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Functional Plant Biology

Mesoporous silica nanoparticle-induced drought tolerance in *Arabidopsis thaliana* grown under *in vitro* conditions

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ABSTRACT

Nanoparticles of varying formats and functionalities have been shown to modify and enhance plant growth and development. Nanoparticles may also be used to improve crop production and performance, particularly under adverse environmental conditions such as drought. Nanoparticles composed of silicon dioxide, especially those that are mesoporous (mesoporous silica nanoparticles; MSNs), have been shown to be taken up by plants; yet their potential to improve tolerance to abiotic stress has not been thoroughly examined. In this study, a range of concentrations of MSNs (0–5000 mg L^{-1}) were used to determine their effects, *in vitro*, on *Arabidopsis* plants grown under polyethylene glycol (PEG)-simulated drought conditions. Treatment of seeds with MSNs during PEG-simulated drought resulted in higher seed germination and then greater primary root length. However, at the highest tested concentration of 5000 mg L^{-1}, reduced germination was found when seeds were subjected to drought stress. At the optimal concentration of 1500 mg L^{-1}, plants treated with MSNs under non-stressed conditions showed significant increases in root length, number of lateral roots, leaf area and shoot biomass. These findings suggest that MSNs can be used to stimulate plant growth and drought stress tolerance.

Keywords: abiotic stress, *Arabidopsis thaliana*, drought tolerance, *in vitro*, Mesoporous Silica Nanoparticles, PEG, root length, seed germination.

Introduction

Our rapidly growing global population has increased the demand for food production, which leads to pressure on agricultural industries to enhance production. This demand is further intensified by adverse environmental conditions caused by dramatic changes in climate, due to global warming and subsequent drought events (IPCC 2022). For example, it was reported that drought reduced global maize and wheat yield by 21% and 40% respectively during the period 1980–2015 (Fahad *et al.* 2017).

Drought negatively affects various plant morphological (seed germination, root growth, plant height and biomass), physiological and biochemical processes (photosynthesis and gas exchange, nutrient uptake and translocation, water relations and oxidative status) (Shao *et al.* 2008; Farooq *et al.* 2012; Kandhol *et al.* 2022). Different approaches have been developed to enhance plant drought stress tolerance, including traditional selection and breeding strategies, modified molecular and genomic approaches and the application of exogenous plant regulators (Hussain *et al.* 2018; Seleiman *et al.* 2021). The use of nanomaterials to ameliorate abiotic stress is in its infancy but recent studies have shown that approaches using nanomaterials are now becoming widely recognised (Weisany and Khosropour 2023). Nanotechnology has emerged as a promising approach to improve crop growth and enhance plant resistance to abiotic stress (Lowry *et al.* 2019; Shang *et al.* 2019; Landa 2021).

Among various metal-based nanoparticles (NPs), silica NPs (Si NPs) were demonstrated to have roles as a plant stimulator (Mathur and Roy 2020; Mukarram *et al.* 2022). For example, Si NPs enhanced seed germination in tomato (Siddiqui and Al-Whaibi 2014) significantly increased shoot biomass, pigment contents, enzymic and non-enzymic antioxidants in barley that had recovered from drought stress (Ghorbanpour *et al.* 2020). As shown for Si NPs several recent studies have reported improvement in plant growth induced by mesoporous silica nanoparticles (MSNs). For example, Sun *et al.* (2016) reported that MSNs (~20 nm) enhanced seed germination, photosynthesis and growth of wheat and lupin grown hydroponically. In research carried out by Lu *et al.* (2020), amine-functionalised MSNs (20 and 50 μg mL^{-1}) were found to significantly increase photosynthesis, growth and yield of *Arabidopsis* plants. In other studies, Sun *et al.* (2018), foliar application of abscisic acid encapsulated within MSNs reduced drought effects on *Arabidopsis thaliana*, as shown by alterations in leaf stomatal aperture, water loss, plant survival rate, and flowering spike numbers. Further, *in vivo* treatment of salicylic acid-loaded MSNs remarkably improved pathogen-related resistance in pineapple (Lu *et al.* 2019).

Although functionalised or biochemically-loaded MSNs have been examined in plants, the study of interactions of bare or non-functionalised MSNs with plants has been limited. *In vitro* culture, which uses sterile and controlled composition media, provides an opportunity to investigate the direct interaction between nanoparticles and plants. Here, we take advantage of *in vitro* culture and a PEG infusion method to examine whether MSNs can influence the response of *Arabidopsis thaliana* to simulated drought conditions.

Materials and methods

MSNs materials and characterisations

Bare mesoporous silica nanoparticles (MSNs) were commercially purchased (Skyspring Nanomaterials Inc., USA, https://ssnano.com/). The characterisations of MSNs that were used in this and similar studies have been detailed in a number of our previous publications (Hussain *et al.* 2013; Sun *et al.* 2018; Lu *et al.* 2020). To confirm the size and porosity of the MSNs used here, we examined, via dynamic light scattering (DLS) on a Malvern Nano Z NANOSIZER, the hydrodynamic diameters and the zeta potential values of the suspended nanoparticles in water (Wang *et al.* 2022*a*, 2022*b*). The porosity across the MSNs' nanostructure and the associated intercalated water molecule retention were evaluated via thermogravimetric analysis (TGA) (Guirguis *et al.* 2022*a*, 2022*b*).

Seed treatment and growth condition

For seed treatment, the method described by Islam *et al.* (2020) was followed. Seeds of *Arabidopsis thaliana* (L.) Hanh. ecotype Col-0 (Lehle, Texas, USA) were surface-sterilised in a solution containing 450 μL sterile distilled water (H_2O), 500 μL ethanol 100% (ChemSupply, Australia) and 5 μL hydrogen peroxide (H_2O_2, Sigma-Aldrich, Australia). The seeds were then centrifuged at 845*g* for 1 min, rinsed three times, suspended in 0.5% (w/v) water agar, and placed in the dark at 4°C (48 h) for seed stratification.

