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Role of silica nanoparticles in enhancing drought tolerance of cereal crops

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Abstract

Cereal crops are essential for providing essential nutrients and energy in the daily human diet. Additionally, they have a crucial role as a significant constituent of cattle feed, hence enhancing meat production. Drought, being an abiotic stressor, adversely affects the growth and yield of numerous crops on a global scale. This issue poses a significant and pressing obstacle to maintaining global cereal crop production and ensuring food security. Nanoparticles have become a valuable resource for improving cereal crop yield and productivity under ongoing rapid climate change and escalating drought conditions. Among these, silica nanoparticles (SiNPs) have demonstrated their potential for agricultural applications in regions with limited water availability. Drought stress has detrimental effects on cereal crops, impacting their growth, metabolic, and physiological processes, hampering water and nutrient absorption, disrupting cellular membranes, damaging the photosynthetic apparatus, and reducing antioxidant activities by altering gene expression. SiNPs help preserve cellular membranes, regulate water balance, and improve water and nutrient absorption, resulting in a substantial enhancement in plant growth under water-deficit conditions. SiNPs also protect the photosynthetic system and enhance its efficiency, facilitate the accumulation of phenolics, hormones, osmolytes, antioxidant activities, and gene expression, thus empowering plants with increased resistance to drought stress. Moreover, SiNPs decrease leaf water loss by promoting stomatal closure, primarily by fostering the accumulation of abscisic acid (ABA) and mitigating oxidative stress damage by activating the antioxidant defence system and reducing reactive oxygen species (ROS). However, a limited number of studies examine the role of SiNPs in cereal crops under drought stress conditions. In this review, we highlighted the promising potential of SiNPs to improve cereal crop resilience by changing morpho-histological traits, antioxidant properties, and gene expression to maintain food security in drought-prone areas. This study will aid researchers in using SiNPs as an environmentally benign way to improving drought resistance in cereal crops in order to fulfill global food supply needs.

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Introduction

Cereal crops belong to the Gramineae family and are typically grown for their edible components, which include germ, endosperm, and brain, forming their botanical structure. The cereal family includes globally significant grain species such as wheat, maize, rice, oat, millet, sorghum, and rye which play a significant role as a primary source of food or caloric intake in many regions of the world (Sharf-Eldin et al., 2023; Toulotte et al., 2022). Among these, wheat and rice are the most dominant and widely cultivated (Arendt and Zannini, 2013). Despite their diverse geographical origins, each of the cereal crops is now extensively grown in a wide variety of climatic conditions. Cereals are considered the most widely cultivated and consumed agricultural commodity worldwide (Stefoska-Needham et al., 2015). Cereals and cereal products serve as popular staple foods in the majority of countries worldwide, contributing more dietary energy than any other crop category, and are primary sources of essential micro or macronutrients (Laskowski et al., 2019). According to the Food and Agriculture Organization (2021), cereals contribute approximately 47% of protein and 51% of calories in an average human diet (FAO, 2021). It was reported that between 2019-2020, the global cereals production was estimated as 2710.7 million tons (Adeboyejo et al., 2023; FAOSTAT, 2023). Asia region holds significant influence over the world cereal trade due to its concentration of production, consumption, and imports of cereals within this region. In 2017, China alone contributed to approximately 20% of global cereal production (Yue et al., 2017). Even though, the global population is projected to reach 9.6 billion by the end of 2050, which demands a 70-100% increase in agricultural yield to encounter the requirements of this growing population (Searchinger et al., 2014).

The rising climate change and global warming, a diminishing availability of fertile land, and an escalation in the severity of abiotic stresses result in significant yield reduction (Malhi et al., 2021; Rivero et al., 2022). Consequently, the decline in agricultural yield poses a serious threat to global food security. Among abiotic stresses, drought stress (DS) has adverse effects on the growth and productivity of crops (Mubarik et al., 2021). In the future both the frequency and severity of DS will upsurge, which will present significant harm to crop production (Nasir and Toth, 2022). DS hinders seed germination, photosynthetic efficiency, hormonal activities, physiological processes, or plant growth (Ahmad et al., 2022; Huang et al., 2020). DS significantly affects the spatial arrangement and morphology of crop roots (Elkelish et al., 2021). DS also lowers chlorophyll production and raises canopy temperature (CT), leading to a decrease in both photosynthesis and overall plant metabolic functions (Elgaml et al., 2022). Moreover, DS results in decreased membrane permeability and increased production of ROS (Mittler et al., 2022), leading to deterioration of membrane veracity, enhanced electrolyte leakage, and harm to proteins, lipids, and DNA (He et al., 2022). In a study, Safian et al. (2022) investigated the influence of DS on the quality and yield of sorghum (Sorghum bicolor) and maize (Zea mays) and determined that DS significantly altered the substrate conformation in these crops (Safian et al., 2022). Plants have naturally evolved mechanisms to alleviate the effects of DS, but their resilience is limited to a specific degree (Shah et al., 2022; Singh and Rao, 2023). To enhance agricultural yield and mitigate the impacts of DS, different approaches such as the application of hormones (Souri et al., 2021), osmolytes (Zhang et al., 2018), nutrients (Akhtar et al., 2021), nano-fertilizers (Behboudi et al., 2018), or screening and breeding of resilient cultivars can be used to boost agricultural yield (Rasheed et al., 2022). Implementing these approaches can protect crops from the adverse effects of DS and significantly enhance agricultural yield to meet food demands (Das et al., 2023).

