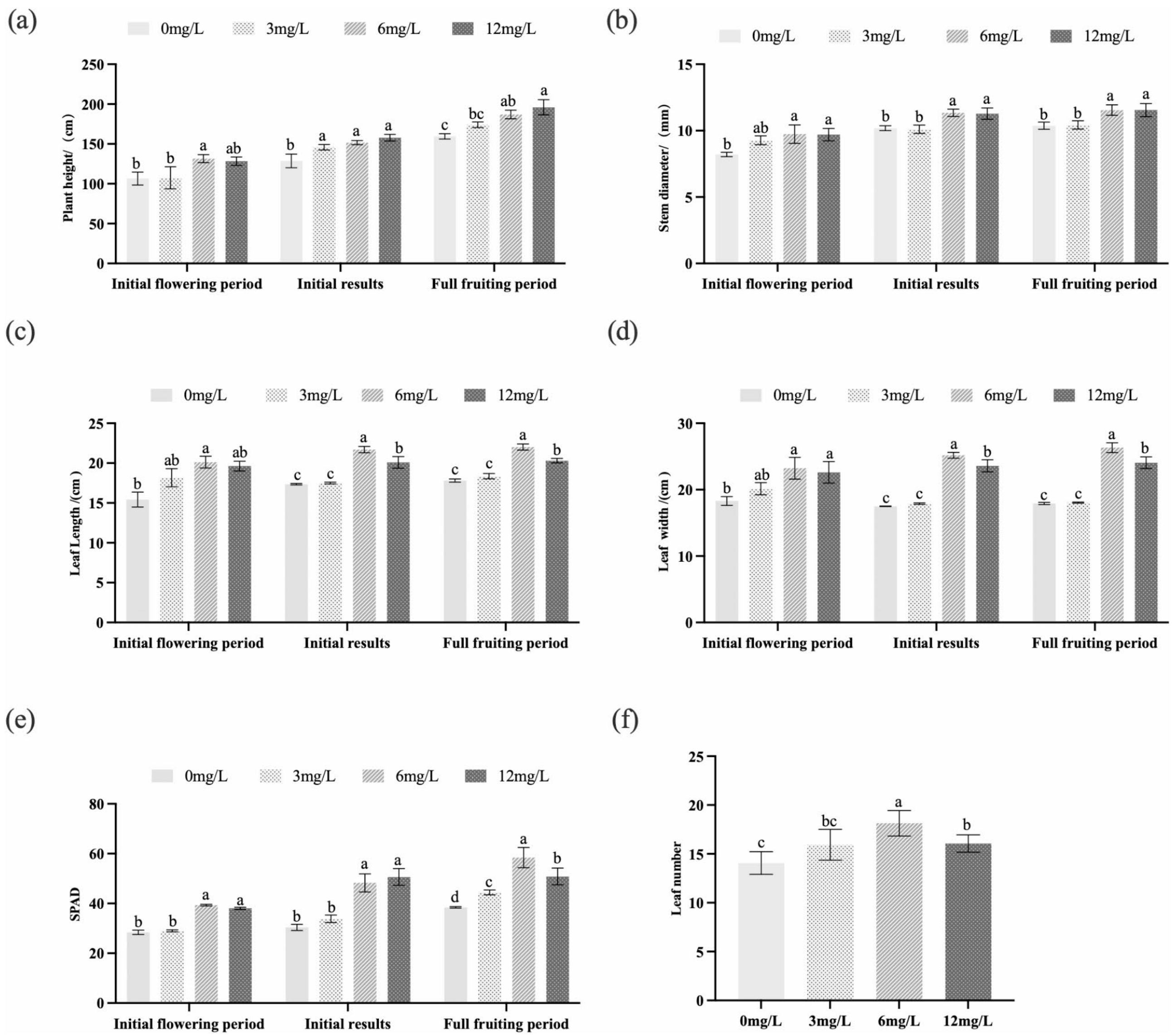

Fig. 1. Effect of biofortification with different selenium concentrations on cucumber growth (n = 30). *Note*: Lowercase letters indicate significant differences between treatments ($P<0.05$) (the same applies below). n is the total number of samples processed for each sampling (the same applies below).

12.27% and 11.67% greater than that in the 3 mg/L treatment, respectively. There was no significant difference between the CK and 3 mg/L treatments, and the difference was insignificant between the 6 mg/L and 12 mg/L treatments. At the fruiting stage, the plant height in the 6 mg/L and 12 mg/L Se treatments was greater than that in the CK and 3 mg/L Se treatments ($P<0.05$), at 11.38% and 11.38% greater than that in the CK treatment and 10.74% and 10.74% greater than that in the 3 mg/L Se, respectively. There were no significant differences between the CK and 3 mg/L Se treatment groups, and the differences were not significant.

The leaf width of cucumber tended to increase but then decreased with increasing Se concentration. In all three periods, the leaf width peaked under the 6 mg/L treatment, and the differences between the CK and 3 mg/L treatments were not significant (Fig. 1c). At the initial flowering stage, the leaf width under the 6 mg/L and 12 mg/L treatments was greater than that under the CK treatment ($P<0.05$) by 29.27% and 25.82%, respectively. In the early fruiting period, the leaf width in the 6 mg/L and 12 mg/L treatments was greater than that in the CK and 3 mg/L treatments ($P<0.05$), and was 43.89% and 34.86% greater than that in the CK treatment, respectively; the leaf width in the 6 mg/L treatment was greater than that in the 12 mg/L treatment ($P<0.05$) by 6.69%. During the fruiting period, the leaf width under the 6 mg/L and 12 mg/L treatments was greater than that under the CK treatment by 46.93% and 34.26%, respectively ($P<0.05$); the leaf width under the 6 mg/L treatment was greater than that under the 12 mg/L treatment by 9.43%.