For soil drying experiments, approximately 50 seeds were sown onto Murashige and Skoog (MS) plates containing 0.44% (w/v) basal salt (Sigma-Aldrich, Australia), 3% (w/v) sucrose (ChemSupply, Australia), 0.8% (w/v) bacteriological agar, and pH adjusted to 5.7. The MS plates were then transferred to a plant growth cabinet (Thermoline Scientific, Australia) with a temperature of 21 ± 1°C under white fluorescent lights (100 μmol m^{-2} s^{-1} photon flux density) and 16:8 h for day:night photoperiod.

Soil-drying simulated drought method

To assess the influence of MSNs on plant grown under simulated drought conditions, three uniform size plants at 2 weeks old, growing in MS plates, were transferred to a 6.9 × 7.6 cm pot (Amazon, Australia) containing a potting mixture (Bunnings, Australia) and then placed in the plant growth chamber under conditions as described above. A volume of 50 mL of water for the control or 50 mL of MSNs-suspended solutions at 500, 1000, 1500, and 2000 mg L^{-1} was applied to the surrounding soil of the plants every 2 days for 14 days. The plants were then subjected to simulated drought condition by completely withholding water while maintaining the same temperature, light intensity and day:night cycle in the growth cabinet. For each treatment, nine plants at 0, 10, 20 days after simulated drought stress were harvested and designated as 'Day 0', 'Day 10', and 'Day 20' samples. The whole experiment was repeated three times, giving a total of 27 samples for each treatment. Physiological parameters, including shoot fresh weight and dry weight, relative chlorophyll content, number of rosette leaves and number of flowers, were then measured for each sample group.

Physiological measurement

For fresh weight measurement, the upper parts of plants (without roots) were harvested and rinsed thoroughly with distilled water three times. The remaining water was then removed using absorbent tissues. The shoot fresh weight (FW) was then measured immediately. To determine shoot dry weight (DW), the samples were maintained at room temperature for 5–10 days until they reached a constant weight. The water content was determined following the formula used by Lu *et al.* (2020): Water content (%) = (FW/DW)/DW × 100.

The relative chlorophyll content of *Arabidopsis* leaves was determined using a chlorophyll meter SPAD-502 (Minolta, Japan) and presented as a SPAD (Soil Plant Analysis Development) value. For each plant, three leaves of similar age were measured at three points along the leaf length (close to the leaf petiole, the middle of the leaf, and close to the leaf tip).

PEG-based simulated drought method

Polyethylene glycol 8000 (Sigma-Aldrich, Australia) was used to simulate, *in vitro*, drought stress at early *Arabidopsis* developmental stages. The PEG infusion method used by Verslues *et al.* (2006) was followed. MSNs-MS Petri plates were prepared by adding MSNs into MS solution (0, 500, 1000, 1500, 2000, and 5000 mg L^{-1}) and then autoclaving at 121°C for 30 min. A volume of 15 mL of the autoclaved media was then poured into 9-cm-in-diameter Petri plates and immediately transferred to a cold room (4°C) for rapid solidification, avoiding the settling of MSNs in the bottom of the media. A volume of 25 mL of PEG at 1%, 10%, 15% and 20% (w/v) made up in MS solution was then pipetted onto the surface of the MSNs-MS Petri plates. Plates were left overnight (12–15 h) to allow PEG to diffuse into the agar. The remaining PEG solution was poured off and the surface of the media was dried using absorbent paper. MSNs-MS media infused with PEG were then used to simulate drought and seed germination rate, main root length and leaf area were determined.

Following MSNs-MS plate preparation, 10 surface-sterilised and stratified *Arabidopsis* seeds were sown onto control plates (No MSNs_No PEG, No MSNs_PEG) or treatment plates (different MSNs concentrations with different PEG concentrations). For one experimental repeat, three plates of each treatment group were used, and the entire experiment was repeated three times. The Petri plates were then placed vertically in a plant growth cabinet with the same conditions as described above. After 7 days, the number of germinated seeds were recorded. Primary root length, the number of lateral roots and leaf area were determined after 14 days using ImageJ software (Maryland, USA, https://imagej.nih.gov/ij/).

Plant growth under non-stressed conditions

After seed treatment, *Arabidopsis* seeds were sown onto MS Petri plates, the surface of which was covered with a layer of MSNs at 1500 mg L^{-1} prepared by using the same method as described for PEG infusion plates. After 14 days, the main root length, number of lateral roots, and leaf area were determined. The seedlings were then transferred to pots using the same set-up as described above for the soil-drying simulated drought method and grown for 7 days under non-stressed conditions. After that, shoot fresh weight (FW), and shoot dry weight (DW) of the plants were measured using the same method as described above for physiological measurements.

Statistical analysis

All experiments were repeated three times independently. Data is presented as mean ± standard deviation (mean ± s.d.). Comparison between treatments were accessed by one-way ANOVA followed by *post-hoc* Tukey's HSD (P-value < 0.05) using IBM SPSS software version 28.0 (IBM Corp., Armonk, NY, USA).

Results

Characterisations of MSNs

The hydrodynamic size and zeta potential of the MSNs were examined via DLS analysis. The MSNs showed an average hydrodynamic size of 80 nm (Fig. 1*a*) and with a zeta potential of −30 mV. The average pore size of MSNs was 5 nm (Fig. 1*b*). The presence of water adsorbed onto the surface of the MSNs was confirmed by TGA analysis over a temperature range from 10°C to 1100°C with a 20°C step (Fig. 1*c*). TGA analysis exhibited three thermal phases. Phase I showed a decrease in the MSNs' mass due to the removal of water molecules at temperatures between 0°C and 130°C. This loss was almost 10% of the total mass of the nanomaterials, followed by only 6% decomposition at the transition temperatures of 170–600°C due to the oxygen-containing functional group pyrolysis, resulting in CO and CO_2 evolution between phase II and III. The MSNs material exhibited good thermal stability, as approximately 85% of the sample was retained at 1100°C. These results revealed, as suggested by Xiao *et al.* (2019), the ability of MSNs to adsorb water from the environment and to sequester it on MSNs' surfaces and within the nanopores of the nanostructures. In this study, we used MSNs with similar properties in size and porosity to the materials used in our previous research (Sun *et al.* 2014; Sun *et al.* 2016; Sun *et al.* 2018; Lu *et al.* 2020). A representative Transmission Electron Microscopy (TEM) result of MSNs obtained by Sun *et al.* (2016) is shown in Fig. 1*d*.