Nanotechnology, an intriguing interdisciplinary science, presents vast prospects for applications in the food industry, global environmental research, or agriculture (Garg *et al.*, 2022; Gul and Beedu, 2023; Javed *et*

al., 2023; Mersha *et al.*, 2023). Among the various methods utilized to enhance plant tolerance to droughtinduced stress, the use of nanoparticles (NPs) is an innovative strategy that has proved its effectiveness in helping plants to tolerate water deficit conditions (Hayat *et al.*, 2023; Kandhol *et al.*, 2022; Rajput *et al.*, 2021). SiNPs, amongst the numerous metal and non-metal NPs, have been reported to enhance plant tolerance to abiotic stresses, particularly drought, by mitigating the adverse effects (Mathur and Srivastava, 2022). The fundamental premise behind employing SiNPs in agriculture is to decrease harmful environmental inputs and high fertilizer costs because they are manufactured utilizing environmentally friendly methods to alleviate adverse effects of various chemicals (Alharbi *et al.*, 2022). Due to their executive properties, including small dimensions and large surface area, SiNPs have a realistic potential for dispersion in plant tissues (Aqeel *et al.*, 2023). SiNPs are reported to endorse plant adaptation and resilience to water deficiency by regulating plant growth and productivity through triggering different responses at the biochemical and physiological levels, including the activation of defence mechanisms and expression of stress-related genes (Etesami *et al.*, 2022; Mahawar *et al.*, 2023).

Even though numerous researchers have discussed the use of SiNPs to enhance plant growth and alleviate stress but their potential in cereal crops under DS is yet to be fully explored (Sayed *et al.*, 2022). Therefore, the objective of this review is to highlight the promising potential of using SiNPs as a strategy to bolster the resilience of cereal crops via modifying morpho-histological characteristics, antioxidant attributes, and gene expression for ensuring food security in increasing DS. This detailed review will serve as a valuable resource for upcoming researchers to implement SiNPs as an eco-friendly approach to increase drought resilience in cereal crops to meet global demand for food production.

Silica nanoparticles (SiNPs): Synthesis, Characteristics, and Transport

Silicon (Si) has been regarded as a valuable element due to its positive contributions to the improvement in the growth of various plants (Brown *et al.*, 2022). While Si is not essential for the survival of plants, therefore, been suggested as a semi-essential element that protects against various types of stresses (Sarkar *et al.*, 2022). Furthermore, the lack of Si has been observed to disrupt the equilibrium of other nutrients in the plant body (Hosseini-Nasr *et al.*, 2023; Teixeira *et al.*, 2020). It is believed to be the sole nutrient that does not cause any detrimental effect even when it accumulates excessively in plant tissues (de Mello Prado, 2023). Silica typically constitutes approximately 0.1-10% of the dry weight of the majority of terrestrial plants (Jinger *et al.*, 2020; Schaller *et al.*, 2021). Hence, plants that naturally hyperaccumulate Si can play a significant role in Si cycle by aiding in the restoration of soil Si levels when dead plant tissues decompose (Zhang *et al.*, 2018).

SiNPs consist of an array of Si-O-Si bonds, typically with sizes smaller than 100 nm. The surface of SiNPs features a hydroxyl group (Si-OH), commonly referred as silanol group (Sarkar *et al.*, 2022). SiNPs have garnered significant attention due to their cost-effective large-scale production, adjustable particle size, hydrophilic properties, and enhanced biocompatibility (Park *et al.*, 2019; Yadav *et al.*, 2022). Owed to these attributes, there has been a surge in the commercial utilization of SiNPs across various domains, including cancer therapy and drug delivery in pharmaceutics (Ahmed *et al.*, 2022; Shahbaz *et al.*, 2023); for disease labelling, imaging and biosensor in diagnostics (Şen Karaman *et al.*, 2021); for packaging, catalysis and manufacturing in industrial sector (Yadav *et al.*, 2022); and in agro-industry for the synthesis of nanoformulations, controlled-release fertilizers, and nano-pesticides, etc. (Fincheira *et al.*, 2023). SiNPs have been suggested as eco-friendly bio-stimulants for promoting plant growth and increasing crop yield and germination rates (Siddiqui *et al.*, 2020). In this sense, SiNPs are recognized to enhance silica uptake in crops which in turn has a beneficial impact on nutrient levels such as the ratio of carbon, nitrogen, and phosphorus, ultimately leading to improved agricultural yield (Ijaz *et al.*, 2023; Roychoudhury, 2020).