The 6 mg/L selenium treatment had the greatest apparent effect on promoting cucumber leaf length, and the impact of selenium on increasing leaf length decreased at a concentration of 12 mg/L (Fig. 1d). At the initial flowering stage, the leaf length in the 6 mg/L treatment group was greater than that in the CK group ($P<0.05$) by

Treatments (mg/L)	Dry matter accumulation (g)	Selenium (mg kg^{-1})	Soluble protein (mg g^{-1})	Acidity%	Soluble solids%
0	2.77 ± 0.71b	0.0337 ± 0.006c	0.35 ± 0.0.009b	2.31 ± 0.23a	3.1 ± 0.16b
3	3.54 ± 0.52ab	0.0371 ± 0.002bc	0.37 ± 0.004a	2.04 ± 0.17b	3.11 ± 0.2b
6	4.46 ± 0.91a	0.0542 ± 0.006ab	0.38 ± 0.006a	1.49 ± 0.15c	3.32 ± 0.17a
12	4.61 ± 1.14a	0.0556 ± 0.010a	0.39 ± 0.001a	1.46 ± 0.16c	3.18 ± 0.07ab

Table 1. Effect of biofortification with different selenium concentrations on the nutritional quality of cucumber (n = 30). Lowercase letters indicate significant differences between treatments ($P < 0.05$) (the same applies below). n is the total number of samples processed for each sampling (the same applies below).

Treatments (mg/L)	Number of fruits per plant/root	Single fruit weight (g)	Single plant yield (g)
0	14.07 ± 0.23c	111.05 ± 8.53b	1562.11 ± 25.05b
3	15.13 ± 0.42bc	112.49 ± 8.79b	1702.39 ± 46.83b
6	17.6 ± 0.2a	126.26 ± 7.92a	2190.84 ± 24.9a
12	17 ± 1.39ab	125.04 ± 9a	2125.74 ± 173.37a

Table 2. Effect of biofortification with different selenium concentrations on cucumber yield (n = 30).

14.73%; the differences between the 3 mg/L treatment group and the CK, 6 mg/L and 12 mg/L treatment groups were not significant, and the differences between the 6 mg/L and 12 mg/L treatment groups were not significant. In the early stage of the study, the leaf length in the 6 mg/L and 12 mg/L treatments was greater than that in the CK and 3 mg/L treatments ($P < 0.05$), with increases of 25.01% and 15.85%, respectively, compared with that in the CK treatment, and increases of 23.94% and 14.86%, respectively, compared with that in the 3 mg/L treatment. The differences were not significant between the CK and 3 mg/L treatments. The leaf length in the 6 mg/L treatment was greater than that in the 12 mg/L treatment ($P < 0.05$) by 7.91%. During the fruiting period, the leaf length in the 6 mg/L and 12 mg/L treatments was greater than that in the CK and 3 mg/L treatments ($P < 0.05$), at 23.53% and 14.04% greater than that in the CK treatment and 19.53% and 10.62% greater than that in the 3 mg/L treatment, respectively, and the difference between the CK and 3 mg/L treatments was insignificant; leaf length in the 6 mg/L treatment was greater than that in the 12 mg/L treatment ($P < 0.05$) by 8.32%.

Treatment with Se-enriched ionic fertilizer with a Se concentration of 6 mg/L resulted in a peak in chlorophyll concentration at the fruiting stage (Fig. 1e). At the early flowering stage, the chlorophyll concentrations in the 6 mg/L and 12 mg/L treatments were greater than those in the CK and 3 mg/L treatments ($P < 0.05$), with increases of 37.7% and 33.29% compared with those in the CK treatment and of 34.77% and 30.46% compared with those in the 3 mg/L treatment, respectively, and the differences were not significant between the CK and 3 mg/L treatments. The differences were not significant between the 6 mg/L and 12 mg/L treatments. At the beginning of the fruiting period, the treatments presented trends consistent with those in the initial flowering period. During the fruiting period, the chlorophyll concentrations in the 3 mg/L, 6 mg/L, and 12 mg/L treatments were greater than those in the CK treatment ($P < 0.05$) by 15.66%, 44.7%, and 32.25%, respectively. The chlorophyll concentration in the 12 mg/L treatment group was greater than that in the 3 mg/L treatment group ($P < 0.05$) and increased by 14.35%.

Compared with those of CK, the effect of the Se-rich Se fertilizer at the three different Se concentrations on the number of cucumber leaves differed (Fig. 1f). The number of leaves in the 6 mg/L treatment was greater than that in the CK, 3 mg/L, and 12 mg/L treatments ($P < 0.05$) by 28.86%, 13.81%, and 12.82%, respectively, and that in the 12 mg/L treatment was greater than that in the CK and 3 mg/L treatments ($P < 0.05$), being 14.21% greater than that in the CK. The difference in the number of leaves between the 3 mg/L treatment and the 12 mg/L and CK treatments was not significant.

Effects of selenium treatment at different concentrations on cucumber yield

Se fertilizer at different concentrations resulted in significant differences in greenhouse cucumber yield (Table 1). When the selenium concentration was 6 mg/L, the cucumber yield increased the most, and the number of cucumber fruits on a single plant, the average weight of a single fruit, and the yield of a single plant were increased by 25.09%, 13.7%, and 40.2% greater than those of the CK, respectively ($P < 0.05$).