Responses of *Arabidopsis* seedlings to MSNs application under drought conditions

In our preliminary study, we utilised a soil drying method to examine the interaction between MSNs and 4-week-old *Arabidopsis* plants after 0, 10 and 20 days exposed to drought (Fig. 2, Supplementary Fig. S1). We observed that applications of 500, 1000, 1500, 2000 mg L^{-1} MSNs remarkably enhanced chlorophyll content after 10 days of being subjected to drought stress as compared to plants without MSNs (Fig. 2*b*). However, no significant differences were recorded between control and MSNs-treated samples for most of the other parameters, including water content (Fig. 2*a*), number of leaves (Fig. 2*c*), and number of flowers (Fig. 2*d*) at Day 0, Day 10 and Day 20 of post-drought exposure. Therefore, experiments were designed to further examine the effects of MSNs on *Arabidopsis* at earlier developmental stages (1–3 weeks) using the PEG-infusion approach.

The germination rate of *Arabidopsis* seeds grown in different MSNs-PEG concentrations were recorded after 7 days (Fig. 3*a*). Although seed germination was reduced by PEG at high concentrations (15 and 20%), germination percentages of MSNs-treated seeds were significantly higher than the no MSNs_PEG samples, except at 5000 mg L^{-1}

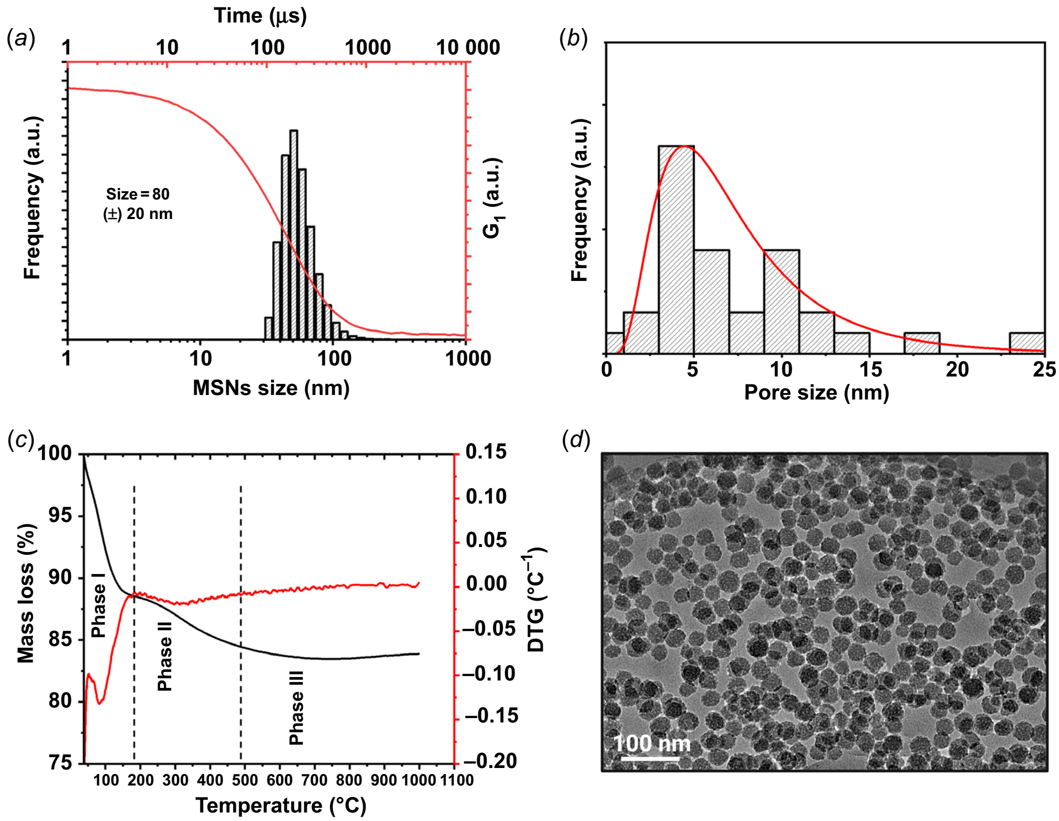

Fig. 1. Characterisations of MSNs. (*a*) Size distribution of MSNs determined by DLS analysis. (*b*) The porosity analysis of MSNs. (*c*) The thermal stability of MSNs assessed by TGA analysis. (*d*) An example of the morphology of MSNs via a TEM image. Abbreviation 'a.u.' stands for arbitrary unit.

MSNs (Fig. 3*a*, *b*). At 15% PEG, seeds treated with all three MSNs concentrations (500, 1000, 1500 mg L^{-1}) increased germination rate by approximately 15% in comparison with the control (no MSNs_PEG) (Fig. 3*a*). Furthermore, the germination percentage of *A. thaliana* in media containing 2000 mg L^{-1} MSNs showed no statistical difference as compared to no MSNs_PEG. Highest concentration of MSNs (5000 mg L^{-1}) remarkably decreased the germination rate to 34.35% under 15%-PEG-based drought (Fig. 3*b*), indicating a negative effect on *Arabidopsis* seeds at high concentrations of MSNs. Moreover, the percentage of seed germination in the no MSNs_PEG media was decreased drastically by 63.58% as compared to no MSNs_no PEG under the 20%-PEG drought condition. Higher germination rates of 55.19% and 54.78% were observed in the media containing 1000 and 1500 mg L^{-1} MSNs, respectively, as compared to no MSNs_PEG and 500 mg L^{-1} MSNs_20% PEG (Fig. 3*a*).