Synthesis of SiNPs

The synthesis of SiNPs is indeed a fascinating process, that involves various techniques, with particular emphasis on green synthesis and sol-gel synthesis methods. Green synthesis is an efficient, cost-effective, and eco-friendly approach to SiNPs production (Sankareswaran *et al.*, 2022). Plant tissues that possess a higher silica content are typically utilized as precursors for the synthesis of SiNPs, including rice husk (Mahalingam and Sivaraju, 2023), rice straw (Osman and Sapawe, 2019), sugarcane bagasse (Boonmee and Jarukumjorn, 2020), sugar beet bagasse (San *et al.*, 2014), etc. Conversely, the sol-gel method is chemical procedure. Stober method is considered the ideal approach for sol-gel synthesis, involving multiple stages such as hydrolysis, gelation, ageing, polycondensation, calcination and drying (Tadanaga *et al.*, 2013). Sol-gel method offers advantages over green synthesis by providing superior control over the morphology and particle size of NPs (Arya *et al.*, 2021). Sol-gel approach entails hydrolysis and condensation of specific precursor substances, such as tetra-ethyl ortho-silicate or sodium silicate (Na₂SiO₃), in the hydrogen chloride or ammonia presence as a catalyst (Horváth and Sinkó, 2022). Furthermore, by amending the Stober method, various kinds of SiNPs can be obtained (Sarkar *et al.*, 2022).

Size of SiNPs

SiNPs are composed of approximately 46.83% silicon and 53.33% oxygen, with sizes typically within the range of 5 to 100 nm (Bhat *et al.*, 2021). According to (Mathur and Srivastava, 2022) SiNPs with a size of less than 20 nm inhibited the germination and growth of rice seedlings due to their small size and large surface area. However, SiNPs larger than 20 nm had beneficial effects on various plant characteristics (Table 1). Likewise, research has revealed that treatment of SiNPs enhanced seed germination of tomato seedlings (Parveen and Siddiqui, 2022).SiNPs possess substantial surface area and intrinsic surface reactivity, making them well-suited for chemical modification.

Concentration of SiNPs

The concentration of SiNPs used for crops varies depending on the specific application and the desired outcome (Table 1). The impact of SiNPs on plants varies because each plant species responds differently to various types of NPs, depending on plant variety, dosage, and mode of application (Giorgetti, 2019; Karimian *et al.*, 2021). For instance, the SiNPs concentration range of 400 to 600 mg L⁻¹ was the best for the growth of rice (Raja *et al.*, 2021) and wheat (Raza *et al.*, 2023).

Uptake and Transport of SiNPs

Plant roots and leaves have the capability to absorb NPs. The absorption and accumulation of NPs can vary among different plant species, depending on their uptake mechanisms, physical characteristics, transport, and distribution in specific plant parts which may trigger defence mechanisms in response to NPs (Verma *et al.*, 2022). Si may be administered either directly to the root system as basal dressing (Fetsiukh *et al.*, 2021), or as foliar spray onto plant's leaves (Sharf-Eldin *et al.*, 2023). The foliar spray can penetrate leaves and then be transported to various plant organs through cuticular layer or stomata (Hellala *et al.*, 2020).

Si uptake and its significance in promoting plant growth and increasing resistance and tolerance to biotic or abiotic stresses has been well studied (Souri *et al.*, 2021). Plants primarily absorb Si in mono-silicic acid form and transport it to various plant parts, including leaves through xylem vessels. In the leaves, it undergoes precipitation and transformed into silica, which is then deposited beneath the cell wall layer (Mathur and Roy, 2020; Savvas and Ntatsi, 2015). Si uptake occurs through both apoplastic and symplastic pathways, the latter one being controlled by influx transporter LSi1 and efflux transporter LSi2 (Wani *et al.*, 2023). Both LSi1 and LSi2 transporters are found within the same cell, LSi2 functions as a proton exchanger, relying on ATP to direct the transport of Si towards the xylem vessels for their subsequent distribution to all plant parts (Yang *et*