Effects of selenium at different concentrations on cucumber quality

The nutritional quality of cucumber fruits differed when cucumber leaves were sprayed with Se fertilizer at different concentrations (Table 2). Dry matter accumulation in cucumber fruits under the different treatments was ranked as follows: 12 mg/L > 6 mg/L > 3 mg/L > CK, with dry matter accumulation in cucumber fruits under the 6 mg/L and 12 mg/L treatments being significantly higher than that in CK by 61.01% and 66.43%, respectively ($P < 0.05$). The selenium content of cucumber fruits in the 6 mg/L and 12 mg/L treatments was higher than that in CK by 60.83% and 49.87%, respectively ($P < 0.05$); and the selenium content of cucumber fruits in the 6 mg/L treatment was not significantly different from that in the 12 mg/L and 3 mg/L treatments. The soluble protein content in cucumber fruits in the selenium treatment groups was greater than that in the CK group ($P < 0.05$) by 5.71%, 8.6% and 11.43%, respectively, and there were no significant differences in soluble protein content in the fruits among the selenium treatment groups. Selenium fertilizer significantly reduced the total acidity of cucumber, at 11.69%, 35.5%, and 36.8% lower than that of CK ($P<0.05$) in the 3 mg/L, 6 mg/L, and 12 mg/L treatments, respectively. The soluble solids content in cucumber fruits under different treatments was 6 mg/L > 12 mg/L > 3 mg/L > CK, in which the soluble solids content significantly increased under the 6 mg/L treatment ($P<0.05$) by 7.1% compared with that under CK.

Effects of selenium at different concentrations on photosynthesis and powdery mildew development in cucumber
The greatest alleviation of leaf photosynthesis inhibition by powdery mildew was achieved at a Se treatment concentration of 6 mg/L (Fig. 2). Compared with those under the CK treatment, the leaf net photosynthetic rate, intercellular CO_2 concentration, stomatal conductance, and transpiration rate under the 6 mg/L treatment increased by 35.69%, 105.9%, 84%, and 99.03%, respectively ($P<0.05$).

Selenium at concentrations of 6 mg/L and 12 mg/L reduced the susceptibility of plants to powdery mildew (Fig. 3). The incidence rate of powdery mildew in the 6 mg/L treatment group at the first flowering stage was lower than that in the CK, 3 mg/L and 12 mg/L treatment groups ($P<0.05$) by 10.46%, 10.46% and 10.46%, respectively. There was no significant difference in the incidence rate of powdery mildew between the 3 mg/L and 12 mg/L treatment groups and CK. The differences in powdery mildew incidence among the CK, 3 mg/L, 6 mg/L, and 12 mg/L treatments were not significant at the early and full fruiting stages, and all the values being more than 90% ($P>0.05$) (Fig. 3a).

The powdery mildew disease indices of the 3 mg/L, 6 mg/L and 12 mg/L treatments at the early flowering stage were lower than those of the CK treatment ($P<0.05$) by 11.36%, 25% and 13.64%, respectively, and there was no significant difference in the powdery mildew disease indices among the 3 mg/L, 6 mg/L, and 12 mg/L treatments. The powdery mildew disease indices of the 6 mg/L and 12 mg/L treatments at the early and fruiting stages were lower than those of the CK and 3 mg/L treatments ($P<0.05$), and the differences between the 6 mg/L and 12 mg/L treatments were not significant (Fig. 3b).