The germinated seeds under the 10% PEG condition were grown vertically for another week and the main root length and leaf area of *A. thaliana* seedlings were measured as shown in Fig. 4*a*–*c*. The seedlings exposed to MSNs at 1500 mg L^{-1} showed the highest increase in root length at 6.82 cm, whereas the root length of plants treated with no MSNs were lowest at 2.90 cm (Fig. 4*b*). Root length of plants grown in the media with added MSNs (500–1500 mg L^{-1}) increased approximately two times more than no MSNs-PEG-treated samples. Interestingly, the exposure to 500, 1000, 1500 mg L^{-1} MSNs increased the root length up to 1.82, 1.69 and 2.39 cm, respectively compared to the control samples (no MSN_no PEG) (Fig. 4*b*). This indicated that MSNs at these concentrations promoted the development of roots over the control level when growing *in vitro*. However, there were no statistical differences in leaf area between MSNs-treated and MSNs-untreated samples (No MSNs_PEG) at 10% PEG (Fig. 4*c*).

Arabidopsis responses to MSN application without simulated drought

Because plants treated with MSNs at 1500 mg L^{-1} showed the highest increases in seed germination and main root length, this concentration was used to investigate its effects on *Arabidopsis* under a non-stressed condition. A similar protocol of PEG infusion was used to prepare 1500 mg L^{-1} MSN-infusion plates without any addition of PEG. Application of 1500 mg L^{-1} MSNs not only improved the root elongation (>2 times) (Fig. 5*a*, *b*) but also increased the number of lateral roots significantly (Fig. 5*c*). Similarly, leaf area of MSNs-treated plants was four times greater than that in the

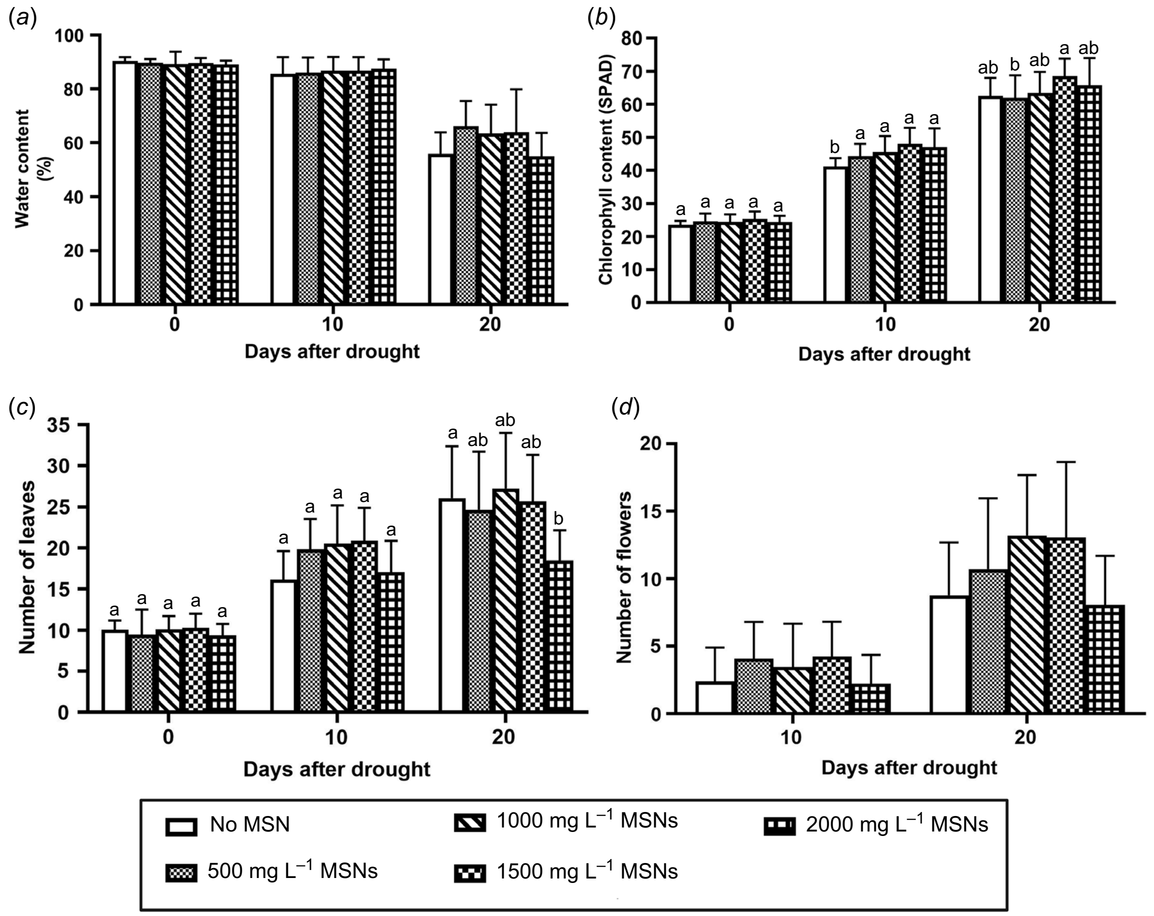

Fig. 2. Physiological parameters for Arabidopsis plants subjected to simulated drought using a soil drying method. Two-week-old Arabidopsis seedlings growing in MS media were transferred to pots and grown for 14 days before being subjected to drought treatment (completely withholding water). Different parameters, including water content (*a*), chlorophyll content (*b*), number of leaves (*c*), and number of flowers (*d*) were measured at 0, 10, and 20 days following drought stress imposition. Data represent the mean ± s.d. of triplicates (n = 27). Different letters above bars indicate significant differences (P < 0.05) between treatments within a common timepoint post-drought simulation, according to Tukey's HSD test.

control (Fig. 5*d*). The 14-day plants from MSN infusion plates were then transferred to pots and fresh weight (FW) (Fig. 6*a*) and dry weight (DW) (Fig. 6*b*) were measured after 7 days. Both FW and DW of seedling shoots treated with 1500 mg L^{-1} MSNs were significantly higher than the control (2.03 and 2.78 times, respectively). These results were consistent with the effects of MSNs on *Arabidopsis* seedlings under the PEG-induced drought condition.