al., 2018). Si is loaded into the xylem vessel by an unknown transporter, although another transporter called LSi6, plays a role in facilitating the subsequent translocation in the leaf tissues (Mathur and Roy, 2020). Nevertheless, there have been limited studies addressing the specific mechanism by which plants uptake SiNPs. Amongst the SiNPs, the uptake of mesoporous forms by roots has been extensively examined and is wellunderstood for its positive impact on the improvement of plant growth (Ghorbanpour et al., 2020). Fluorescein isothiocyanate (FITC) labelled monodisperse mesoporous SiNPs uptake was explained using the combined application of transmission electron microscopy, confocal laser scanning microscopy, and protoninduced X-ray emission elemental analysis (Nair et al., 2011). It was determined that uptake in plant roots occurred through apoplastic and symplastic pathways, followed by translocation to the shoots via the xylem vessels. Furthermore, FITC-labelled NPs were taken up by the endocytosis pathway in Liriodendron hybrid cell suspension (Xia et al., 2013). In a study conducted by Sun et al. (2016), it was found that mesoporous SiNPs were highly effective in infiltrating chloroplasts, which had beneficial impact on photosynthetic rate of lupin and wheat plants (Sun et al., 2016). As per research by Schaller et al. (2013), the uptake of SiNPs occurred through a mechanism similar to that of other silicates, although, the precise chemical mechanism of their uptake could not be determined. However, it was observed that expression levels of LSi1 gene responsible for Si uptake were comparatively lower in plants exposed to sodium silicate compared to those treated with SiNPs (Asgari et al., 2018). These findings somewhat suggest that the primary uptake of SiNPs occurs via the apoplastic pathway (Figure 1).



Figure 1. Schematic diagram of SiNPs uptake and transportation in plant body (Created with Biorender.com)

Effect of Drought Stress on Cereal Crops

Despite their economic and nutritional value, cereal crops remain sensitive to climate change because they often lack the adaptive characteristics needed to withstand extreme weather conditions. At present, DS affect approximately 23 million hectares of rainfed rice fields, leading to a significant reduction in global production by about 18 million tons annually (Pandey and Bhandari, 2009; Pandey *et al.*, 2007). Furthermore, it is estimated that extensive drought events will lead to a substantial decrease in global wheat by 21% and maize by 40% (Cai *et al.*, 2020; Zhang *et al.*, 2018).

DS can cause different molecular, biochemical, physiological, and morphological alterations in the root and aerial tissues of cereal crops (Elkelish *et al.*, 2021). When the water content is decreased, plant faces a reduction in leaf water potential or a loss of turgor pressure. During DS leaf curling, reduction in cell growth and expansion, complete or partial closure of stomata, and reduced internal CO₂ levels leading to a decline in photosynthetic activity are among the physiological changes (Aslam *et al.*, 2015; Rao *et al.*, 2016; Razi and Muneer, 2021). These changes result in a decrease in leaf area and development (Aslam *et al.*, 2015; Kadioglu *et al.*, 2012), thickening of roots (Asch *et al.*, 2005; Tahere *et al.*, 2000) and leading to overall reduction of plant growth. If the stress becomes too severe, it may stop photosynthesis, disrupting overall metabolic processes or ultimately causing plant death (Kapoor *et al.*, 2020). In triticale, drought during the pre-anthesis stage accelerates the time of flowering, whereas drought occurring post-anthesis shortens the duration of grain filling (Estrada-Campuzano *et al.*, 2008). The primary adverse effect of DS on crop plants is a decrease in both fresh and dry biomass production (Jaleel *et al.*, 2009), which results in reduced grain size and number in wheat (Wang *et al.*, 2017), and grain yield in maize (Sabagh *et al.*, 2018; Sathish *et al.*, 2022). However, the application of NPs significantly enhances plant performance or confers significant resilience to DS in crops.

Effect of SiNPs in Enhancing Drought Stress Tolerance of Cereal Crops

NPs can enter the plant through leaves and roots, once inside the plant, they trigger a range of biochemical, physiological, molecular, or morphological changes (Kandhol et al., 2022). The extent of these changes in plant growth is mainly depending on size, concentration, and method of application (Aqeel et al., 2023). Amongst NPs, the existing evidence indicates that SiNPs mitigate the negative impacts of DS or substantially enhance cereal crop growth and development (Rasheed et al., 2022). Application of SiNPs through irrigation and foliar spray has proven to be an effective approach in increasing crop productivity, enhancing the quality of grains, especially under stress conditions and supporting root development or photosynthetic CO₂ assimilation (Dhakate *et al.*, 2022; Verma *et al.*, 2022). Overall, DS leads to a reduction in the uptake of important minerals like calcium, manganese, nitrogen, iron, sodium, silicon, copper, zinc, etc (El-Mogy et al., 2022). However, the application of SiNPs increases the uptake of potassium, nitrogen, and other nutrients in wheat during DS (Akhtar and Ilyas, 2022; Raza et al., 2023), with accumulation of SiNPs in leaves, which results in the closure of stomata to avoid water loss in barley (Ghorbanpour et al., 2020). DS increases the production of ROS, resulting in excessive production of MDA and ultimately causing oxidative damage. Although, SiNPs have been found to increase antioxidant enzyme activities and decrease MDA concentration during DS (Riaz et al., 2023; Riaz et al., 2022). The effect of SiNPs on morpho-histological, antioxidant attributes, and gene expression of cereals under DS are discussed below.

