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Ahmed El Moukhtari, Mariem Ksiaa, Walid Zorrig, Cécile Cabassa, Chedly Abdelly, et al.. How silicon alleviates the effect of abiotic stresses during seed germination: A review. Journal of Plant Growth Regulation, 2023, 42, pp.3323-3341. 10.1007/s00344-022-10794-z . hal-03765797

HAL Id: hal-03765797

https://hal.sorbonne-universite.fr/hal-03765797v1

Submitted on 31 Aug 2022

How silicon alleviates the effect of abiotic stresses during seed germination: A review.

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Short title: Silicon and seed germination

Acknowledgments

The authors are grateful to the Referees for their constructive comments and recommendations which definitely help to improve the review. This work was supported by the Hubert Curien Maghreb Partnership - PHC Maghreb, No.19MAG41- governed by the agreement signed between the French Ministry of Europe and Foreign Affairs and the Algerian, Moroccan and Tunisian Ministries of Higher Education and Scientific Research.

Abstract

Rapid synchronized seed germination is desirable to ensure seedling establishment and improve crop yield. However, abiotic stresses from drought, salinity, and heavy metals have a negative impact on seed germination. The application of silicon (Si) has emerged as a promising approach for improving seed germination, especially under unfavorable conditions. However, the mechanisms of Si action have not been systematically studied in germinating seeds under conditions of abiotic stress. Considering the potential importance of sustainable agriculture, here we review recent findings of how seeds of numerous species, including several important crops, respond to Si treatment under abiotic stress. Exogenous Si has multiple effects on embryo viability, reserve mobilization, hormone/enzyme activity, membrane integrity, antioxidant metabolism, and regulation of gene expression in seed germination.

Keywords: Silicon, salinity, drought, heavy metals, seed germination, tolerance mechanisms.

Introduction

Seed germination is the crucial stage when individual progeny of plant sexual reproduction become established (Waterworth et al. 2019) and the environment of the future growth and development of the plant is determined (Hubbard et al. 2012; Ali and Elozeiri 2017). Germination is naturally very sensitive to abiotic stresses, including those caused by heavy metals, salinity, and drought (Dehnavi et al. 2020; Farissi et al. 2011; Ghavami and Ramin 2007; Seneviratne et al. 2017; Xiao et al. 2016). Abiotic stresses either delay or entirely prevent seed germination through osmotic stress and/or ionic toxicity (Debez et al. 2018; Haghighi et al. 2012; Farissi et al. 2011). Some abiotic stresses also increase reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2) and superoxide anion (O_2^-) in seeds (Bailly 2019), that may be produced during desiccation, germination, and aging (Pulido et al. 2009). In imbibed seeds, it has been reported that the metabolic activity in the different cell compartments such as NADPH oxidase activity in the plasma membrane, respiratory activity in mitochondria, purine catabolism in peroxisomes and lipid metabolism in glyoxysomes contribute to ROS production (Bailly 2004; Gomes and Garcia 2013). ROS disturb cellular metabolism by causing the peroxidation of proteins, lipids, and nucleic acids leading to seed deterioration and germination failure (Parvin et al. 2019). The exposure of seeds to salinity, drought, or heavy metals therefore induces modifications in protein structure, which diminishes hydrolytic enzyme activities so mobilization of seed reserves is compromised (Farissi et al. 2011; Hameed et al. 2021; Kranner and Colville 2011; Liu et al. 2018; Muscolo et al. 2014; Seneviratne et al. 2017).

Si is the second most abundant element after oxygen in the earth's crust. Exogenous application of Si has improved seed germination and embryo viability under various abiotic stresses (El Moukhtari et al. 2021; Lamsaadi et al. 2022; Rizwan et al. 2015; Siddiqui et al. 2020). An example of Si improving the seed viability of *Medicago sativa* L. under salt stress is illustrated in Fig. 1. Under drought, salinity, or heavy metal stresses, the addition of Si was found to improve seed germination rates in various plant species by influencing reserve mobilization, membrane integrity, ROS detoxification, antioxidant system, phytohormone metabolism, and gene expression (Ayed et al. 2021; Delavar et al. 2017; Gou et al. 2020; Khan and Gupta 2018). The beneficial effects of exogenous Si on plant tolerance to various abiotic stresses have been the subject of several reviews (El Moukhtari et al. 2021; Rizwan et al. 2015; Siddiqui et al. 2020) covering effects on plant growth, photosynthesis, water nutrition, and productivity of different crops under various abiotic stresses. Here we focus on reviewing the effect of exogenous Si on seed germination under abiotic stresses. First, we briefly highlight how different abiotic stresses affect seed germination, purposely considering evidence from a wide range of species. Then within this framework, the possible modes of Si action on seed germination are critically reviewed. Future areas of research to deepen our understanding of the mechanisms triggered by Si during seed germination are discussed.