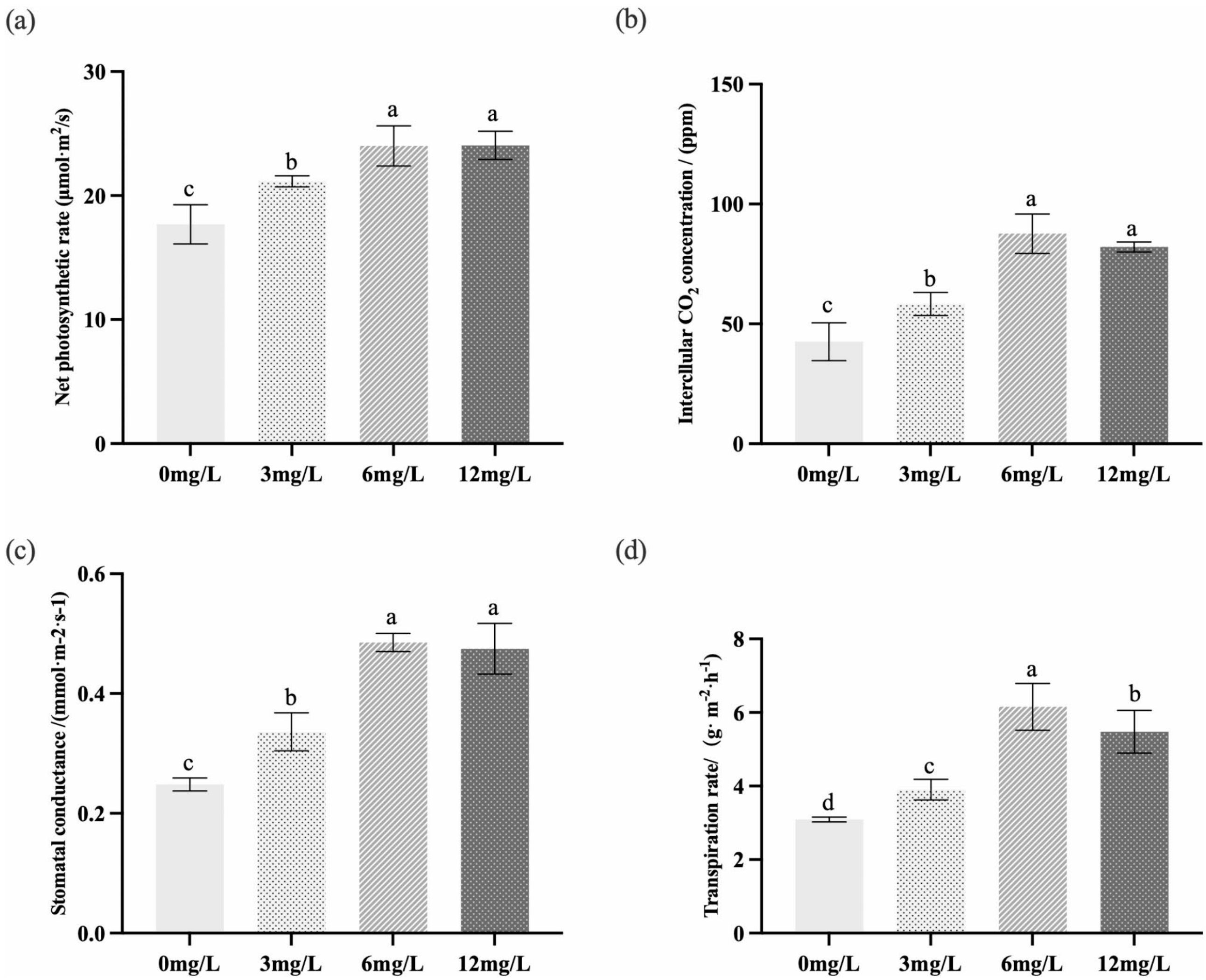

Fig. 2. Effect of biofortification on photosynthesis at different selenium concentrations (n = 30).

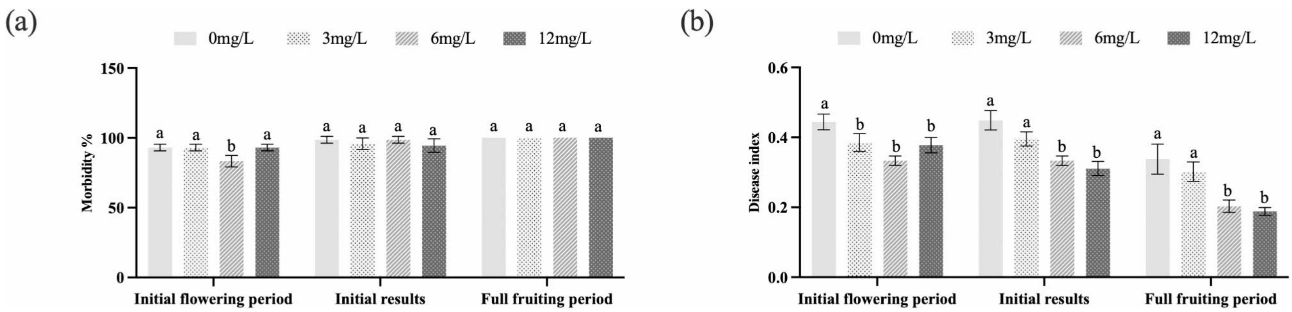

Fig. 3. Effect of biofortification with different selenium concentrations on powdery mildew of cucumber (n = 132).

Treatments	Height (cm)	Stem thickness (mm)	Total fresh weight (g)	Total dry matter accumulation (g)
CK	11.11 ± 0.3c	8.51 ± 0.03b	11.66 ± 0.05c	0.68 ± 0.02d
MJ	11.43 ± 0.84c	8.89 ± 0.29ab	11.58 ± 0.16c	0.78 ± 0.01c
XX	13.17 ± 0.27b	9.1 ± 0.16a	12.99 ± 0.16b	0.95 ± 0.07b

Table 3. The effect of selenium biological enhancement on the growth of cucumber seedlings (n = 15). CK: water control treatment; MJ: fungicide control (probiotic); XX: selenium-enriched ionic fertilizer.

Treatment groups	Disease index before spraying	Disease index after spraying	Therapeutic effect (%)
CK	0.58	0.69	–
MJ	0.56	0.26	59.53a
XX	0.67	0.36	56.09ab

Table 4. The therapeutic effect of selenium bio enhancement on cucumber powdery mildew (n = 27).

Treatment groups	Disease index	Preventive effect (%)
CK	0.74a	–
MJ	0.4b	45.08a
XX	0.43b	41.72a

Table 5. The preventive effect of selenium bio enhancement on cucumber powdery mildew (n = 27).

Effects of selenium biofortification on cucumber powdery mildew disease and its pathogens

Effect of selenium biological enhancement on the growth of cucumber seedlings

The plant height, stem thickness, and total fresh weight under the 6 mg/L selenium-enriched ionic fertilizer treatments were greater than those under the two control treatments ($P < 0.05$), and the differences between the CK and MJ treatments were not significant. Compared with that in the CK and MJ treatments, dry matter accumulation was greater under selenium-rich ionic fertilizer treatment, and dry matter accumulation was greater in the MJ treatment than in the CK treatment ($P < 0.05$) (Table 3).

The effect of selenium bioenhancement on powdery mildew

Compared with CK, 6 mg/L selenium-enriched ionic fertilizer had a certain inhibitory effect on cucumber powdery mildew (Table 4). Compared with CK, the incidence of powdery mildew in seedlings decreased by 59.53% with the application of selenium-enriched ionic fertilizer.

The effect of selenium bioenhancement on powdery mildew prevention

The effect of selenium fertilizer on cucumber powdery mildew prevention is shown below (Table 5). When the water control treatment was not considered, the preventive effect of the different treatment groups was less than 1; the preventive effect of selenium-enriched ionic fertilizer on powdery mildew reached levels similar to those of standard fungicide prevention.