SiNPs enhance morpho-histological attributes

The effects of DS can be seen throughout the entire life cycle of plant, from germination to maturity. It diminishes plant yield and overall performance by disrupting a variety of biochemical, physiological or morphological processes (Ansari *et al.*, 2019; Wahab *et al.*, 2022). DS in crops leads to significant changes, including decreased photosynthetic activity (Du *et al.*, 2022), altered stomatal closure (Kapoor *et al.*, 2020) and transpiration rates (Tran *et al.*, 2023), reduced relative water content (Kaur *et al.*, 2021) or increased electrolyte leakage (Ansari *et al.*, 2019; Yadav *et al.*, 2020).

Raza et al. (2023) reported that SiNPs played a significant role in crucial stages of wheat plant growth under drought conditions. The application of SiNPs at 300 to 900 mg L^{-1} was observed to alleviate adverse

impacts of drought and enhance plant height by 7% as compared to control (Raza *et al.*, 2023). Likewise, Behboudi et al. (2018) stated that in wheat plants, SiNPs application on the root had a better effect on leaf area (LA), chlorophyll content, relative water content (RWC) of leaves, plant height and biomass. In rice treated with 3000 mg L⁻¹ of SiNPs, roots were thicker and longer than the control and notable changes in the expression of root growth related genes resulted in promoted root development (Du *et al.*, 2022). Similarly, SiNPs were found to increase both leaf area index (LAI) and dry matter (DM) accumulation with increasing SiNPs concentration in rice (Table 1) (Elshayb *et al.*, 2021).