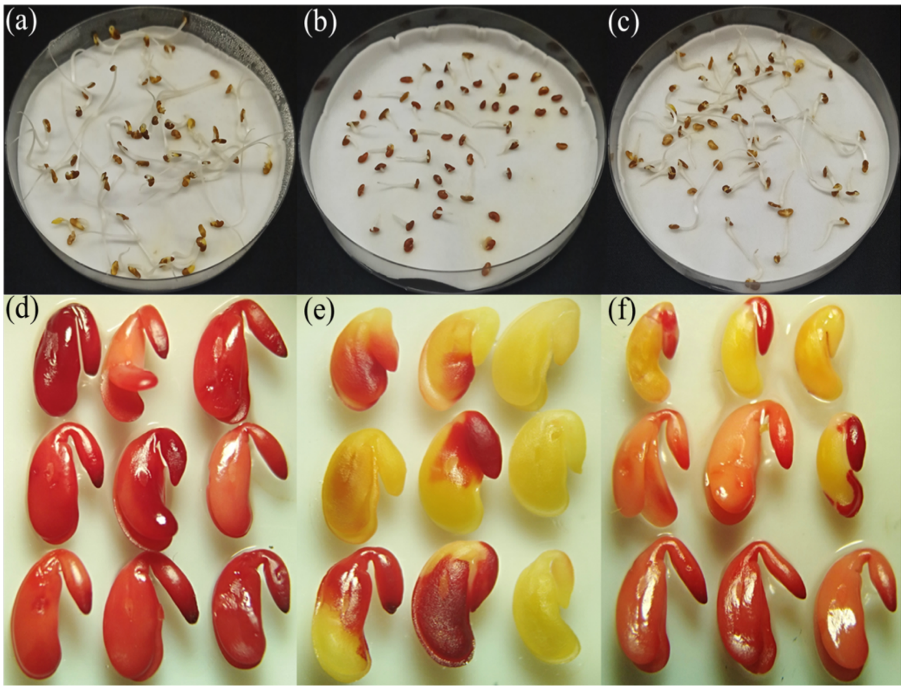

Fig. 1 Germination (a, b, and c) and embryo viability (d, e, and f) of seeds of the Moroccan *Medicago sativa* L. Demnate 201 variety treated with water (a, d), with 200 mM NaCl (b, e), or with 200 mM NaCl and 3 mM silicon in the form of $CaSiO_3$ (c, f). The germination rates were (a) 100%, (b) 51%, and (c) 85% after seven days of treatment. Embryo viability was evaluated after 12 hours of treatment using the 2,3,5 triphenyltetrazolium chloride (TTC) method in which viable embryos are stained red due to the reduction of TTC by respiratory activity of the cells. Images were taken under a binocular magnifying glass with 10x magnification.

Relationship between seed dormancy and germination

Seed formation itself is a key strategy adopted by plants, especially annuals, to overcome unfavorable environments (Boesewinkel and Bouman 1984). Mature seeds are spread from the mother plant into the soil, where they germinate or stay dormant. Seeds can sense the surrounding environment and cannot germinate in the absence of appropriate environmental conditions (Baskin and Baskin 2004; Finch-Savage and Footitt 2017). Environmental factors such as temperature, nitrate, light, water, oxygen, smoke, and allelochemicals may all form an integrative signal to determine whether and when seeds germinate or stay dormant (Graeber et al. 2012; Sano and Marion-Poll 2021; Yan and Chen 2020).

Seed dormancy is an orchestrated process during which the germination of viable seeds is blocked or delayed to withstand unfavorable environmental conditions (Finkelstein et al. 2008), which is key for the survival of the offspring. Dormancy is established during seed maturation and reaches a maximum level in freshly harvested seeds (Nakabayashi and Leubner-Metzger 2021). Seed dormancy therefore counters the phenomenon of preharvest sprouting, which is a major detrimental issue in cereal production (Tai et al. 2021). Abscisic acid (ABA) initiates and maintains dormancy (Koornneef et al. 2002). Carles et al. (2002) found that ABA-deficient *A. thaliana* seeds (*abi4-1, abi5-2* and *abi5-5*) germinated under osmotic stress, even with as much as 175 mM NaCl or 300 mM mannitol in the growth medium, but the seedlings died 7 days after germination. This example shows that ABA serves to inhibit germination in environmental conditions that are too extreme for the proper establishment of the seedlings. In contrast, it is well-known that gibberellic acid (GA) breaks seed dormancy and triggers seed germination (e.g. Stejskalová et al. 2015). For example, seeds of the GA biosynthesis *A. thaliana* mutant *ga1-3* only germinate if exogenous GA is applied (Hauvermale and Steber 2020). A key step in the germination process is the rupture of seed coat by the emerging radicle and GA stimulates radicle growth by mediating the activation of cell division in the embryonic root apical meristem (Ravindran and Kumar 2019). In tomato and Arabidopsis, GA promotes embryo growth and weakens the structures surrounding the embryo (Yamaguchi and Kamiya 2001). GA also stimulates the synthesis and translation of specific mRNAs, particularly those encoding α-amylase, a hydrolytic enzyme required for the digestion of seed reserves needed for germination (Ali and Elozeiri 2017; Muralikrishna and Nirmala 2005).

Overview of the effects of abiotic stresses on seed germination

Drought stress

Water is a major factor necessary for the imbibition and germination of seeds (Bradford 2017). Drought decreases external water potential, limiting the seed's ability to take up water and impairing germination (Balestrazzi et al. 2011; Campos et al. 2020). This effect has been observed in numerous Fabaceae species, including *Medicago sativa* (Han et al. 2017; Wang et al. 2009), *Glycine max* (Wijewardana et al. 2018, 2019), and *Lens culinaris* (Aniat-ul-Haq and Agnihotri 2010). Water stress was found to reduce several positive seed germination traits in some crop species of the Poaceae, Solanaceae, Asteraceae and Brassicaceae families. For example, germination percentage, germination rate, and vigor index are lowered by water stress in *Triticum aestivum* (Kizilgeci et al. 2017), *Hordeum vulgare* (Barati et al. 2015), *Oryza sativa* (Ali et al. 2020), *Solanum lycopersicum* (Galviz-Fajardo et al. 2020), *Helianthus annuus* (Toscano et al. 2017) and *Brassica napus* (Xiong et al. 2018). According to Llanes et al. (2015), drought stress can influence seed germination by changing endogenous plant growth regulator levels. For example, water deficit mediated by PEG treatment triggered an increase in ABA and a decrease in GA in *Trifolium repens*, impairing seed germination (Hassan et al. 2021). When less GA is available under water shortage, reserve mobilization is compromised, because the synthesis of various hydrolytic enzymes is not stimulated (Bewley 2001). In fact, Muscolo et al. (2014) and Hameed et al. (2021) reported that water deficiency significantly impaired the activities of α- amylase, β-amylase and proteases in the endosperm of lentil and wheat seeds, respectively, which consequently hampered seed reserve mobilization. In *Medicago truncatula* water deficit also alters embryo respiration and seed viability (Balestrazzi et al. 2011). In drought-stressed wheat, a decrease in germination rate appeared to result from the induction of oxidative stress, where a higher level of malonyldialdehyde (MDA) was noted together with an increase in H_2O_2 and O_2^- (Guo et al. 2017).

