Effect of Silicon Nutrition on Oxidative Stress Induced by *Phytophthora melonis* Infection in Cucumber

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Abstract

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The effect of silicon nutrition on root rot of cucumber caused by *Phytophthora melonis* was studied in a greenhouse experiment. Two cucumber cultivars (*Cucumis sativus* 'Dominus' and 'Super Dominus') fertilized with three concentrations of Si (0.0, 1.0, and 1.7 mM Si in the form of sodium silicate) were not inoculated or were inoculated with *P. melonis*. The *P. melonis* isolate significantly decreased root dry weights, although the magnitude of growth reduction varied with cultivar and Si concentration. Silicon nutrition at either concentration significantly reduced disease severity relative to the treatment that

received no silicon. There was a significant negative correlation between the extent of root rot caused by *P. melonis* and the extent of electrolyte leakage of roots. Roots infected with *P. melonis* had greater root catalase (CAT) and ascorbate peroxidase (APX) activities. There was a positive correlation between silicon concentrations and CAT and APX activities in plants inoculated with *P. melonis*. Silicon improved activity of antioxidant enzymes, resulting in enhanced crop resistance to oxidative stress induced by *P. melonis* infection and improved cucumber growth.

Silicon (Si) is the second most abundant element in the lithosphere (13). Although Si is not known as an essential plant nutrient, many plants accumulate Si from 0.1 to 10% of dry matter of the plant tissue (13). Absorption of silicon by plant roots is highly dependent on plant species and mechanisms of Si uptake and transport (25,27).

The beneficial effects of Si nutrition in plants include enhancement of growth and yield and improvement of physical properties (e.g., stature, soil penetration by roots, exposure of leaves to light, resistance to lodging, reduction of transpiration, and increasing crop resistance to drought, salinity, and metal toxicity stresses) (13,26,27). The beneficial effects of Si on plant enzyme activities and resistance to pathogens also have been reported (13,26,27). Silicon also may amend nutrient imbalances that often occur as a result of biotic and abiotic stresses in the plants (28,32,36). Some beneficial roles of Si in plants are associated with the bioactivity of monosilicic acid, whereas others are likely to derive from the deposition of amorphous silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) in plant cell walls (31).

Root and crown rotting pathogens, in particular *Phytophthora* spp., cause yield reductions of several greenhouse crops in Iran, particularly cucumber. Although production of cucumber (*Cucumis sativus* L.) is negatively influenced by root rot, symptoms of the disease can be easily overlooked until the plants suddenly wilt (14). In Iran, cantaloupes, melons, and cucumbers occupy more than 250,000 irrigated hectares that are often affected by a severe wilt disease, known locally as "green death", caused by *Phytophthora melonis* Tucker (2).

Plants exposed to biotic and environmental stresses produce reactive oxygen species (ROS), including superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH), and singlet oxygen (O_2) (28). ROS significantly damage cell membranes and other essential macromolecules such as photosynthetic pigments, proteins, nucleic acids, and lipids (15). An antioxidant system nor-

mally maintains the ROS balance within plant cells. Superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) are antioxidative enzymes involved in detoxification of the ROS. The CAT and peroxidase can convert H_2O_2 to water and oxygen, and the APX reduces H_2O_2 using ascorbate as an electron donor (43).

It has been reported that soluble Si activates defense mechanisms in cucumber against *Pythium* spp. by increasing activity of chitinases, peroxidases, and polyphenoloxidases (39). Soluble Si absorbed by plants tends to accumulate in the apoplast, particularly in epidermal cell walls (28,30,38). Addition of Si also may increase content of phenolic compounds, which are fungitoxic, in the infected cells (8,29). Silicon binds to hydroxyl groups of proteins strategically included in signal transduction (4,11). Silicon also can interfere with cationic cofactors of enzymes influencing pathogenesis-related events (5).

Since Si affects physiological and biological mechanisms in cucumber to alleviate disease, the aim of the present study was to investigate the interaction of Si and *P. melonis* on growth, antioxidant enzyme activities, reactive sulfhydryl groups, root membrane permeability, and severity of disease development in cucumber plants.

Materials and Methods

Plant growth and pathogen inoculation. Seeds of cucumber cultivars (*Cucumis sativus* 'Dominus GRC' and 'Super Dominus'), obtained from the National Institute of Seed Preparation and Distribution, Karaj, Iran, were thoroughly rinsed with distilled water and germinated on moist filter paper in an incubator at 28°C.