Discussion

Although MSNs have been widely discussed in relation to smart drug delivery systems, findings related to interaction and application of MSNs in plants are still limited, especially plants under drought stress. In this study, PEG at 15% and 20% caused drought effects and significantly reduced germination rate and root length of *Arabidopsis* seedlings as compared with non-stressed controls. That PEG is able to simulate drought stress in plants has been widely reported (Hatami *et al.* 2017; Ahmad *et al.* 2020; Basal *et al.* 2020). PEG treatment is one of a number of experimental drought models available, which belong to three major groups: soil-based, aqueous culture–based and agar-based techniques (Osmolovskaya *et al.* 2018). For at least 50 years, soil drying methods have been applied to conduct drought-related experiments due to their close similarity to the natural environment (Munns *et al.* 2010). However, simply withholding irrigation to soil may cause fast drying rates; precise control of soil water content is difficult and usually requires expensive control systems (Marchin *et al.* 2020). An alternative approach to adequately control water availability is the application of osmotic substances such as polyethylene glycol (PEG) and mannitol.

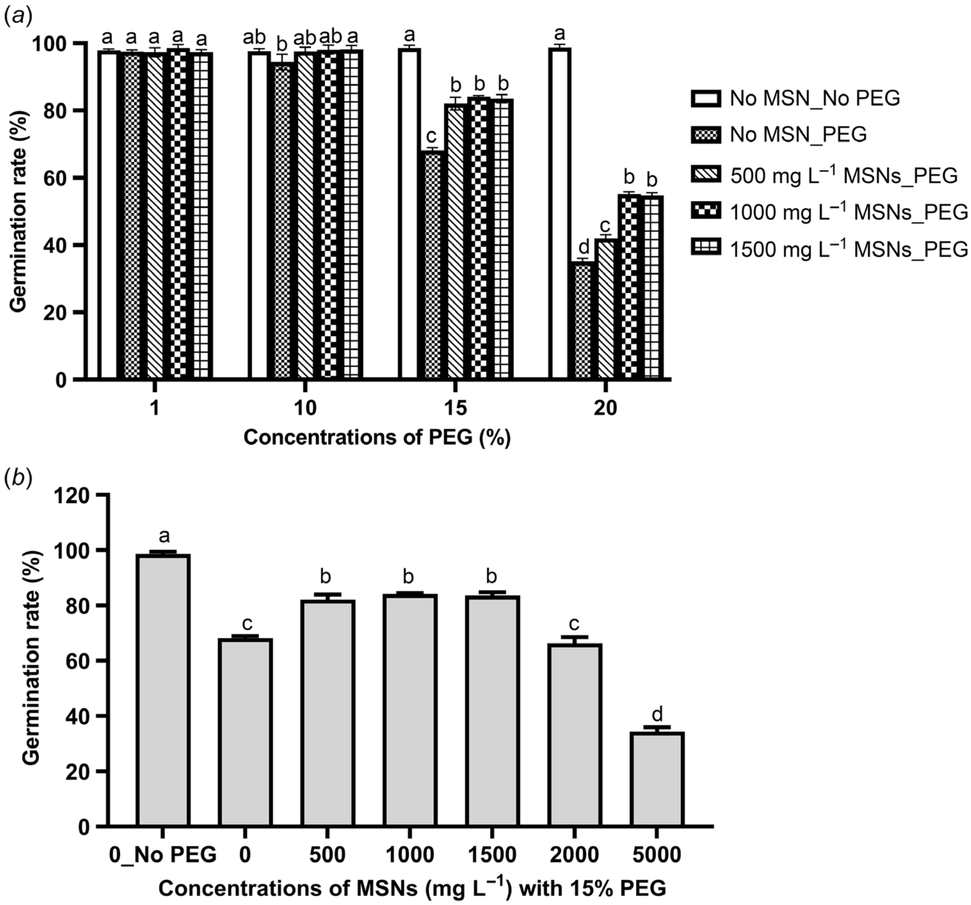

Fig. 3. Germination rate of *Arabidopsis* seeds growing on PEG-infusion agar media. (*a*) Germination rate of seeds grown on MS Petri plates containing different concentrations of MSNs in combination with different concentrations of PEG. (*b*) Germination rate of seeds on MS Petri plates containing different concentrations of MSNs under *in vitro* simulated drought conditions using 15% PEG. Data represent the mean ± s.d. of triplicates ($n = 90$). Different letters above bars indicate significant differences ($P < 0.05$) between treatments within the same concentration of PEG, according to Tukey's HSD test.

Increased concentrations of osmolytes in the growth medium trigger similar effects to those found with low water content due to a reduction in water potential of plant tissues, causing osmotic stress, and simulating drought conditions (Verslues *et al.* 2006). PEG with high molecular weight (>6000 Da) has been commonly used to mimic drought stress. PEG does not enter plant cells to cause toxicity, as do lower-molecular-weight osmolytes such as sodium chloride, and unlike nonionic osmolytes such as mannitol, PEG is not involved in cellular metabolism (Gopal and Iwama 2007; Mahmoud *et al.* 2020). However, due to high viscosity, the addition of PEG in soil or hydroponic media may reduce the diffusion of oxygen to the roots, especially at high concentrations (Osmolovskaya *et al.* 2018; Marchin *et al.* 2020). This problem can be solved by using a PEG-infused agar method, which allows roots to grow on the agar surface when the agar medium is placed vertically (van der Weele *et al.* 2000) as in our study. Therefore, PEG infusion agar generates a more stable, highly accurate and reproducible model to simulate drought relative to soil-based models; and due to its solid form is closer to natural conditions than, for example, aqueous hydroponic culture. In addition, as has been shown by other researchers (for example, Verslues *et al.* 2006; Paudel *et al.* 2016), an agar-based PEG infusion method is the most suitable method to study drought tolerance in small-sized species such as *A. thaliana* that have a fine root system and therefore, are difficult to investigate using conventional soil-based media (van der Weele *et al.* 2000; Verslues *et al.* 2006; Paudel *et al.* 2016; Frolov *et al.* 2017; Mawodza *et al.* 2022).