Salinity stress

Salinity causes serious abiotic stress, severely hindering seed germination and delaying seedling emergence. When seeds are germinated on filter paper, salinity affects indexes such as percentage, rate, and speed of germination of various plant species, including *Sorghum bicolor* (Dehnavi et al. 2020), *M. sativa* (Farissi et al. 2011), *Silybum marianum* (Ghavami and Ramin 2007), *Suaeda salsa* and *Phragmites australis* (Xiao et al. 2016), *Buchloe dactyloides* and *Bouteloua gracilis* (Zhang et al. 2012). Salinity is even reported to delay the germination of some halophytes such as *Cakile maritime* (Debez et al. 2004, 2018), *Salicornia europaea* (Calone et al. 2020), *Spartina maritima*, and *Spartina densiflora* (Infante-Izquierdo et al. 2019) as the times for 50% germination of viable seeds (T_{50}) are longer when the level of salt stress is high.

Salinity inhibits seed germination through various metabolic changes. In addition to the effects of osmotic stress, salinity may induce ionic toxicity due to an excess of Na^+ and Cl^- (de Oliveira et al. 2013). Salinity drastically decreased the activities of α- and β-amylase in *Amaranthus caudatus* (BiaŁecka and Kępczyński 2009), with negative consequences on seed reserve mobilization (Farissi et al. 2011). A similar effect was observed in *O. sativa*, where salinity reduced the expression of the α-amylase gene and the activity of the enzyme (Liu et al. 2018). Similarly, catabolism of starch and lipids during *Cucumis sativus* seed germination was inhibited and delayed under salinity (Zhang et al. 2017). In *Pancratium maritimum* seeds, salinity affects cell division and causes DNA fragmentation, micronucleus formation, and chromosomal abnormalities (Mohamed et al. 2018). Salt can also disturb the homeostasis of phytohormones leading to failure of seed germination (Miransari and Smith 2014). Moreover, either through osmotic stress and/or ionic toxicity, salinity mediates an over-accumulation of ROS, leading to damage of nucleic acids, lipids, proteins, and carbohydrates which limits seed germination (Ibrahim 2016).

Heavy metals

Heavy metals have been shown to negatively influence seed germination and seedling growth of various plant species (El Rasafi et al. 2020; Seneviratne et al. 2017). There have been numerous descriptions of cadmium (Cd) delaying or completely inhibiting germination. For example, wheat grain germination was reduced by 47% at 0.12 mM Cd (Guilherme et al. 2015), while no *O. sativa* grains germinated at 1 mM Cd (Ahsan et al. 2007). Mercury (Hg), another toxic metal, is known to suppress seed germination and seedling growth. In *Vigna radiata*, 7 mM Hg reduced seed germination, seedling elongation, and dry weight accumulation by 42%, 70%, and 47%, respectively, compared to the control (Muhammad et al. 2015). Copper (Cu) also has a harmful impact on seed germination, even at low concentrations. For example, 10 µM Cu reduced seed germination of *H. vulgare*, *T. aestivum*, and *O. sativa* by more than 7%, 39%, and 63%, respectively (Mahmood et al. 2007). When *M. sativa* seeds were sown on solid media, 24% fewer seeds germinated when treated with 40 ppm nickel (Ni) (Aydinalp and Marinova 2009). Lead (Pb) inhibits seed germination in various plant species, including *L. culinaris* (Cokkizgin and Cokkizgin 2010). When 4.5 mM Pb was applied to lentil seeds, the germination percentage and vigor index were 67% and 83% lower than controls without Pb, respectively, and the mean germination time was 17% longer. Seed germination inhibition by other metalloids has been reported, including aluminum (Al) (Rodrigues et al. 2019), arsenic (As) (Mridha et al. 2021), and chromium (Cr) (Khan et al. 2020).

How heavy metal stress prevents seed germination is a complex biochemical process. Heavy metals can block aquaporins by binding to a cysteine residue close to the pore of the protein (Daniels et al. 1994) thereby impeding water uptake by seed cells and limiting seed imbibition (Cardoso et al. 2015; Lefèvre et al. 2009). Similar effects have been observed in *Pisum sativum* under $HgCl_2$ and $ZnCl_2$ stresses (Kshetrimayum et al. 2017). Furthermore, enzymes participating in reserve mobilization, such as α- and β-amylases, proteases, leucine amino peptidases as well as cysteine-, aspartic-, and metallo-proteases, are altered by heavy metals, resulting in lower enzyme activity that has a negative effect on germination (Seneviratne et al. 2017). Heavy metal stress may also alter endogenous phytohormone homeostasis in seeds (Seneviratne et al. 2017). In *Cicer arietinum*, the negative effect of Pb or zinc (Zn) stress on seed germination was due to an increase in ABA and a decrease in GA content (Atici et al. 2005). Heavy metals can also reduce seed germination by inducing oxidative stress, reducing cell viability, and altering embryo growth (Gonzalez-Mendoza et al. 2009; Li et al. 2005; Sethy and Ghosh 2013).

To summarize, abiotic stresses, including drought, salinity and heavy metals, have a significant negative impact on seed germination of various species of plants. The negative effects include altered ion and water uptake, reduced reserve mobilization, modifications of proteins/enzymes and oxidative stress resulting in reduced seed viability and vigor (Table 1).