These two cultivars of cucumber are the ones most commonly grown in Iran. The germinated seeds were sown in sterilized quartz sand (four plants in each pot) and continuously irrigated with Johnson nutrient solution (20). The nutrient solution contained the following: 1.0 mM KNO_3 , 1.0 mM $\text{Ca}(\text{NO}_3)_2$, 1.0 mM $\text{NH}_4\text{H}_2\text{PO}_4$, 1.0 mM MgSO_4 , 50 μM FeEDTA, 50 μM KCl, 25 μM H_3BO_3 , 2.0 μM MnSO_4 , 2.0 μM ZnSO_4 , 0.5 μM CuSO_4 , 1.0 μM NiSO_4 , 0.02 μM $\text{H}_2\text{MoO}_7\text{O}_4$, and 2 mM MES [2-(*N*-morpholino) ethanesulfonic acid] adjusted to pH 6 with KOH as a pH buffer.

The daily photoperiod in the greenhouse was 12 h, with average daily maximum and minimum temperatures of 30 and 18°C, respectively. The pH of the nutrient solution was adjusted to 6.0 daily using 0.1 M H_2SO_4 . Treatments were three levels of Si (0.0, 1.0, and 1.7 mM Si as sodium silicate) and two *P. melonis* infection

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levels (0 and 10^6 spores/ml). The silicon levels were chosen based on previous studies where 1 or 1.7 mM silicon (9,10,24,44) stimulated cucumber growth and increased tolerance to pathogens. Soluble silicon was fed to the plants by amending the nutrient solution with 1.0 or 1.7 mM silicon in the form of Na_2SiO_3 . All solutions were renewed every day.

P. melonis was isolated from infected cucumber plants in greenhouses of Isfahan Province. Inoculation with *P. melonis* was performed 40 days after planting.

Zoospores for inoculation were produced by the procedure described by Ristaino (37). *P. melonis* was grown on V8 agar petri plates for 1 week. The agar with fungal hyphae was then cut into 0.5-cm squares and placed in a sterile petri dish with sterile distilled water. The solution was replaced with fresh water every 3 days. After 1 week, the sporangia were given a cold shock (1 h at 4 to 6°C), followed by a 1-h equilibration at room temperature. The zoospores were separated from the solution by filtering through 2 layers of cheesecloth. Zoospores were applied to the plant within 30 min of filtering.

Plant roots were inoculated by adding 1 ml of the suspension (10^6 zoospores/ml) into the supplied nutrient solution. Plants were examined daily for wilting, desiccation, and stem collapse (2).

Pathogen isolation and disease assessment. The presence of *P. melonis* was confirmed by taking root samples every 5 days after inoculation. Symptomatic root samples from two or three plants in each treatment were selected arbitrarily, dissected, washed thoroughly in distilled water, surface-disinfested in 3% aqueous sodium hypochlorite for 5 min, rinsed for a few minutes in distilled water, blotted dry, and plated onto a selective medium composed of corn meal agar (CMA) (42), to which 250 ppm ampicillin, 10 ppm rifampicin, 100 ppm PCNB, and 20 ppm benomyl were added for each liter of medium. Plates were placed in an incubator at 25°C. The presence of *P. melonis* was determined after 7 days of incubation based on morphological features.

P. melonis is heterothallic, and sporangia are ellipsoid and relatively large ($\sim 34 \times 55 \mu\text{m}$) with tapered bases. Characteristically, they have a unique cross wall which forms higher in the sporangium. Angular hyphal swellings occur in chains, and maximum temperature for colony growth is greater than 35°C. Studies by Mostofizadeh-Ghalamfarsa et al. (33) on a worldwide collection of *Phytophthora* species isolated from cucurbit and noncucurbit hosts revealed that all of the cucurbit isolates previously identified in Iran as *P. drechsleri* were distinct, which was regarded as *P. melonis* and placed in a different clade from *P. drechsleri*.

Banihashemi and Mirtalebi (3) reported that all of the *Phytophthora* isolates from cucurbits in Iran are *P. melonis*, while they have previously been misidentified as *P. drechsleri*.

Koch's postulates were fulfilled 10 days after inoculation by placing the necrotic roots on semi-selective CMA medium and recovering the causal agent and confirming its identification.