The effect of selenium bioenhancement on enzyme activity

Compared with CK, Se-enriched ionic fertilizer application increased the SOD activity of cucumber under disease stress, and under Se-enriched ionic fertilizer application, the maximum value of SOD activity was reached at 48 h after inoculation. At 0 h after injection, the SOD activity under fungicide treatment (MJ) was greater than that under the other two treatments ($P<0.05$), and at this point, the difference in enzyme activity between the water control (CK) treatment and the selenium-enriched ionic fertilizer treatment was insignificant. At 6 h after injection, the SOD activity in all the treatments tended to increase, and that in the selenium-enriched ionic fertilizer treatment was greater than that in the CK treatment ($P<0.05$). At 12 h after injection, the SOD activity in the CK and fungicide treatments began to decrease gradually, and the SOD activity in the selenium-enriched ionic fertilizer treatment increased slowly up to 48 h after injection. At 72 h after injection, the SOD activity in the water control treatment was lower than that in the other two treatments ($P<0.05$) (Fig. 4).

The activity of the enzyme POD in all the treatments tended to increase but then decreased (Fig. 5). At 0 h after injection, POD activity in the selenium-enriched ionic fertilizer treatment (XX) and fungicide treatment (MJ) groups was greater than that in the control group ($P<0.05$), and the difference among the three treatment groups was not significant. At 6–24 h after injection, POD activity in each treatment group increased with time elapsed after injection, and POD activity in the selenium-enriched ionic fertilizer treatment and fungicide treatment groups was greater than that in the CK treatment group ($P<0.05$). However, POD activity did not continue to increase and began to decrease as the inoculation time reached 24 h. During the period from 24 to 72 h after injection, the difference in POD activity between the selenium-enriched ionic fertilizer treatment and fungicide treatment was insignificant. Nevertheless, these values were greater than those in the CK treatment ($P<0.05$) (Fig. 5).

Microscopic observation of the inhibition of powdery mildew pathogen conidia

The application of Se fertilizer effectively inhibited the germination of powdery mildew spores and the production of germ tubes (Fig. 6). At 24 h after leaf inoculation, the spore germination rate was the lowest in the control group, at only 30.19%, while the spore germination rate of the CK group was the highest, reaching 64.4%. The spore germination rate in the selenium treatment group (XX) was lower than that in the water control group ($P<0.05$), and the average number of germ tubes produced in the CK treatment was greater than that in the other treatment groups within 24 h ($P<0.05$). The ability of Se fertilizer to inhibit the germination of white powder spores within 24 h reached levels similar to that under fungicide treatment (Table 6).

At 48 h after injection, the spore germination rate in the CK treatment was greater than that in the other treatments ($P<0.05$), and the germination rate reached 72.38%. The number of buds produced in the CK treatment reached 1.24, while the number of buds produced in the fungicide control was lower than that produced under selenium fertilizer application ($P<0.05$).

At 72 h, the bud tubes of powdery mildew spores began to elongate to form mycelia, and the mycelium formation rate under fungicide treatment was lower than that under CK ($P<0.05$). As shown in Fig. 6 below, many mycelial colonies formed by 96 h. At 120 h, the number of cascade conidia in the water control treatment

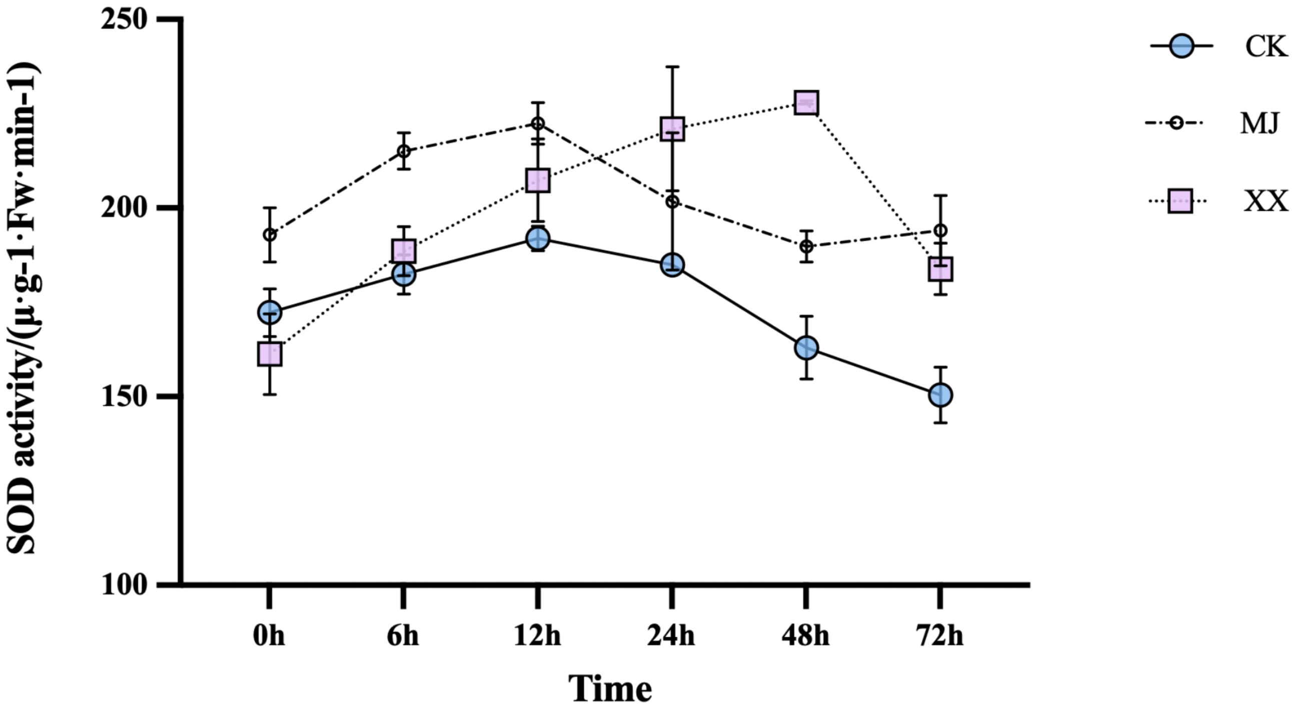

Fig. 4. Effect of selenium biological enhancement on SOD enzyme activity in facility cucumber (n = 9).