Table 1 Effects of abiotic stresses on germinating seeds of different plant species compared to non-stressed controls

Abiotic stress			Plant species	Effects on germination	References
Type of stress	Agent	Stress level			
Drought stress	Mannitol	-0.3, -0.6, -1.2 and -2.4 MPa	*Glycine max*	Lower germination indexes Shorter hypocotyl and root More abnormal seedlings	Machado Neto et al. (2004)
	PEG	15%	*Brassica napus*	Lower germination indexes Lower seed vigor index More ROS accumulation More lipid peroxidation More non-enzymatic antioxidants Increased activity of antioxidant enzymes More ABA	Xiong et al. (2018)
	PEG	10%	*Gossypium hirsutum*	Lower germination indexes Increased ABA/GA ratio Less α-amylase More ROS accumulation More lipid peroxidation Delayed water absorption capacity of testa	Bai et al. (2020)
	PEG	13.6 and 20.4%	*Hordeum vulgars*	Lower germination indexes Fewer primary roots Shorter maximum root length Shorter shoots	Barati et al. (2015)
	PEG	0.5-2.5 MPa	*Juglans regia*	Lower germination indexes Less water in radicle and plumule More lipid peroxidation Increased activity of antioxidant enzymes More antioxidant compounds More ABA, SA and JA Less GA and IAA More polyamines	Lotfi et al. (2019)
	PEG	10-21%	*Lens culinaris*	Lower germination indexes Less water in germinating seeds Less α-amylase More proline	Muscolo et al. (2014)

	PEG	-0.40, -0.50 and -0.75 MPa	*Lens culinaris*	Lower germination percentage Reduced seedling survival Shorter root and shoot	Aniat-ul-Haq and Agnihotri (2010)
	PEG	35%	*Medicago sativa*	Lower germination indexes More ROS accumulation More lipid peroxidation Increased activity of antioxidant enzymes	Wang et al. (2009)
	PEG	20%	*Oryza sativa*	Lower germination indexes Less water in seeds More ROS accumulation More lipid peroxidation More ABA Upregulated *OsNCED3* expression Upregulated SOD and CAT related gene expression	Liu et al. (2019)
	PEG	-0.3, -0.6 and -0.9 MPa	*Oryza sativa*	Lower germination indexes Shorter plumules Shorter roots Shorter seedlings	Ali et al. (2020)
	PEG	17%	*Trifolium repens*	Lower germination indexes Less cytokinin More ABA Less β-amylase Less total amylase More starch and soluble sugar More ROS accumulation More lipid peroxidation Increased CAT activity	Hassan et al. (2021)
Heavy metals	$AlCl_3$	30 mmol L^{-1}	*Triticum aestivum*	Lower germination indexes Lower amylase and esterase activity More ROS accumulation More lipid peroxidation	Zhang et al. (2010)
	$AlCl_3$	2 mmol L^{-1}	*Oryza sativa*	Lower germination indexes Lower GA/ABA ratio Downregulation of the expression of ABA catabolism genes (*OsABA8ox*$_1$ and *OsABA8ox*$_2$) Lower α- and β-amylase activity More lipid peroxidation Increased antioxidant enzyme activity	Xu et al. (2017)

	Cd	100-500 µM	*Brassica napus*	Induced ROS accumulation Induced lipid peroxidation Ultrastructural changes in cells of germinating seeds	Ali et al. (2015)
	$CdCl_2$	5 mM	*Phaseolus vulgaris*	Lower germination indexes Reduced embryo growth Lower α-amylase and invertase activity Induced lipid peroxidation	Sfaxi-Bousbih et al. (2010)
	$CdCl_2$	10-30 mg L^{-1}	*Trigonella foenum-graecum*	Lower germination indexes	Espanany et al. (2015)
	$CdCl_2$	1-5 mM	*Triticum aestivum*	Lower germination indexes Shorter coleoptile and radicles Lower amylase activity Induced lipid peroxidation	Hu et al. (2015)
	$CuSO_4$	100-500 µM	*Hordeum vulgare*	Lower germination indexes Shorter radicles Lower *α*- and *β*-amylase, acid phosphatase, and alkaline phosphatase activities Induced lipid peroxidation Induced proline accumulation	Kalai et al. (2014)
	Cr^{3+}	50-800 mg L^{-1}	*Arabidopsis thaliana*	Lower germination indexes Less embryo viability Increased seed coat permeability	de Silva et al. (2021)
	Cr (VI)	100 µM	*Triticum aestivum*	Lower germination indexes Lower α-amylase activity Fewer free amino acids Induced ROS accumulation Induced lipid peroxidation	Lei et al. (2021)
	$K_2Cr_2O_7$	30-300 mg L^{-1}	*Lepidium sativum*	Lower germination indexes	Pavel et al. (2013)
	$PbCl_2$	0.5-4.5 mM	*Lens culinaris*	Lower germination indexes Shorter plumules and radicles	Cokkizgin and Cokkizgin (2010)
	$Pb(NO_3)_2$	0.05-1 g L^{-1}	*Triticum aestivum*	Induced lipid peroxidation, Increased proline accumulation Lower α-amylase activity Increased antioxidant enzyme activities	Lamhamdi et al. (2011)
Salinity	NaCl	150-300 mM	*Arabidopsis thaliana*	Lower germination indexes Induced ROS accumulation Induced lipid peroxidation	Luo et al. (2021)

			Less embryo viability	
NaCl	150 mM	*Gossypium hirsutum*	Lower germination indexes Less α-amylase and β-galactosidase Lower GA/ABA ratio Less melatonin	Chen et al. (2021)
NaCl	150 mM	*Gossypium hirsutum*	Lower germination indexes Downregulated ABA catabolism (*CYP707A2*) and GA biosynthesis (*GA20ox1*) genes Upregulated ABA biosynthesis (*NCED2*, *NCED5* and *NCED9*) and GA catabolism (*GA2ox1*) genes	Kong et al. (2017)
NaCl	50 and 100 mmol dm^{-3}	*Gossypium hirsutum*	Lower germination indexes Lower α-amylase activity Less reduced-sugar Less total amino acids	Ashraf et al. (2002)
NaCl	100 mM	*Lactuca sativa*	Lower germination indexes Lower phosphatase and phytase activities	Nasri et al. (2012)
NaCl	200 mM	*Limonium bicolor*	Reduced germination indexes Lower GA/ABA ratio Lower amylase and α-amylase activities Decreased *GA20ox*, *GA3ox* and *CYP707A1* gene expression Increased *NCED1* and *NCED3* gene expression More Na^+ and Cl^-	Li et al. (2019)
NaCl	50-200 mM	*Medicago sativa*	Lower germination indexes Less reserve mobilization Ionic toxicity	Farissi et al. (2011)
NaCl	100-200 mM	*Sorghum bicolor*	Lower germination indexes Lower salinity tolerance index Higher stress susceptibility index	Dehnavi et al. (2020)
NaCl	200 mM	*Trigonella foenum-graecum*	Lower germination indexes Less seed reserve mobilization Reduced seed viability Induced ROS accumulation Induced lipid peroxidation Ionic toxicity	Lamsaadi et al. (2022)
NaCl	60 and 120 mM	*Triticum aestivum*	Lower germination indexes Less water uptake Lower α-amylase activity	El-Hendawy et al. (2019)