Silicon analysis. Four weeks after inoculation (approximately 2 months after seeding), the cucumber plants were harvested and separated into roots and shoots. Plant materials were washed with distilled water and dried at 70°C for 48 h. Silicon concentration was measured in the plant tissues as described by Elliot and Snyder (12). Dried plant samples (0.5 g) were wetted with 2 ml of 50%

H_2O_2 in 100-ml polyethylene tubes previously rinsed with 0.1 M NaOH and demineralized water (DM). To each tube, 4.5 g of 50% NaOH was added at ambient temperature, and each tube was gently vortexed. The tubes were individually covered with loose-fitting plastic caps and autoclaved at 138 kPa for 1 h. Afterward, the tubes received distilled water until the volume within reached 50 ml. Silicon concentration in the extracts was determined by the colorimetric molybdate blue method (21).

Reactive sulfhydryl group assay. Roots of intact cucumber seedlings were analyzed as described by Norvell and Welch (35) using sulfhydryl-reactive reagent DTNB (5,5'-dithio-bis(2-nitrobenzoic acid)). The DTNB reacts with sulfhydryl groups to form the nitromercaptopbenzoic acid anion, which has an intense yellow color. Seedling roots were immersed in 100 ml of sulfhydryl reaction buffer (0.2 M Tris-HCl plus 0.02 M Na-EDTA adjusted to pH 8.2 with NaOH). One milliliter of 10 mM DTNB, dissolved in absolute methanol, was added to the reaction buffer at time zero. After 15 min, the roots were removed from the reaction buffer. Reactive sulfhydryl groups in 2.0-ml aliquots of sulfhydryl buffer solution were immediately assayed after collection through spectrophotometer for increasing in absorption at 412 nm. Sulfhydryl concentrations were calculated from standard curves prepared from Cys standards made immediately before the assay.

Root leakage conductivity: an indicator of root membrane permeability. Root cell membrane permeability was assessed using a modification of the method described by Yan et al. (43). Washed root segments of 1 cm length were placed in a beaker containing 10 ml of deionized water and incubated at 30°C for 3 h. The electrical conductivity (EC) of the solution was measured at 25°C. The samples were then boiled for 2 min and cooled to room temperature (25°C), and conductivity was measured. The electrolyte leakage (EL) was calculated as follows:

$$\text{EL}(\%) = (\text{EC1}/\text{EC2}) \times 100$$

where EC1 and EC2 are the electrical conductivities measured before and after boiling, respectively.

Enzyme assay. The plant root samples (buffer volume: fresh weight, 3:1) were homogenized in a pestle and mortar with 100 mM TRIS-HCl buffer (pH 8) containing 2 mM EDTA, 5 mM DL-dithiothreitol, 10% glycerol, 100 mM sodium borate, 4% (wt/vol) insoluble polyvinylpyrrolidone (PVP), and 1 mM phenylmethylsulfonylfluoride (PMSF). The homogenate was filtered through four layers of muslin cloth and centrifuged at $12,000 \times g$ for 40 min. The supernatant was stored in separate aliquots at -80°C prior to enzyme analyses. Total protein was determined using the Bradford method (6).

Catalase (CAT). Catalase (EC 1.11.1.6) activity was determined according to Cakmak and Marschner (8). The reaction mixture contained 25 mM sodium phosphate buffer (pH 7.0) plus 10 mM H_2O_2 in a total volume of 3 ml. The reaction was initiated by the addition of 100 μl of root extracts to the reaction mixture, and the enzyme activity was determined by measuring the initial rate of disappearance of H_2O_2 at 240 nm ($E = 39.4 \text{ mM}^{-1} \text{ cm}^{-1}$) for 30 s.