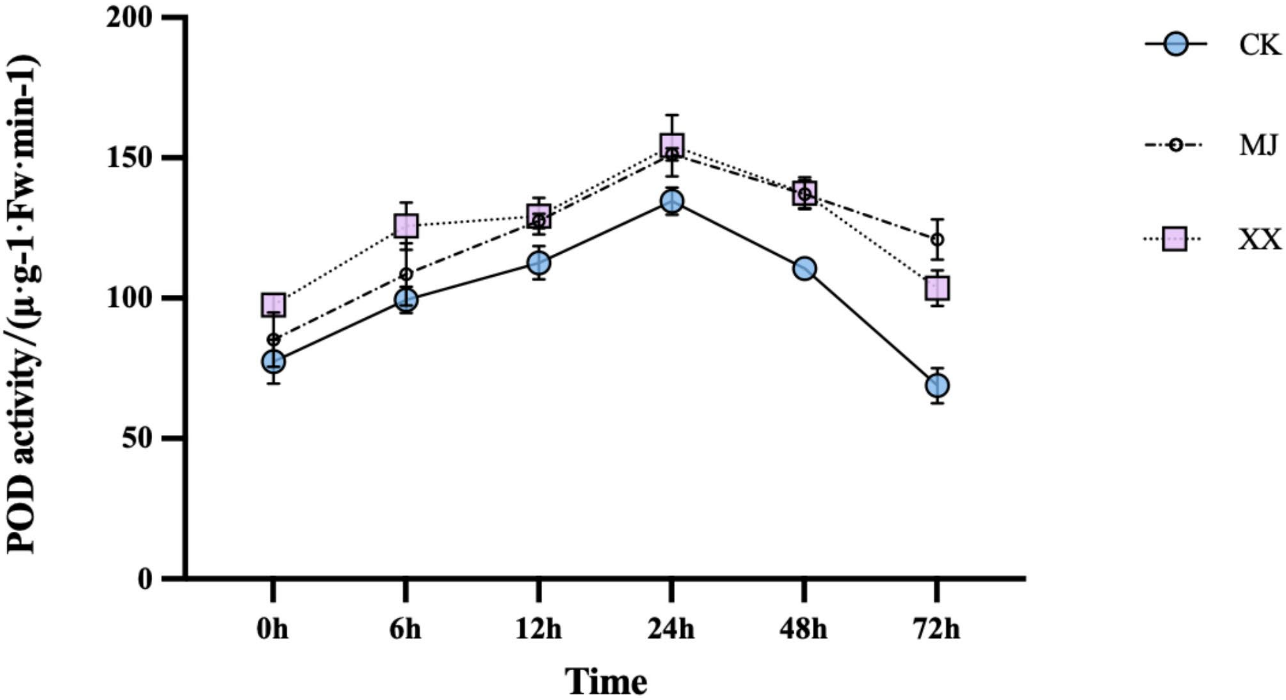

Fig. 5. Effect of selenium biological enhancement on POD enzyme activity in facility cucumber (n = 9).

group had increased to 5–7, whereas those in the selenium-enriched ionic fertilizer treatment group had only increased to 2–3.

Discussion

Effect of biofortification with different selenium concentrations on cucumber growth

The human body can only absorb low doses of selenium. Currently, the primary method of selenium supplementation to prevent selenium deficiency is the consumption of plants that are rich in selenium[30]. Our research group previously studied the effects of three selenium fertilizers on cucumber growth and determined that the application of selenium-rich ionic fertilizer had the greatest effect. Therefore, in this study, selenium-enriched ionic fertilizer was selected as the test material according to previous experimental results to investigate the effects of selenium at different concentrations on the growth of cucumber. According to the results of previous studies, the concentration range of selenium fertilizer applied to vegetables is 2–15 mg/L[31–33]. Selenium has effects on the growth of plants, animals, and humans. Studies have shown that applying Se at low concentrations promotes vegetable growth and increases yield, whereas at high concentrations, Se can inhibit plant growth[34–37]. Therefore, in this study, we referred to previous research on selenium fertilizer application to vegetables to determine appropriate concentrations and utilized four selenium solutions at different concentrations to investigate their effects on cucumber growth.

Plants respond differently to different levels of selenium. At 6 mg/L, selenium fertilizer can promote increases in cucumber plant height and stem thickness, increase leaf chlorophyll concentration, and increase fruit yield. Several studies have shown that at appropriate concentrations, selenium fertilizer significantly increases the growth and yield of watermelon[38], cucumber[27,39], and tomato[40,41]. In addition, selenium fertilizer increases the soluble sugar, soluble solid, and selenium contents in these fruits and vegetables. Nutritional quality is an important indicator of fruit value, with selenium content being a primary factor in selecting organic, selenium-rich fruits. A study confirmed that increasing selenium levels can promote tomato plant growth and increase soluble sugar and selenium contents in fruits. The increase in organic acid content was most significant when a Se treatment exceeding 5 mg/L was applied to leaves[40]. This study also revealed that Se fertilizer at a concentration of 6 mg/L increased the content of soluble solids, Se, and other substances in cucumber while also reducing the total acidity of the fruit.