NaCl	120 mM	*Oryza sativa*	Lower germination indexes Less bioactive GA Lower α-amylase activity Downregulated α-amylase gene expression	Liu et al. (2018)
NaCl	50-200 mM	*Pancratium maritimum*	Lower germination indexes Affects cell division DNA fragmentation, micronucleus formation, and chromosomal abnormalities	Mohamed et al. (2018)
Na_2CO_3	50 mM	*Oryza sativa*	Lower germination indexes Less bioactive GA Lower α-amylase content	Li et al. (2019)
$NaHCO_3$	90 mmol L^{-1}	*Cucumis sativus*	Lower germination indexes Shorter hypocotyl and radicles Lower α- and β-amylase activity Increased lipid peroxidation	Sun and Luo (2014)

PEG, polyethelene glycol; GA, gibberellic acd; ABA, abscisic acd; Na_2CO_3, sodium carbonate; $NaHCO_3$, sodium hydrogen carbonate; Pb $(NO_3)_2$, lead (II) nitrate; $PbCl_2$, lead chloride; Cr(VI), chromium hexavalent; Cr^{3+}, chromium; $CuSO_4$, copper sulfate; $CdCl_2$, cadmium chloride; Cd, cadmium; $AlCl_3$, aluminum chloride.

Si improves seed germination under abiotic stresses

Si has repeatedly been found to have a positive effect on seed germination under abiotic stress (e.g. Rizwan et al. 2015; Siddiqui et al. 2020), and several of the reports are listed in Table 2. Elemental Si increases seed germination percentage, germination index, and seedling vigor of *C. sativus* exposed to stress caused by 200 mM NaCl (Gou et al. 2020). Investigations by Almutairi (2016) indicate that 1 mM nano-silicon increased germination percentage and germination rate of *S. lycopersicum* seeds under different NaCl concentrations (150-200 mM). In a different study by Zhang et al. (2015), germination rate, germination index, and vitality indexes of *Glycyrrhiza uralensis* seeds grown under salt stress (150 mM NaCl) were all improved upon Si treatment. In *Trigonella foenum-graecum* seeds germinating under NaCl induced salinity stress, the application of $CaSiO_3$ improved the germination percentage, germination speed, velocity index, germination energy, peak value and vitality index, all in a shorter mean germination time (Lamsaadi et al. 2022). Alsaeedi et al. (2017) showed that Si in the form of nano-silica restricted Na^+ uptake by *Phaseolus vulgaris* seeds resulting in a final germination percentage and germination rate that were 19.7% and 22.6% higher, respectively, than Na^+-stressed *P. vulgaris* seeds not supplied with Si. Toxicity of NaCl on germination of *T. aestivum* (Azeem et al. 2015), *Zea mays* (Naguib and Abdalla 2019), and *L. sativa* (Alves et al. 2020) was alleviated by Si application.

Si added as an exogenous compound was also beneficial as it improved seed germination under other abiotic stresses, such as drought and heavy metal stress (Arif et al. 2021). Under drought stress, Ayed et al. (2021) reported that Si in the form of sodium metasilicate ($Na_2SiO_3H_2O$) increased germination percentage, germination, and seedling vigor indexes of *T. turgidum* by 22%, 62%, and 39%, respectively. Furthermore, under 100 µM Cd stress, SiO_2 supplements improved *Phyllostachys edulis* seed germination (Emamverdian et al. 2021). In *O. sativa*, 5 mM silicic acid increased germination percentage under 150 µM As stress from 56% to 78% (Khan and Gupta 2018). In seed germination experiments with *Z. mays*, the toxic effects of Al were alleviated by exogenous application of Si (Delavar et al. 2017). Si in the form of Na_2SiO_3 can also augment seed germination in *C. sativus* under 3-phenylpropionic acid induced stress (Bu et al. 2018) and in *C. melo* under autotoxicity stress (Zhang et al. 2020). The studies above indicate that Si has an amelioratory effect on the germination of seeds grown under various abiotic stressors.

Table 2 Potential modes of Si action during seed germination under various abiotic stresses

Plant species	Si			Stress		Mode of action	References
	Form	Technique	Concentration	Type	Level		
Cucumis melo	Na_2SiO_3	Soaking	2 mM	MPWE	20 mg L^{-1}	Germination traits Reserve mobilization Gene expression Antioxidant activities Membrane integrity	Zhang et al. (2020)
Cucumis sativus	Na_2SiO_3	Soaking	2 mM	3-PPA	2 mM	Germination traits Reserve mobilization Gene expression	Bu et al. (2018)
Cucumis sativus	Na_2SiO_3	Soaking	0.3 mM	NaCl	200 mM	Germination traits Reserve mobilization Membrane integrity ROS detoxification Antioxidant activities Phytohormones Gene expression	Gou et al. (2020)
Lactuca sativa	Ca_2SiO_4	Priming	0.05-0.1 mM	NaCl	50 mM	Germination traits Antioxidant activities Membrane stability	Alves et al. (2020)
Lathyrus odoratus	nano-Si	Priming	20 mg L^{-1}	NaCl	21.60 dS m^{-1}	Germination traits	El-Serafy et al. (2021)
Lens culinaris	Na_2SiO_3	Soaking	2 mM	PEG	18%	Germination traits Reserve mobilization Antioxidant activities ROS detoxification Membrane stability	Biju et al. (2017)
Oryza sativa	$H_4SiO_2^-$	Priming	5 mM	As	150 uM	Germination traits Antioxidant activities Gene expression	Khan and Gupta (2018)
Oryza sativa	SiO_2	Priming	350 mg L^{-1}	PEG	-0.9 Mpa	Germination traits Antioxidant activities Membrane stability	Gana Ali et al. (2021)
Phaseolus vulgaris	nano-Si	Soaking	300 mg L^{-1}	Na^+	1-5 g L^{-1}	Germination traits Nutrient homeostasis	Alsaeedi et al. (2017)