Ascorbate peroxidase (APX). Ascorbate peroxidase (APX) activity was determined according to Nakano and Asada (34). The reac-

Table 1. Analysis of variance for root and shoot dry matter yield, activity of root catalase (CAT) and ascorbate peroxidase (APX), and concentration of sulfhydryl (SH) groups and Si in roots of cucumber cultivars as affected by Si addition and *Phytophthora melonis*

Treatment	df	<i>P</i> > <i>F</i>						
		Root dry matter yield	Shoot dry matter yield	Root membrane permeability	CAT	APX	SH groups	Si
Cultivar	1	0.0392	0.0231	0.0004	0.0011	0.0085	0.0320	0.0032
<i>P. melonis</i>	1	0.0498	0.1021	0.0349	0.0179	0.0094	0.7027	0.0355
Si	2	0.0465	0.0011	0.0400	0.0410	0.8510	0.0160	0.0214
Cultivar $\times$ <i>P. melonis</i>	1	0.0504	0.1151	0.0214	0.0050	0.0066	0.0019	0.0461
Cultivar $\times$ Si	2	0.0563	0.0507	0.0641	0.0041	0.0010	0.0026	0.0393
<i>P. melonis</i> $\times$ Si	2	0.0371	0.0803	0.0308	0.0012	0.0013	0.0034	0.0428
Cultivar $\times$ <i>P. melonis</i> $\times$ Si	2	0.0426	0.0906	0.0582	0.0019	0.0904	0.0051	0.0064

tion mixture, with a total volume of 3 ml, consisted of 25 mM sodium phosphate buffer (pH 7.0), 0.1 mM EDTA, 0.25 mM ascorbate, 1.0 mM H₂O₂, and 100 µl of the root extract. H₂O₂-dependent oxidation of ascorbate was followed by a decrease in the absorbance at 290 nm ($E = 2.8 \text{ mM}^{-1} \text{ cm}^{-1}$).

Statistical analysis. The experiment was conducted as a completely randomized factorial design; each treatment contained four replicates. All values reported in this work are means of three independent experiments. There was homogeneity of variances, and no significant difference was found between the experiments in the measured parameters. Therefore, the combined analysis of three experiments was performed. Analysis of variance procedures were conducted with the PROC GLM procedure of SAS (40). Mean separations were performed using Fisher's protected least significant difference (LSD) method at $P < 0.05$.

Results

Disease severity and plant growth. After 4 weeks, most of the plants inoculated with *P. melonis* in the Si-free treatment showed root rot symptoms. Silicon nutrition significantly reduced disease severity, although no significant difference was found between the 1.0 and 1.7 mM Si levels (Table 1 and Fig. 1).

Root and shoot dry weight of both cucumber cultivars were significantly increased by Si application (Table 1 and Figs. 2 and 3). There was no significant difference in the cucumber shoot and root dry weight between the 1.0 and 1.7 mM Si levels. Inoculation of cucumber with *P. melonis* resulted in significant decrease in the root dry weight of cucumbers, and this effect was greater in Super Dominus (Table 1 and Fig. 2). The root dry matter in the Dominus cultivar was greater than in the Super Dominus. No difference in shoot dry weight was observed between the cucumber seedlings infected with *P. melonis* and the noninfected plants.

Silicon nutrition led to a significant increase in the root and shoot Si concentration (Table 1 and Figs. 4 and 5). No significant difference was found between the shoot Si concentration in the plants grown at the 1.0 mM Si compared with those that received 1.7 mM Si. Silicon concentration in the Super Dominus was significantly higher than that in the Dominus. Infection with *P. melonis* significantly decreased the root Si concentration in both cultivars, whereas the infection had no significant effect on the shoot Si concentration (Table 1 and Fig. 4).

Root electrolyte leakage. The root electrolyte leakage, as an indicator of plasma membrane permeability, was higher in the Super Dominus than for Dominus (Table 1 and Fig. 6). In both cultivars, Si nutrition resulted in a significant decrease in root electrolyte leakage. The root electrolyte leakage of Super Dominus plants infected with *P. melonis* was significantly greater than for plants without infection. The interaction between Si nutrition and *P. melonis* infection also was significant (Table 1 and Fig. 6).

Fig. 1. The *Phytophthora melonis* infection score of cucumber cultivars as affected by Si addition. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Reactive sulfhydryl group concentration. Silicon nutrition significantly increased the reactive SH group concentration in the cucumber roots (Fig. 7). The enhancement of the SH group concentration by Si addition was greater in Dominus than in Super Dominus. There was no significant difference in the reactive SH group concentration between plants grown at 1.0 and 1.7 mM Si treatments. No significant difference was observed between the reactive SH group concentration of the plant infected with *P. melonis* and noninfected plants (Table 1 and Fig. 7). The interaction between Si nutrition and cultivar and the interactions between Si nutrition, cultivar, and *P. melonis* infection were significant (Table 1).