Seed germination is considered one of the most important stages of plant growth. It requires sufficient water to initiate the metabolic processes needed for germination. In our study, treatment with MSNs significantly enhanced the germination rate of *Arabidopsis* seedlings subjected to PEG-simulated drought. Similarly, several reports of enhanced seed germination following treatment with Si NPs have been found for cucumber (Alsaeedi *et al.* 2019*a*), maize (Karunakaran *et al.* 2016),

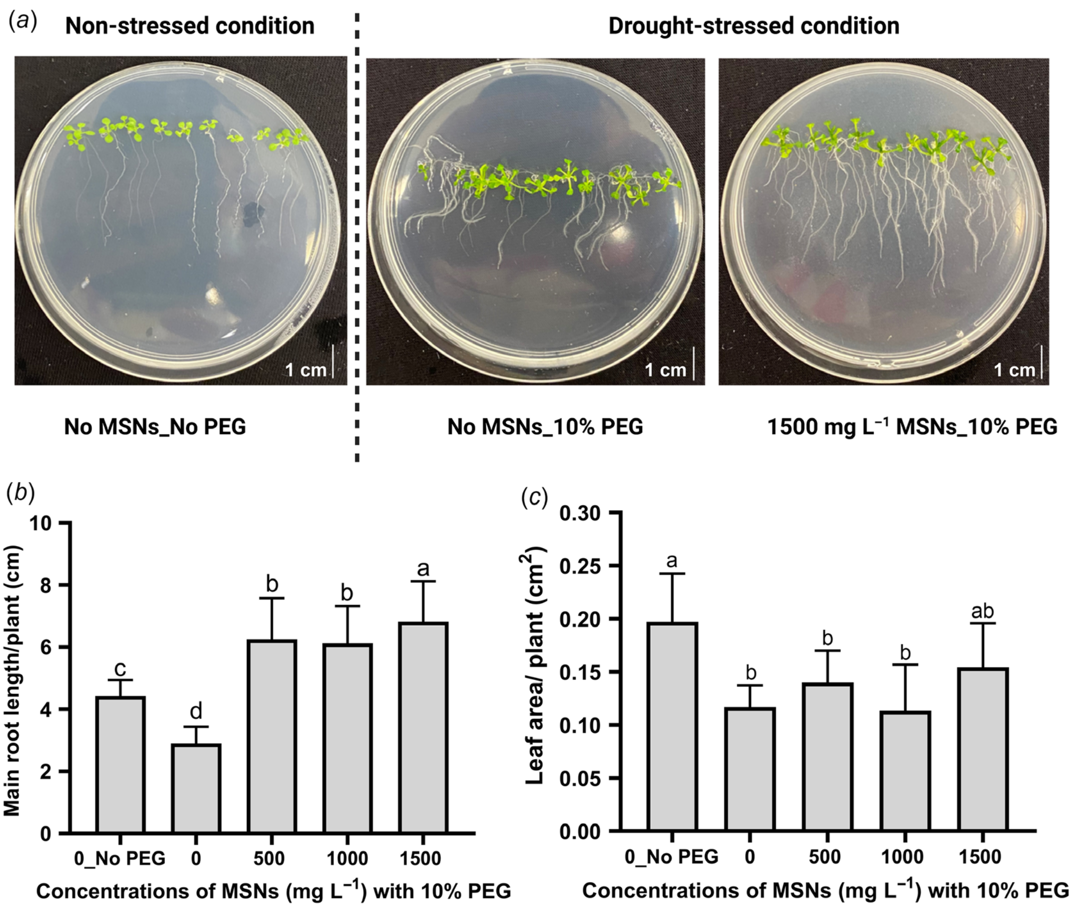

Fig. 4. *Arabidopsis* seedlings growing on MSNs-MS media supplemented with 10% PEG. (*a*) Representative images of *Arabidopsis* plants after 14 days growth *in vitro* under non-stressed conditions (No MSNs_No PEG) or drought-stressed conditions (No MSNs_PEG and 1500 mg L^{-1} MSNs_PEG). Root length (*b*) and leaf area (*c*) of plants grown for 14 days under these conditions. Data represent the mean ± s.d. of triplicates ($n = 90$). Different letters above bars indicate significant differences ($P < 0.05$) between treatments according to Tukey's HSD test.

and sunflower (Janmohammadi *et al.* 2016). Rahimi *et al.* (2021) found that marigold (*Calendula officinalis* L.) seed priming with Si NPs increased germination percentage following various PEG-induced drought periods.

Based on our current work and that of others, we propose potential mechanisms for the interaction of MSNs with *A. thaliana* seeds and seedlings (Fig. S2). Due to their small size, nanoparticles may penetrate the seed coat and regulate the activities of reactive oxygen species (ROS), which become primary messages that mediate various downstream physiological responses (Khodakovskaya *et al.* 2009; Azimi *et al.* 2014; Kim *et al.* 2017) (Fig. S2A). For example, Acharya *et al.* (2020) confirmed by transmission electron microscopy (TEM) that silver NPs (Ag NPs, ~29 nm) penetrated through watermelon seed coats and were then located in embryo cells. The activated ROS signals induced by NPs can lead to loosening of cell wall structure, facilitating the uptake of water and oxygen into seed cells (Mahakham *et al.* 2017). ROS-stimulated accumulation of the α-amylase enzyme may weaken endosperm cell walls and increase starch hydrolysis to provide sugars for initiation of germination (Rahimi *et al.* 2021; Nile *et al.* 2022) (Fig. S2A).