Phyllostachys edulis	nano-Si	Soaking	200 µM	Cd	100 µM	Germination traits	Emamverdian et al. (2021)
Solanum lycopersicum	Na_2SiO_3	Soaking	0.5 mM	PEG	10%	Germination traits Antioxidant activities ROS detoxification Membrane integrity	Shi et al. (2014)
Solanum lycopersicum	nano-Si	Soaking	0.5-3 mM	NaCl	150-200 mM	Germination traits Gene expression	Almutairi (2016)
Trigonella foenum-graecum	$CaSiO_3$	Soaking	3 mM	NaCl	200 mM	Germination traits Reserve mobilization Embryo viability Antioxidant activities ROS detoxification Membrane integrity Compatible osmolytes K^+/Na^+ ratio	Lamsaadi et al. (2022)
Triticum aestivum	K_2SiO_3	Priming	1.5 mM	NaCl	up to 20 dS m^{-1}	Germination traits	Feghhenabi et al. (2020)
Triticum turgidum	Na_2SiO_3	Priming	15-20 mg L^{-1}	PEG	150 g L-1	Germination traits	Ayed et al. (2021)
Zea mays	Na_2SiO_3	Soaking	2 mM	NaCl	75 mM	Germination traits Phytohormones Reserve mobilization	Delavar et al. (2017)
Zea mays	Na_2SiO_3	Soaking	2 mM	Al	10 mM	Germination traits Phytohormones Reserve mobilization	Delavar et al. (2017)
Zea mays	nano-Si	Priming	10 mg L^{-1}	NaCl	150 mM	Germination traits Embryo respiration Reserve mobilization Antioxidant activities Phytohormones Membrane integrity ROS detoxification	Naguib and Abdalla (2019)

MPWE: Melon plant water extract; PEG: Polyethelene glycol; 3-PPA: 3-phenyl-propionic acid

Si treatment enhances seed reserve mobilization under abiotic stress

Si application improves the germination of seeds under abiotic stress conditions by modulating reserve mobilization (Fig. 2). For example, in drought-stressed germinating seeds of *Eleusine coracana*, Mundada et al. (2021) recently found that Si increased the breakdown of glucose to acetyl CoA via pyruvate, which was diverted to lipid biosynthesis instead of the tricarboxylic acid cycle. This is good evidence that Si has a role in lipid metabolism. Additionally, Si augmented the activity of α-amylase, β-amylase, and α-glucosidase in osmotically stressed seeds of *L. culinaris* (Biju et al. 2017). Similar findings were reported in *C. sativus* (Ning et al. 2020). In wheat, seed priming with Si nanoparticles increased amylase activity under drought stress (Rai-Kalal et al. 2021). Similarly, in *C. sativus* under salt stress, application of 0.3 mM sodium silicate alleviated the negative effects of 200 mM NaCl and significantly increased α-amylase activity (Gou et al. 2020). Recently, Lamsaadi et al. (2022) observed that the enhanced seed germination rate of Si-treated *Trigonella foenum-graecum* seeds under salt stress was due to better reserve mobilization and embryo viability. Seed priming with nano-silica improved embryo respiration by increasing aldolase and isocitrate lyase activities (Naguib and Abdalla 2019). Under Al stress, the activity of amylase was 45% higher in Al-stressed seed with $NaSiO_3$ compared to Al-stressed seed without the addition of Si (Delavar et al. 2017). In a study of *C. melo* seeds, the application of Si increased α-, β- and total-amylase activities under autotoxicity stress (Zhang et al., 2020). The same was observed under 3-phenylpropionic acid induced stress in *C. sativus*, where Si supplementation improved α-, β- and total-amylase activities, and finaly seed germination (Bu et al. 2018). Exogenous Si may therefore alleviate the negative effects of abiotic stresses on seed germination by promoting reserve mobilization, but more detailed studies, including testing for embryo viability and monitoring gene expression and the activity of other enzymes related to reserve mobilization, are required.

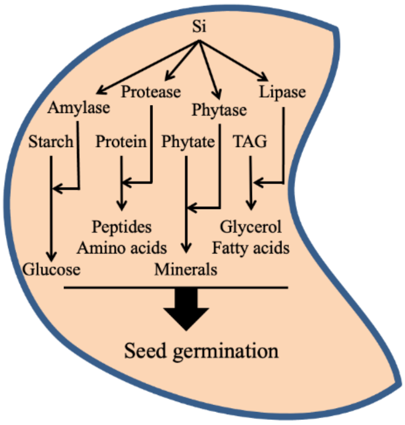

Fig. 2 Proposed effects of Si on seed reserve mobilization during seed germination under abiotic stresses. TAG, triacylglycerol

Exogenous Si mediates seed germination by modulating phytohormone balance

The effects of Si on phytohormone synthesis in stressed plants during vegetative growth have been reviewed by El Moukhtari et al. (2021) and Rizwan et al. (2015). Only a few reports show a link between Si treatment and plant hormone metabolism during seed germination (Fig. 3). A recent study demonstrated that seed priming with nano-silica increased *Z. mays* seed germination under 150 mM NaCl stress, and this was correlated with a higher GA/ABA ratio (Naguib and Abdalla 2019). The authors also revealed that changes in hormone metabolism were sufficient to explain the effect of Si on seed germination, particularly under unfavorable conditions. Another interesting study demonstrated that under 75 mM NaCl or 10 mM Al stress, *Z. mays* seeds that were soaked in 2 mM Na_2SiO_3 solution contained more GA and less ABA compared to the control, leading to a higher germination rate (Delavar et al. 2017). According to Gou et al. (2020), the increased GA in NaCl-treated *C. sativus* treated with Si was the result of downregulated expression of GA catabolism gene *GA2ox*, while the decreased ABA was the result of downregulated expression of ABA anabolism genes such as *NCED1* and *NCED2*. The combined effect was to raise the GA/ABA ratio to the level needed for dormancy release and germination. In PEG-stressed seeds of *E. coracana*, the application of Si modulates jasmonic acid (JA) synthesis during germination, especially under stressed conditions (Mundada et al. 2021). These results provide evidence that Si is effective in improving seed germination through the modulation of GA, ABA, and JA metabolism. Further investigations are necessary to understand the mode of action of Si and any signaling crosstalk in modulating phytohormones in seeds during abiotic stress.