Antioxidant responses. Both in the presence and absence of *P. melonis*, Si nutrition significantly increased CAT activity in roots (Table 1 and Fig. 8), whereas it had no significant effect on APX activity (Table 1 and Fig. 9). The activity of CAT and APX was not affected by increasing the Si level from 1.0 to 1.7 mM (Figs. 8 and 9). Both CAT and APX activities were significantly higher in plants with diseases. However, CAT and APX activities were greater for Dominus than for Super Dominus (Figs. 8 and 9).

Discussion

Infection of cucumber with *P. melonis* resulted in a significant decrease in the root dry weight, although the magnitude of this decrease depended upon the cultivar and Si level in the media. Regardless of the cultivar, the severity of damage induced by *P. melonis* in the cucumbers grown with added Si was significantly lower than in those plants that did not receive Si. Similarly, Si nutrition has been reported to improve resistance of cucumber to *Pythium aphanidermatum* (9), *Fusarium wilt* (5), *Didymella bry-*

Fig. 2. Root dry matter weight of cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Fig. 3. Shoot dry matter weight of cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

oniae, and *Botrytis cineria* (38). Miyake and Takahashi (31) also reported the positive effect of Si on reducing the severity of Fusarium wilt disease in cucumber. The reduced severity of the disease in the Si-supplied cucumber plants in comparison with those grown in Si-free nutrient solution was partly due to the role of Si in the alleviation of oxidative stress induced by *P. melonis*.

In our study, the detrimental effect of *P. melonis* on growth of cucumber plants was associated with oxidative stress induced by reactive oxygen species (ROS). The activated oxygen species are produced when plants are subjected to abiotic and biotic stresses that seriously damage membrane integrity (7). The ROS produced in plants under stress conditions oxidizes membrane lipids, proteins, and nucleic acids (17) and increases membrane permeability.

Higher root membrane permeability is indicative of root cell membrane damage under oxidative stress conditions (7). In our study, infection with *P. melonis* affected the root leakage conductivity of cucumber cultivars that was measured as an indicator of root membrane permeability. Accordingly, a positive correlation ($R^2 = 0.93$) was found between disease severity and root membrane permeability (Fig. 10). In contrast, Si significantly decreased permeability of the plasma membrane and conserved the membrane integrity of cucumber under disease stress induced by *P. melonis*. This is in agreement with the study by Liang (23) in which Si addition decreased the permeability of the plasma membrane of leaf cells and reduced lipid peroxidation in barley.

Another piece of evidence for the positive role of Si in maintaining root membrane integrity was a significant increase observed in the reactive sulfhydryl group concentrations in cucumber plants supplied with Si compared with those grown in Si-free medium. Also, a negative correlation ($R^2 = -0.67$) was found between the SH group concentration and the severity of root and crown rot.

Fig. 4. Root Si concentration in cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Fig. 5. Shoot Si concentration in cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Most of the nonprotein SH groups in plants represent glutathione (18), which is an important antioxidant in plant cells and is involved in the detoxification of ROS (19). Addition of Si may enhance sulfhydryl protein contents at the cell surface and impair the action of respiratory enzymes within the cells (28). Alleviation of disease stress caused by *P. melonis* in cucumber by Si also may be related to deposition of Si in the cell walls and increased stability of components in plasma membranes (28). It is possible that Si nutrition inhibited the structural and functional deterioration of cell membranes of the cucumber plants inoculated with *P. melonis* infection.

One of the mechanisms affecting crop tolerance to biotic stresses is related to the enzymatic antioxidative defense capacity of plants (7). In previous studies, less attention has been paid to the antioxidant mechanisms of plants against diseases. Plants have different defense systems for regulating reactive oxygen species and combating destructive oxidative reactions (15). Antioxidant enzymes are the key elements in defense mechanisms of plants against biotic and abiotic stresses. Plants with high levels of antioxidants are mostly resistant to oxidative damage and thus have a greater tolerance to stresses (41,43). Different tolerance to *P. melonis* of the studied cucumber cultivars might partly be due to their different antioxidative capacity. In this regard, concentration of nonprotein SH groups and activity of CAT and APX in the roots of the studied cultivars varied significantly. In the present experiment, 4 weeks after infecting the cucumber seedlings with *P. melonis*, a significant increase in CAT and APX activities in the roots was observed. Similarly, Cherif et al. (10) reported increased activity of antioxidant enzymes, such as peroxidase, in cucumber in the presence of *Pythium ultimum*. The increase in activity of antioxidant enzymes also has been reported in wheat infected with *Blumeria graminis* f.