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Plant species	Administration	Drought stress severity	Size of SiNPs	Concentration of SiNPs	Experimental outcomes	References
Rice (<i>Oryza sativa</i> cv. 'EHR1')	Foliar	3, 6, and 9 Days	30 nm	30, 60, and 90 ppm	 Increased LAI, number of filled grains/panicles, dry matter production, number of panicles m², 1000 grain weight, as well as Chl. Content. Gradually enhanced the proline levels and antioxidant enzymes. 	(Elshayb <i>et al.</i> , 2021)
Rice (<i>Oryza sativa</i> cv. 'CO39')	Foliar and Soil	20 Days	39 ±7 nm	3000 mg L ⁻¹	 Due to soil application leaf water loss rate decreased. Promotes root growth and development. Root growth did not enhance through foliar treatment. 	(Du <i>et al.</i> , 2022)
Rice (<i>Oryza sativa</i> cv. 'CO54 and CO53')	Foliar	22 Days	Not specified	200, 400, 600, 800, and 1000 ppm	 400 ppm had maximum value on TCC, SPC, RWC, CSI, and MSI while a decrease in antioxidant enzymes of CAT, and proline accumulation. 	(Raja <i>et al.</i> , 2021)
Wheat (<i>Triticum</i> <i>aestivum</i> cv. 'Pakistan-13')	Seed priming	10% PEG-6000	45.69 to 48.73 nm	100, and 150 mg L ⁻¹	 Increased the GP to 93.66% in non-stress and 48.66% in stress conditions and SVI by 60.24%. 	(Akhtar <i>et al.,</i> t 2021)
	Soil	40% FC		150 mg kg^{-1}	 Increased dry and fresh weight at rate of 48.11% and 19.02% respectively. Increased Chl. <i>a</i>, Chl. <i>b</i>, or carotenoid content by 35.71%, 116.66%, and 236.36% respectively. Enhanced photosynthesis, production, and yield by 9.15%, 27.47%, and 32.06% respectively. 	
Wheat (<i>Triticum</i> aestivum cv. 'Pakistan-13')	Seed priming	10% PEG-6000	Not specified	150 mg L ⁻¹	 Enhanced GP, GI, and GVI to 16.78%, 8.33%, and 44.82% respectively. 	(Akhtar and Ilyas, 2022)
	Soil	45% FC		150 mg kg ¹	 Enhanced root and shoot length by 10.76% and 9.39% respectively. An increase of 19.01%, 13.20%, 24.02%, 16.48%, and 20.30% in Chl. a, Chl. b, carotenoid content, proline, and SSC respectively. The increase in CAT, POD and, SOD was 32.80%, 52.29% and, 57.53% respectively. 	
Wheat (<i>Triticum</i> <i>aestivum</i> cv. 'Pishtaz')	Foliar and Soil	15 Days	40 ± 9.5 nm	30, 60, and 90 ppm	 Improved RWC and leaf greenness (SPAD) by 84.04 and 12.54% respectively. Increased yield by 17.81 and 25.35% by soil and foliar spray. 	(Behboudi <i>et al.</i> , 2018)
Wheat (<i>Triticum</i> <i>aestivum</i> cv. 'Stava')	Soil	7 Days	30 ± 3.1 nm	50 µg mL-1	 Triggered EPS content which increased PGPR WHC and osmotic pressure of biofilm matrix, leading to increased biomass. 	(Fetsiukh <i>et al.</i> , 2021)
Wheat (<i>Triticum</i> <i>aestivum</i>)	Foliar	35 and 70% FC	≤ 50 nm	25, 50, and 100 mg L ⁻¹	 Improved photosynthesis, growth, leaf defence system, or Si concentrations in tissues while reducing Cd level, especially in grains. Under 100 mg L⁻¹ 46% reduction in H₂O₂ Concentration. Reduced MDA content by 18%, 21%, and 43% in 25, 50, and 100 mg L⁻¹ respectively. 	(Adrees <i>et al.</i> , 2022)
Wheat (<i>Triticum</i> <i>aestivum</i> cv. 'kalar1 and kalar2')	Seed priming	5-6 Days	20-30 nm	50 mg L ⁻¹	 Increased SLA, Chl., soluble carbohydrate, CAT enzyme activity, phosphor, and potassium. 	(Jasem and Khalil, 2022)
Wheat (<i>Triticum</i> <i>aestivum</i> cv. 'Glaxy-2013')	Seed priming	30% FC	63.09 ± 6.2 nm	300, 600, and 900 mg L ⁻¹	 Seed priming increased plant height, spike length, grains per spike, 1000 grains weight, grain and biological yield. Improved Chl. a or b concentrations, though reduced electrolyte leakage or increased SOD and POD activities. 	(Raza <i>et al.</i> , 2023)
Wheat (<i>Triticum</i> <i>aestivum</i>)	Foliar	50% FC	Not specified	30, 60, 90, and 120 ppm	 Lowered H₂O₂ and MDA content and increased RWC, antioxidant enzyme activities (APX, CAT, and SOD). Chl content and proline content 	(Boora <i>et al.</i> , 2023)

Table 1. Effect of SiNPs on morpho-histological, antioxidant enzymes and gene expression of cereal cropsunder drought conditions

					 Upregulated stress-related genes (DREB2, MYB33 MYB3R, WRKY 19, and SnRK 2.4). 	
Wheat (<i>Triticum</i> <i>aestivum</i>)	Soil	35 and 70% FC	≤ 50 nm	25, 50, and 100 mg kg ¹	 Reduced production of H₂O₂, electrolyte leakage, or MDA contents, and increase in SOD and POD activities. Plant height increased by 18.7%, 32.7%, and (Khan et 41.2% with the dosage of 25, 50, and 100 mg kg⁻¹, respectively. Increased Chl. a or Chl. B content. 	al., 2020)
Wheat (<i>Triticum</i> <i>aestivum</i> cv. 'HI 1544')	Seed priming	Not specified	Not specified	$15 \text{ mg } L^{\cdot 1}$	 Improved the production of ROS and antioxidant enzymes like POD, CAT, and SOD. Enhanced electron transport rates, number of active reaction centres, and absorbance. 	lal <i>et al.</i> , 21)
Maize (Zea mays)	Foliar	-0.03, -0.6, and - 1.2 MPa	Not specified	100-200 ppm	 Enhanced nutrient absorption efficiency. No significant impact on P, Ca, Na, or Cu elements in seeds, or Ca and Na in shoots. 	al., 2020)
Maize (<i>Zea mays</i> cv. 'Egaseed 81')	Foliar	5 and 7 Days	~126 nm	0.25 g L ⁻¹	 Improved RFW, Chl. a, Chl. b, TCC, RWC, and proline levels while a decrease in the concentration of H₂O₂. Increased activity of enzymes (SOD, CAT, G-POX), except APX. Increased the expression of D2 protein. 	ldin <i>et al.</i> , 23)
Maize (Zea mays)	Foliar	60 and 80% FC	Not specified	1.5 and 3 mM	 Improved levels of significant osmolytes, like phenol and proline, and sustained most of their photosynthetic pigments (PN, gs, Ci, and E). 	kadem <i>et</i> 2023)
Maize (<i>Zea mays</i> cv. 'Hybrid single cross 10')	Foliar	12, 15, and 18 Days	10-20 nm	500 mg L-1	 Improvement in enzymatic activity (POD, SOD, and CAT) or ion balance (K⁺/Na⁺). Increased RWC, photosynthetic pigments, photosynthetic rate, and gs, along with reduced lipid peroxidase, proline content, or electrolyte leakage. 	al., 2021)
Millet (Panicum miliaceum)	Foliar	40, 60, 80, and 100% FC	20-30 nm	100, 200, 300, 400 and 500 mg L ⁻¹	 Increased grain yield, harvest index, and water (Mok productivity. 	ari and our, 2020)
Barley (<i>Hordeum</i> vulgare cv. Giza 129, Giza 136, and Giza 133')	Foliar	40, 60, and 80% FC	< 50 nm	25, 50, and 100 ppm	 Increment in growth parameters, 1000 kernel weight, grain and straw weight, Chl. content, Fe and Zn content, and WHC while a decrease in Mn content. 	la <i>et al.</i> , 20)
Barley (<i>Hordeum</i> vulgare cv. 'G1- G20')	Foliar	Natural rainfall	100 nm	20 ppm	 Increased spike length and yield component. (Ghorban 20 	1ian <i>et al.</i> , 17)
Barley (Hordeum vulgare)	Soil	25, 50, 75, and 100% FC	20-30 nm	125-250 ppm	 The lower dose of 125 ppm was associated with the extensive distribution of SiNPs in cells and the development of consistent porous patterns in roots. TCC (up to 17.1%) and carotenoid (up to 24.1%) content were significantly enhanced. 	11.020)