We have previously shown that, under non-stressed conditions, the applications of MSNs in *Arabidopsis* (Lu *et al.* 2020), wheat and lupin (Sun *et al.* 2016) did not cause oxidative stress and membrane damage as indicated by no changes in the concentration of H_2O_2 and malondialdehyde (MDA). On the other hand, under abiotic stress conditions, such as drought or extreme temperatures, plants experience an increase in the generation of ROS, which can cause damage to cellular components, such as proteins, lipids, and DNA, leading to impaired plant growth and development (Kim *et al.* 2017). Si NPs have been demonstrated to have a protective effect on plants by enhancing ROS scavenging through the regulation of antioxidant systems (Mathur and Roy 2020; Mukarram *et al.* 2022). In a recent study by Hajizadeh *et al.* (2022), Si NPs have been shown to enhance the tolerance of rose (*Rosa damascena* Mill.) to PEG-induced drought stress by reducing the concentration of H_2O_2 and increasing the

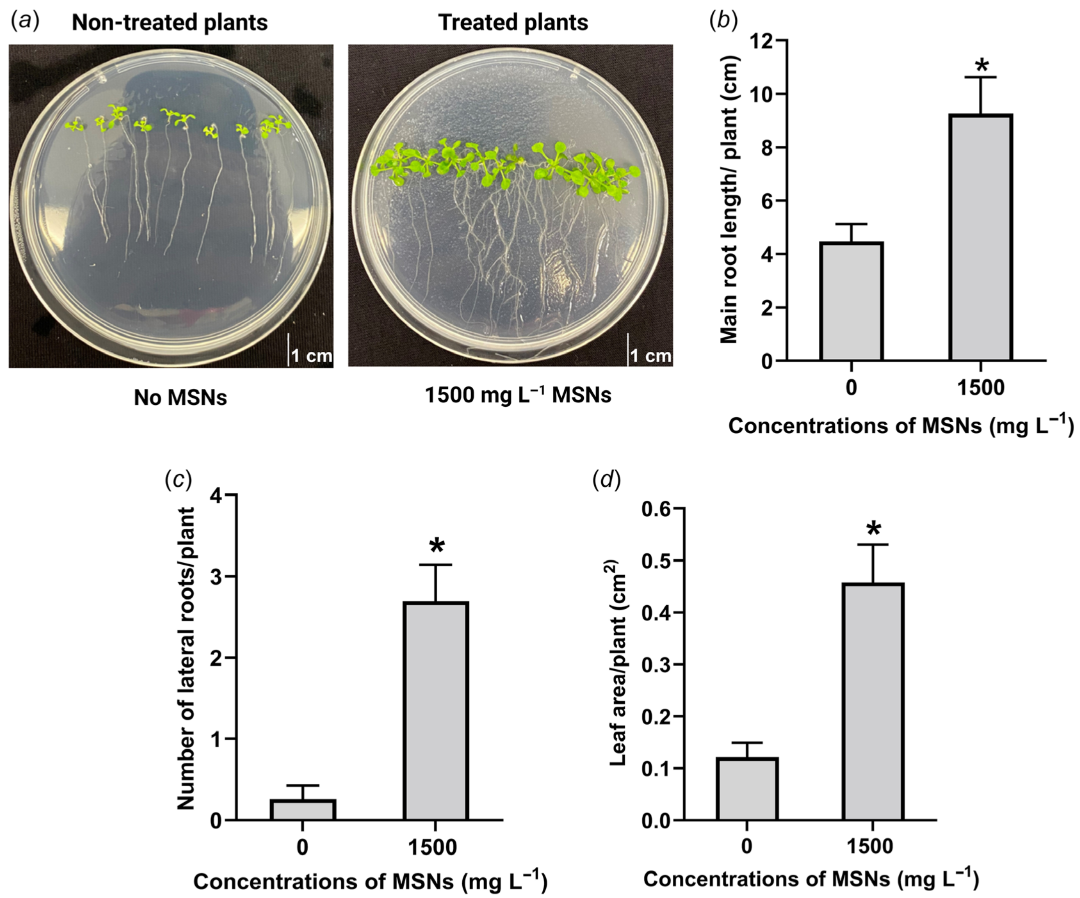

Fig. 5. *Arabidopsis* seedlings grown in MSNs-MS media under non-stressed conditions. (*a*) Representative images of *Arabidopsis* plants after 14 days growing on the media with and without MSNs. (*b–d*) Main root length, number of lateral roots and leaf areas of 14-day plants growing in the media with and without MSNs, respectively. Data represent the mean ± s.d. of triplicates ($n = 90$). The asterisk (*) indicates a significant difference ($P < 0.05$) between the control and the MSNs-treated samples according to one-way ANOVA analysis.

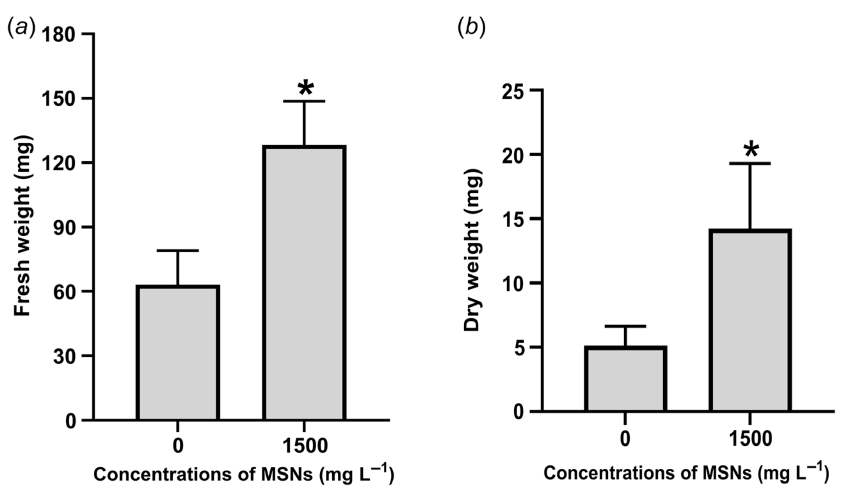

Fig. 6. Effect of treatment with MSNs on shoot fresh weight (*a*) and shoot dry weight (*b*) of Arabidopsis plants after 14 days following transfer into soil in pots. Data represent the mean ± s.d. of triplicates ($n = 90$). The asterisk (*) indicates a significant difference ($P < 0.05$) between the control and the MSNs-treated samples according to one-way ANOVA analysis.

activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GOX), and peroxidase (POD). Furthermore, NP uptake may impact the complex phytohormone-mediated signalling based on the interplay between abscisic acid (ABA) and gibberellin (GA) to break seed dormancy (Mathur and Roy 2020).