When the same form of Se is applied, low concentrations ($\leq$ 10 mg/kg) can promote celery growth, whereas high concentrations (> 20 mg/kg) inhibit celery growth[42]. A research concluded that the application of a foliar spray of 2.5 mg/L sodium selenite had a yield-increasing effect on radish fruits, whereas 40 mg/L sodium selenite significantly inhibited the growth of radish fruits[43]. According to the analysis of comprehensive growth indicators, spraying 3 mg/L selenium fertilizer had no significant effect on promoting cucumber growth; when the Se concentration in the spray reached 6 mg/L, the growth-promoting effect was highly significant. However, when the selenium concentration was greater than 6 mg/L, the growth-promoting effect of selenium on cucumber did not decrease with increasing selenium concentration. However, it did not continue to increase with increasing Se concentration either, which may have occurred due to the relatively weak Se enrichment capacity of cucumber. At 3 mg/L, the selenium concentration was not enough to satisfy the plants' growth

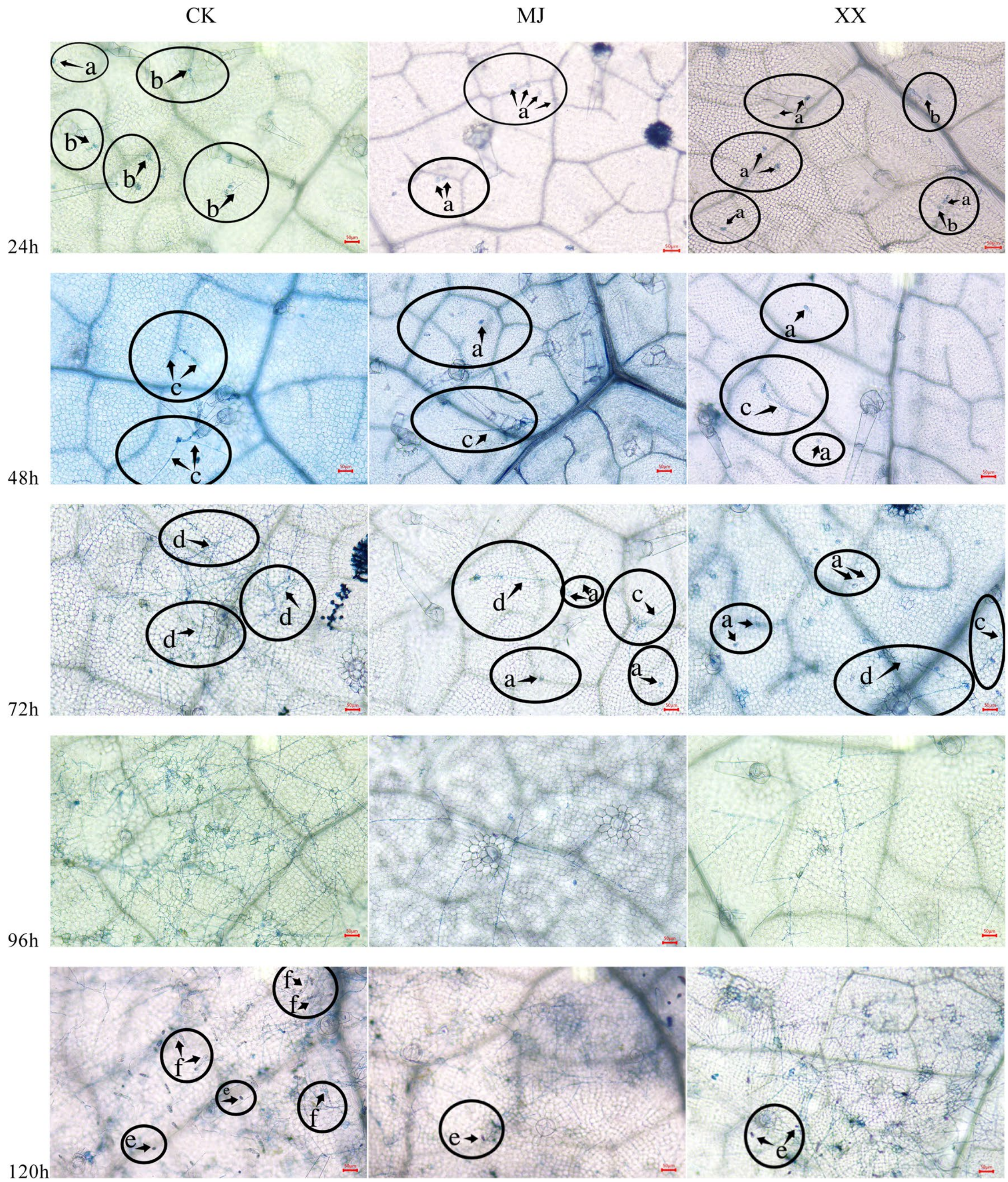

Fig. 6. Effect of selenium fertilizer on spore germination and growth of cucumber powdery mildew pathogen (n = 9). *Note* (**a**) Pathogenic spore; (**b**) Conidia formed one germ tube; (**c**) Bud tube elongation; (**d**) Hyphal formation; (**e**) Conidiophore; (**f**) Conjugate conidia.

demand. However, at 12 mg/L, the Se was not fully absorbed and transformed in the cucumber plants. Selenium can increase the competitive ability of plant leaves for light resources[44]. Some studies also reported that selenium can increase cucumber photosynthetic capacity[45,46]. Upon powdery mildew development, photosynthesis is one of the first processes to be inhibited in plant leaves. Our study revealed that a foliar spray of selenium at a concentration of 6 mg/L or 12 mg/L could increase photosynthetic capacity in cucumber leaves, and the greatest alleviation of leaf photosynthesis inhibition by powdery mildew was achieved when the selenium concentration was 6 mg/L. Mohammadi's study revealed that foliar spraying of selenium at low concentrations had beneficial effects on plant cell metabolism[47,48]. In the study of the effects of selenium fertilizer on the occurrence of cucumber powdery mildew, it was initially reported that 6 mg/L and 12 mg/L selenium-rich ionic fertilizers have similar effects on reducing the leaf powdery mildew disease index in cucumber; the goal is to mitigate cucumber powdery mildew damage. The differences between the fertilizers at the two different concentrations on mitigating powdery mildew are not significant.