SiNPs: Silica nanoparticles, PEG: Polyethylene glycol, GP: Germination percentage, GVI: Germination vigour index, GI: Germination index, SVI: Seedling vigour index, LAI: Leaf area index, Chl.: Chlorophyll, TCC: Total chlorophyll content, SPC: Soluble protein content, SSC: Soluble sugar content, CSI: Chlorophyll stability index, MSI: Membrane stability index, RFW: Root fresh weight, SLA: Specific leaf area, CAT: Catalase, POD: Peroxidase, SOD: Superoxide dismutase, MDA: Malondialdehyde, H₂O₂: Hydrogen peroxide, APX: Ascorbate peroxidase, G-POX: Guaiacol peroxidase, ROS: Reactive oxygen species, SPAD: Soil and plant analysis development, RWC: Relative water content, EPS: Exopolysaccharides, WHC: Water holding capacity, PGPR: Plant growth-promoting rhizobacteria, NP: Net photosynthetic rate, gs: Stomatal conductance, Ci: Intercellular CO₂ concentration, E: Transpiration rate, FC: Field capacity, MPa: Mega Pascal.

The performance of plants are dependent on various processes such as biochemical, physiological and anatomical mechanisms, and these functions are connected to the internal anatomy (Rasheed *et al.*, 2022). The application of SiNPs resulted in membrane stability, enhanced anatomical parameters, and nutrient status (Figure 2) (Nawaz *et al.*, 2023). In a study conducted by Adress *et al.* (2022) on wheat, it was observed that foliar application of SiNPs leads to increased Si content in both roots or shoots. Similarly, according to Aqaei *et al.* (2020), SiNPs were found to mitigate DS in rice by reducing transpiration. Transpiration in leaves is regulated through stomata and cuticle. Rice plants typically have a thin cuticle, and the development of the Sicuticle double layer substantially reduces cuticular transpiration. In maize, Sharf-Eldin et al. (2023) found the reduction in aquaporins (AQPs) and cysteine-rich protein known as osmotin (OSM-34) expression in SiNPs-treated plants indicates improved membrane and RWC integrity as compared to untreated plants under DS.





Figure 2. Role of SiNPs in improving drought tolerance of cereal crops (Created with Biorender.com)