Interestingly, our study also showed that a high concentration of MSNs at 5000 mg L^{-1} caused a significant decrease in seed germination of *in vitro* grown *Arabidopsis* under drought stress. To date, studies on the toxicity of silica nanoparticles are still limited. Si NPs (14, 50 and 200 nm) with concentrations up to 1000 mg L^{-1} do not affect stem length, biomass and rosette leaf size of *A. thaliana* grown in pH-adjusted hydroponic media (Slomberg and Schoenfisch 2012). Sun *et al.* (2016) also reported no side effects of MSNs at 2000 mg L^{-1} in terms of oxidative status or cell membrane integrity of both wheat and lupin, whereas, the same concentration of Si NPs (>30 nm) decreased the root and shoot biomass and plant height in cotton (*Gossypium hirsutum*) (Le *et al.* 2014). The effect of the high concentration of MSNs used in our study may be attributed to increased alkalinity or pH caused by the silanol groups of the MSNs (Slomberg and Schoenfisch 2012). However, the exact mechanism needs to be further investigated.

During the germination process, the radicle or primary root is the first organ to interact directly with NPs. Our study showed that MSNs increased primary root length and number of lateral roots and leaf area in *Arabidopsis* grown under both non-stressed and drought conditions. Our previous report has demonstrated that MSNs were taken up by roots via either symplastic or apoplastic pathways and eventually transported to leaves via the xylem (Sun *et al.* 2014) (Fig. S2B). In a recent review by Mukarram *et al.* (2022), the impacts of Si NPs treatment on phytohormone production has been shown. For example, the application of Si NPs altered both the concentration of key phytohormones such as indole-3-acetic acid (IAA), gibberellic acid (GA), and abscisic acid (ABA) in the roots and the expression of genes that are regulated by them (Lang *et al.* 2019). Here, the enhancement of primary root elongation induced by MSNs may be attributed to the uptake of MSNs into the root system, which may stimulate the production of hormones, such as IAA, that play a key role in regulating root growth. The development of lateral roots leads to higher surface areas of the root system, enhancing uptake of water and nutrients. NPs may pass readily through lateral roots via the apoplast due to underdeveloped cuticles or in regions of disconnection of the casparian strip with the main root (Lv *et al.* 2019). Increased root growth of MSN-treated plants may be attributed to the penetration and increased content of cellular Si inside plant cells. This is correlated to our finding that increased fresh weight and dry weight were recorded in *Arabidopsis* treated with MSNs after 14 days of being transferred to pots. Overall, MSNs improved the growth of *Arabidopsis* under both non-stressed and drought conditions.

The beneficial effects of Si NPs on plant growth were further demonstrated in various species such as tall wheatgrass (*Agropyron elongatum* L.) (Azimi *et al.* 2014), the tuberose (*Polianthes tuberosa* L) (Karimian *et al.* 2021), and lemongrass (*Cymbopogon flexuosus* (Steud.) Wats) (Mukarram *et al.* 2021). During water deficit induced by PEG-8000 treatment, application of 150 mg L^{-1} Si NPs increased *in vitro* grown banana shoot growth and chlorophyll content and reduced electrolyte leakage (Mahmoud *et al.* 2020). Alsaeedi *et al.* (2019*b*) reported that Si NPs increased the content of nitrogen and potassium by more than 30% in cucumber, contributing to increased chlorophyll content, plant height and fruit yield grown under water deficient conditions.

How might MSNs be taken up by plants? It was demonstrated that the unmodified MSN surface comprised of numerous silanol groups (SiOH), which are hydrophilic and negatively charged under various pH conditions (Pyo and Chang 2021). The silanol groups are likely to react with water molecules via electrostatic interactions to generate mono-silicic acid, $Si(OH)_4$ (Xiao *et al.* 2019), which was hypothesised to be taken up by plants via similar pathways as those of Si in its bulk form, using silica-specific aquaporin transporters such as Lsi1 and Lsi2 (Ma *et al.* 2006; Nazaralian *et al.* 2017). Indeed, the Lsi1 aquaporin channel, an influx transporter, was suggested to facilitate the transportation of Si NPs through the epidermis, cortex, and endodermis via the symplastic pathway in roots, while the Lsi2, an efflux transporter, could transport Si NPs into the xylem to travel to the leaves (Mukarram *et al.* 2022).

Importantly, in contrast to solid Si NPs, nanopores distributed across MSNs are likely to increase the absorption of water and nutrient ions (such as Na^+, K^+ and Ca^{2+}) into their porous structure, providing a greater opportunity for water and ions to be delivered to plants subjected to drought stress (Wang *et al.* 2020; Fig. S2B). From the TGA analysis result, even when the MSNs were completely dry, they had still adsorbed water electrostatically, and this water may be available for root uptake. Recently, Mitra *et al.* (2022) demonstrated the beneficial roles of MSNs over conventional Si NPs for enhancing plant growth, reducing stress, and promoting basic metabolic rates in the dicot *Vigna radiata*. These authors also proposed that the pores of MSNs were filled with ions present in the MS media, which may increase their availability to emerging seedling roots. Similarly, Adams *et al.* (2020) demonstrated that unmodified MSNs could interact with ions in nutrient solution to increase nutrient delivery of limiting nutrients such as Ca, K, Mg, Zn and Mn to zoysiagrass (*Zoysia japonica* Steud.), enhancing its establishment in the field.

Conclusion

The use of nanoparticles has emerged as a promising strategy for improving drought tolerance in plants and thereby enhancing crop production and management. We discovered that MSNs at 500, 1000 and 1500 mg L^{-1} concentrations improved seed germination, primary root length, lateral root numbers, leaf area and shoot biomass of *Arabidopsis* seedlings under optimal and PEG-induced drought condition.

Notably, MSNs at high concentrations (up to 2000 mg L^{-1}) had no measurable negative effects on growth. It is evident that Si NPs can penetrate into the plant body, trigger signalling pathways to break seed dormancy, assist in photosynthesis, and enhance water and nutrient uptake, thereby contributing to sustained and even increased plant growth under drought stress. Finally, our study illustrates and highlights that the application of MSNs to plants is a promising solution to improve crop performance under drought conditions, contributing to enhanced agricultural productivity in the context of climate change.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study are available in the article and accompanying online supplementary material.

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