Treatment groups	Germination rate of conidia%		Average number of germ tube per conidium		Hyphal formation rate%
	24 h	48 h	24 h	48 h	72 h
CK	64.4a	72.38a	0.66a	1.24a	0.46a
MJ	30.19b	32.75b	0.32b	0.34c	0.29b
XX	39.61b	42.3b	0.42b	0.64ab	0.35ab

Table 6. Inhibition effect of selenium biological enhancement on the growth of cucumber powdery mildew pathogen (n = 9).

Effect of selenium biofortification on the control of cucumber powdery mildew disease and its pathogen

Studies have shown that the exogenous input of selenium in the form of selenium fertilizer at different concentrations can promote the growth of cucumber and result in high-quality seedlings[24,39]. Under selenium biofortification using selenium-enriched ionic fertilizer, the growth of cucumber seedlings was promoted. This was reflected mainly in an increase in plant height and stem thickness as well as an increase in fresh weight and dry matter accumulation in the seedlings. Selenium fertilizer inhibits cucumber powdery mildew; similar to local and foreign international research studies on selenium treatment for tomato disease[49,50]. Selenium has the potential to prevent tomato gray mold and reduce the incidence of fusarium wilt. Under selenium treatment, the germination of spores of the pathogen for gray mold in tomato fruits is inhibited, effectively preventing the occurrence of gray mold. Inoculation of tomato pretreated with sodium selenite with *F. oxysporum* can significantly reduce the incidence rate of tomato fusarium wilt[49,50].

Selenium can increase plant resistance and control pathogen activity, thereby controlling plant diseases[51–54]. Scholars have reported that exogenous selenium can increase the activity of plant antioxidant enzymes and promote the accumulation of ascorbic acid and glutathione, thus alleviating the oxidative damage caused under stress conditions[55], improving the functioning of enzyme systems (SOD, POD), and enhancing resistance[56]. Foliar spraying of selenium fertilizer also increased the activities of SOD and POD in cucumber leaves under powdery mildew stress. The activities of the two enzymes tended to increase but then decrease, which effectively eliminated attack from free radicals and alleviated disease stress caused by the infestation of pathogenic bacteria in cucumber plants. Selenium enhances the ability of plants to resist pathogenic bacteria and inhibits pathogen growth in four main ways, namely, via physiological, biochemical, morphological and structural, and defense gene expression routes[49,54,57]. In this study, microscopic observations of pathogen-inoculated leaves revealed that selenium fertilization effectively inhibited the growth of powdery mildew pathogen conidia. This finding is similar to the results of a bacteriostatic test of selenium-enriched juice extracted by Duan[58]; the selenium-enriched garlic juice inhibited the growth of brewer's yeast, *Aspergillus flavus*, *Aspergillus niger*, and *Staphylococcus aureus*. In addition, Razak reported that 10 mg/kg sodium selenite could stop the growth of *Fusarium*, *Streptomyces*, and *Aspergillus*[59]. According to Cheng[60,61], selenium is a potential fungicide. Selenium resulted in a reduction in the pathogenicity of *S. sclerotiorum,* and Se-enriched agricultural byproducts inhibited the mycelial growth of *S. sclerotiorum*. However, the effect of selenium on the growth of pathogenic microorganisms cultured under isolation conditions manifests mainly as inhibitory effects rather than lethal effects. The authors of this study believe that in the practical application of selenium fertilizers, a small number of chemical agents must be combined, with staggered application, to achieve the best results for the prevention and control of powdery mildew disease. In this study, we focused on physiological and biochemical investigations to preliminary determine that selenium fertilizer has an inhibitory effect on cucumber powdery mildew pathogens. Further studies would be needed to check the effects of selenium fertilizer on the morphological structure of powdery mildew pathogens to control powdery mildew in cucumber.

Conclusion

At a concentration of 6 mg/L Se, selenium-enriched ionic fertilizer had the greatest effect on promoting the growth and improving the quality of greenhouse cucumber. This method can be used to safely produce selenium-enriched cucumber. Selenium biofortification has preventive and control effects on cucumber powdery mildew, mainly through physiological and biochemical means, to increase the tolerance and defense capacity of the host. Selenium-enriched ionic fertilizer at a concentration of 6 mg/L can also be used to cultivate high-quality cucumber seedlings. It affects the antioxidant enzyme activity of cucumber seedlings to increase plant resistance and inhibits the germination of powdery mildew pathogen conidia, the number of conidia that germinate in shoot tubes and mycelium formation, reducing the degree of damage caused by powdery mildew.

Data availability

The dataset generated and/or analyzed during the current research period can be obtained from the corresponding author upon reasonable request.

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Author contributions

This study was conceived and led by K.P. and X.D.X., who conducted field experiments and collected samples through X.D.X. and Z.B.C., X.D.X., Z.B.C. and W.R.W. finished all lab work. X.D.X. and Z.B.C. analyzed the data and wrote the manuscript. All authors discussed the results and their implications and commented on the manuscript as it progressed.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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