SiNPs improve the antioxidant defence system

The scarcity of water leads to oxidative stress elevation of H₂O₂, MDA, and ROS levels, resulting in increased oxidative damage (Mohamed et al., 2009 Alam et al., 2022; Kirova et al., 2021). SiNPs have great potential to enhance antioxidant activity, thereby alleviating the negative effects of drought-induced stress. Utilization of SiNPs notably enhanced activities of CAT, SOD, or POD, leading to a reduction in oxidative damage of DS (El-Beltagi and Mohamed, 2010; Afify et al., 2011; Afify et al., 2012; Al-Mokadem et al., 2023; Elshayb et al., 2021; Pinedo-Guerrero et al., 2020; Sutuliene et al., 2021). Raza et al. (2023) reported that the treatment of SiNPs on wheat plants resulted in improved antioxidant enzyme activities. The SiNPs seed priming at 300, 600, and 900 mg L⁻¹ concentrations showed 2, 10, and 16% increase in SOD activity and enhance POD by 5, 11, and 17% respectively (El-Beltagi et al., 2020; Raza et al., 2023). Furthermore, Adrees et al. (2022) also confirmed that wheat plants exhibited maximum leaf POD and SOD activities, when subjected to the highest dose of SiNPs in foliar form. Similarly, Elshayb et al. (2021) in their study on rice concluded that a significant increase in SOD and CAT activity was observed in plants watered every 6 days, while the maximum POD activity in plants watered every 9 days, treated with 60 ppm SiNPs. According to Al-Mokadem et al. (2023), foliar application of 3 mM SiNPs significantly increased activities of antioxidant enzymes like CAT, SOD, POX, GR, and APX of Zea mays under water deficit conditions. Similarly, the application of SiNPs increased the activities of CAT, SOD, or G-POX, except for APX, of maize plants subjected to DS (Figure 2) (Sharf-Eldin et al., 2023).

SiNPs improve the expression of drought-tolerant genes

The usage of NPs pointedly upregulated the expression of various drought-responsive genes, such as GmERD1, GmDREB2, GmRD20A, GmMYB174, GmWRKY27, GmMYB118, GmNAC11, and GmFDL19 (Kandhol et al., 2022). Sharf-Eldin et al. (2023) reported that the application of SiNPs increased relative expression of D2 protein of photosystem II (PsbD) in maize plants, while gene expression of osmotic-like protein (OSM-34) and aquaporin (AQPs) was downregulated under DS. In this case, downregulation of OSM-34 and AQPs gene expression in SiNPs treated plants indicates an improvement in the integrity of membrane and RWC when compared with untreated plants under water deficit conditions. Moreover, Yang et al. (2018) observed that ZnO-NPs or CuO-NPs application significantly upregulated expression of drought tolerance associated genes in roots of wheat plants. Similarly, Raeesi Sadati et al. (2021) examined certain transcription factors (TFs) expression patterns in wheat under water stress conditions, and found that Zn-NPs application substantially upregulated expression of zinc transporter (ZIPI), heavy metal transporter (HMA2), and DNA binding protein transcription factor (WRKY1) genes, leading to notable enhancement of water stress resilience. These findings revealed that the use of NPs results in gene increase expression, subsequently improving drought tolerance in planta via promoting antioxidant activities, hormone signalling, and synthesis of secondary metabolites. However, further research is required to explore precise mechanisms and SiNPs-induced gene activation in cereal crops under DS.

Conclusions

Cereal crops play a crucial role in providing food and diets worldwide. Drought stress can induce different molecular, biochemical, physiological, and morphological alterations in both the root system and above-ground tissues of plants. However, the application of SiNPs significantly enhances the performance of cereal crops and provides significant resilience to the adverse effects of DS. The relatively nontoxic nature, best absorption, small size, favourable bio-distribution and porosity make SiNPs a promising candidate for use as plant growth regulators especially under water deficit conditions. Application of SiNPs significantly improved drought tolerance of cereal crops through morpho-histological changes, antioxidant enzyme activation, and expression of stress-responsive genes. Therefore, the synthesis of nano-silica-based fertilizers has unlocked new areas of research for agronomists to develop eco-friendly innovative products that can boost agricultural yields to mitigate the challenges of global food security.

Further research should concentrate on unravelling the molecular mechanism underlying the regulation of genes mediated by SiNPs, particularly concerning the growth and development of specific organs in cereal crops exposed to DS. Additionally, different -omic techniques, such as transcriptomics, metabolomics, proteomics, and genomics, are essential to comprehensively assess the influence of SiNPs on crops. Moreover, exploring the role of SiNPs in the synthesis of various osmolytes, hormones, enzymes or their linkage with specific genes are of quite importance. Simultaneously, crop improvement approaches should be assumed rather than promoting the enhancement of SiNPs absorption in plants. Sufficient research should be conducted to assess the beneficial as well as harmful impacts of SiNPs on various crops, animals and environment. Future studies should focus on the synthesis and utilization of SiNPs in the form of nano-insecticides, nano-pesticides etc.

Authors' Contributions

Conceptualization: S, HSEB, and AA; Data curation: S and MFNH; Funding acquisition; HSEB, WFS and MLH; Investigation: S; Project administration: S, HSEB and AZ; Supervision: AZ; Validation: S and

MFNH; Visualization: S; Writing - original draft: S; Writing - review and editing: AZ, HSEB and MFNH. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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