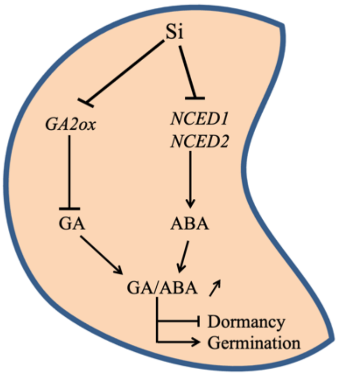

Fig. 3 Proposed effects of exogenous Si application on phytohormone balance during seed germination under abiotic stresses. *NCED, nine-cis-Epoxycarotenoid dioxygenases*; *GA2ox, Gibberellin 2-oxidases*; GA, gibberellic acid; ABA, abscisic acid

Si enhances antioxidant machinery and improves integrity, functionality, and stability of membranes during seed germination

During environmental stresses, the generation of ROS is enhanced (Nadarajah 2020). At high levels, ROS causes proteins, lipids, and nucleic acid peroxidation, hence causing cell damage and death (Hasanuzzaman et al. 2020). Maintaining membrane integrity and functionality during environmental change is a challenge for sessile plants (Rogowska and Szakiel 2020). Antioxidative defense systems, including both enzymatic and non-enzymatic antioxidants, play a major role preventing ROS build-up in cells (Kasote et al. 2015). Si has been reported to lower ROS activity and restore damaged plant membranes during seed germination by enhancing the antioxidant system (Debona et al. 2017; Mostofa et al. 2021). In drought-stressed *S. lycopersicum* (Shi et al. 2014) and *L. culinaris* (Biju et al. 2017), Na_2SiO_3 increased the activity of ascorbate peroxidase (APX), peroxidase (POX), catalase (CAT), and superoxide dismutase (SOD), consequently decreasing how much H_2O_2, O_2^-, and malondialdehyde were generated, with less lipid peroxidation as a result. Parallel evidence using the Evans Blue method is that under 200 mM NaCl *C. sativus* seed membrane integrity was improved by Si-treatment (Gou et al. 2020). The latter effect was linked to the ability of Si to limit ROS generation by modulating the activity of SOD, POX, CAT and APX. Likewise, *Trigonella foenum graecum* seeds supplied with 3 mM $CaSiO_3$ and exposed to 200 mM NaCl solution showed increased SOD and polyphenol oxidase (PPO) activities, and a greater content of total polyphenol, flavonoids, glycine betaine and proline, while displaying lowered levels of H_2O_2, O_2^-, MDA and electrolyte leakage (Lamsaadi et al. 2022). Similar findings were reported by Naguib and Abdalla (2019), who showed that the decreases in both lipid peroxidation and ROS accumulation in salt-stressed *Z. mays* seeds were associated with the higher activities of SOD, POX, and PPO in response to nano-silica applied as a priming agent. Again as a priming agent, Si stimulated the activities of antioxidant enzymes, particularly CAT, decreasing lipid peroxidation in Cd-stressed lettuce seeds (Pereira et al. 2021). Si supplementation to *C. melo* seeds triggered an increased SOD, CAT and POD activities and a reduced MDA content under autotoxicity stress (Zhang et al. 2020). It is clear from the above studies that Si improves seed germination under multiple abiotic constraints by enhancing enzymatic and non-enzymatic antioxidant activities and thus maintaining the integrity and stability of membranes. Currently studies related to the molecular mechanisms and the metabolic pathways of Si-mediated stress tolerance are still limited.

Si modulates gene expression during seed germination

The complex process of seed germination is governed by the expression of specific sets of genes (Rajjou et al. 2012). Si has been reported to regulate transcript levels of various abiotic stress-related genes during seed germination. The example of 0.3 mM Na_2SiO_3 downregulating the expression of *NCED1* and *NCED2* encoding nine-cis-epoxycarotenoid dioxygenases involved in ABA synthesis and *GA2ox* encoding gibberellin 2-oxidase, which deactivates bioactive Gas, was already cited (Gou et al. 2020). In another case, as ABA is known to activate *Mitogen-activated protein kinase* (*MAPK*) expression, which are genes involved in signal transduction pathways (Lu et al. 2002), the lower levels of ABA due to Si treatment (Delavar et al. 2017) may be the reason *MAPK2* and *MAPK3* are downregulated in Si-treated salt-stressed *S. lycopersicum* (Almutairi 2016). ABA was also shown to regulate the expression of *Ethylene response factor* (*ERF*), a key transcription factor in abiotic stress signaling (Müller and Munné-Bosch 2015). In *S. lycopersicum*, the application of Si downregulates the expression of *Ethylene response factor 5 (ERF5)*, and this was associated with lower levels of ABA (Almutairi 2016). Moreover, *ERF* controls *Respiratory burst oxidase* (*RBOH*) (Yao et al. 2017), and the reduction of *ERF5* expression in salt-stressed *S. lycopersicum* in response to Si treatment downregulates *RBOH1* (Almutairi 2016).