Fig. 6. Electrolyte leakage in the root of cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Fig. 7. Reactive sulfhydryl group concentration in the root of cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

sp. *tritici* (4) and in cucumbers infected by powdery mildew (16). The magnitude of the increase in activity of CAT and APX in cucumber roots infected with *P. melonis* was dependent on the crop cultivar. Zhu et al. (44) also showed that the effects of disease stress on antioxidant enzymes varied by plant species and the kind of stress. The disease differently affected the studied antioxidant enzymes because the activity of APX was higher than CAT under disease stress.

In a trend similar to that of root growth, Si nutrition significantly increased the activity of CAT and APX in cucumber plants infected with *P. melonis*, although this increase was less for APX. It has been shown that Si stimulates chitinase activity and rapid activation of peroxidase and polyphenoloxidase after fungal infection (21,22). Zhu et al. (44) reported that Si application increased SOD and APX activities in cucumber under salt stress. Addition of Si also increased SOD and CAT activities but decreased APX activity in tomato seedlings exposed to salt stress (44). In the present study, the increased activity of CAT and APX in the *P. melonis*-infected cucumber plants treated with Si might have resulted in decreased root membrane permeability and increased reactive SH group contents. Increasing the activity of antioxidant enzymes may be an important factor in enhancing crop resistance to the oxidative stress induced by *P. melonis* infection and improving cucumber growth even in the presence of infection. Accordingly, a significant correlation was found between the root CAT activity and root disease severity (Fig. 11), but there was no significant correlation between the root APX activity and root disease severity.

According to the results, the Si level of 1.0 mM in the nutrient solution was effective in reducing the damage of *P. melonis* infection on the cucumber plants. By increasing the Si level in the media to 1.7 mM, there was no further increase in antioxidative re-

sponse of the cucumber plants; thus, root growth improvement was observed. The result of Si analysis in the plant tissues also indicated no further increase in Si uptake when Si in the nutrient solution was increased from 1.0 to 1.7 mM.

Although mechanisms for Si uptake and transport in plants are still unclear, two general mechanisms in higher plants have been suggested: their relative contribution is dependent on plant species and Si supply level (1,24). Some researchers have reported that Si absorption by cucumber roots is a passive process (27), whereas others think that Si uptake in cucumber is active and independent of external Si concentrations (24).

Conclusion. Infection of cucumber with *P. melonis*, depending on the cultivar and Si level in the media, resulted in a significant decrease in root dry weight. The detrimental effect of *P. melonis* on growth of cucumber plants was associated with the oxidative stress induced by ROS. The root electrolyte leakage of plants infected with *P. melonis* was significantly greater than that of the plants that were not infected. Both CAT and APX activities were significantly higher in plants with disease. In contrast, Si significantly decreased the permeability of the plasma membrane and conserved the membrane integrity of cucumber under disease stress induced by *P. melonis*. In addition, the reactive sulfhydryl group concentration and antioxidant enzyme (i.e., APX and CAT) activities of cucumber plants were increased by Si. According to the results, increased activity of antioxidant enzymes in cucumber plants is an important

Fig. 8. Catalase (CAT) activity in the root of cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Fig. 9. Ascorbate peroxidase (APX) activity in the root of cucumber cultivars as affected by Si addition and *Phytophthora melonis* infection. Bars with the same letter are not significantly different at $P < 0.05$ according to Fisher's protected LSD.

Fig. 10. Correlation between root membrane permeability and severity of disease. Disease score shows the severity of *Phytophthora melonis* infection assessed based on progressive development of necrotic symptoms on roots. * indicates that the correlation is significant at $P < 0.05$.

Fig. 11. Correlation between root catalase (CAT) activity and severity of disease. Disease score shows the severity of *Phytophthora melonis* infection assessed based on progressive development of necrotic symptoms on roots. * indicates that the correlation is significant at $P < 0.05$.

factor in enhancing crop resistance to oxidative stress induced by *P. melonis* and improving growth even in the presence of infection. This result has great practical importance for cucumber production in soilless systems where Si has to be added to the nutrient solution.

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