The accumulation of compatible osmolytes, including proline, is one of the most common strategies to overcome adverse environmental conditions (El Moukhtari et al. 2020). This response is mediated by several genes, including *delta-1-Pyrroline5-carboxylate synthetase* (*P5CS*) involved in proline biosynthesis (Szabadoz and Savouré 2010). In a study by Almutairi (2016), the application of Si increased the expression of *P5CS* in *S. lycopersicum* during NaCl-induced salinity stress. This suggests that Si may be involved in mediating osmotic adjustment in germinating seeds during osmotic stress. Another mechanism of plant resistance to salt stress is to decrease Na^+ uptake and accumulation (Bargaz et al. 2015) through the action of the Na^+/H^+ antiporters of the plasma membrane (Rizwan et al. 2015). To investigate how Si controls Na^+ uptake by the seeds, Almutairi (2016) studied the effect of Si on the expressions of *Na^+/H^+ antiporter 6* (*NHX6*) in salt-stressed seeds of *S. lycopersicum*. The results showed that Si under salt stress up-regulated this gene expression, preventing Na^+ uptake by the seeds. Abscisic Acid-Responsive Element-Binding Protein (AREB) is required for the establishment of *Arabidopsis* seedlings (Sharma et al. 2011). During salinity stress, Si-treatment upregulated *AREB* expression in *S. lycopersicum* as compared to controls (Almutairi 2016). Acid phosphatase and esterases belonging to a group of hydrolytic enzymes that catalyze the hydrolysis of the seed reserve are required for the germination process (Kantharaju and Murth 2014; Senna et al. 2006). In Cd-stressed lettuce, the use of Si as a priming agent triggered the expression of genes associated with esterase and acid phosphatase (Pereira et al. 2021). The upregulation of *Low silicon 2* (*OsLSi2)* and *OsLSi6* genes and the downregulation of the *OsLSi1* gene, which all encode Si-transporters, were reported in *O. sativa* supplemented with Si under 150 µM As stress (Khan and Gupta 2018). These findings indicate that *O. sativa* seeds may take Si up from the soil via OsLsi2 and/or OsLSi6 transporters. Moreover, seven days after rice seed imbibition, Si upregulated the expression of genes encoding Nitrate reductase (*NR*), Nitrite reductase (*NiR*), Glutamine synthetase (*GS*), Glutamate synthase (*GOGAT*), high affinity Nitrate transporter protein (*NRT2*), high affinity Ammonium transporter protein (*AMT1*), high affinity Phosphate transporters 1 and 2 (*PHT1*, *PHT2*), Acid phosphatases (*APase*), Potassium channel protein (*KAT1*) and Potassium transporter protein (*HAK10*) during As induced stress (Khan and Gupta 2018). In *C. sativus*, expression of *AMY* and *BMY* genes encoding α-amylase and β-amylase, respectively, were upregulated after 36h of stress from 10% PEG in the presence of Si, indicating that Si contributes to reserve mobilization of the embryo (Ning et al. 2020). In line with this, the positive effects of 2 mM Si on *C. sativus* under toxicity induced by 2 mM 3-phenylpropionic acid were attributed to the higher *AMY* and *BMY* transcript levels (Bu et al. 2018).

Si uptake by germinating seeds

Si has been reported to be taken up by plants in three different modes: active, passive, and rejective (Rizwan et al. 2015; Zhu and Gong 2014). Si assimilation by plants from soil was reported to be facilitated by the specialized Si-transporters Lsi1 and Lsi2 (Coskun et al. 2021). *Lsi1* was first discovered in *O. sativa* by Ma et al. (2006), where the suppression of its expression resulted in less Si uptake. Soon after another gene named *Lsi2* was identified in a rice mutant which accumulates less Si than the wild type and does not display any deleterious symptoms when grown in the presence of germanium, a toxic analog of Si (Ma et al. 2007). Other Si transporters, Lsi3 and Lsi6, have since been documented (Ahire et al. 2021). Most of the studies have investigated the uptake of Si by plants during vegetative stages, showing particularly that Si transporters are localized in roots. However, there is little information on the presence and role of functional Si-transporters in seeds. Strong evidence comes from a report by Khan and Gupta (2018) who demonstrated that Si supplementation to *O. sativa* seeds germinating under As stress upregulated the expression of *Lsi1*, *Lsi2* together and *Lsi6* (analog to *Lsi1*). These findings indicate that seeds express Si-transporter genes potentially allowing Si uptake.

Investigation of Si application for improvement of seed germination

Numerous reports have documented a beneficial effect of Si on seed germination of several plant species, particularly under unfavorable conditions (Ayed et al. 2021; Pereira et al. 2021; Sun et al. 2021). Si has the potential to induce various physiological changes inside seeds, but the effects on seed germination may depend on how Si is applied. To date, the most widespread method is to soak seeds in a solution with an optimal concentration of Si (Haghighi et al. 2012; Zhang et al. 2020). For example, the germination percentage of *L. culinus* seeds under 18% PEG stress was higher if they were soaked in 2 mM Na_2SiO_3 (Biju et al. 2017). The authors suggested that the induction of seed reserve mobilization mediated the improved seed germination. Under salinity stress, the improved germination percentage observed for *G. uralensis* seeds soaked in low Si concentrations was mediated by better membrane integrity and antioxidant systems (Zhang et al. 2015). Soaking *C. sativus* seeds in 0.3 mM

$NaSiO_3$ increased seed germination under 200 mM NaCl by triggering the expression of some genes related to dormancy release and seed germination (Gou et al., 2020). Soaking seeds with Si was also reported to increase seed germination by modulating plant hormone metabolism, especially ABA and GA (Delavar et al. 2017).

Priming seeds with Si is another method (Khan and Gupta 2018) that is widely used to synchronize the germination of individual seeds in a population, resulting in enhanced, faster, and more vigorous germination (Marthandan et al. 2020; Sharma et al. 2014). With this method, Si generally enhances the metabolic processes in the seed, which makes it efficient in responding more quickly to abiotic stress (Abdel Latef and Tran 2016; Hameed et al. 2013). For example, *Triticum turgidum* seeds primed with sodium metasilicates showed improved germination parameters, including germination percentage, germination index, and seedling vigor index under drought stress compared to unprimed seeds (Ayed et al. 2021). Consistent with this, Alves et al. (2020) observed that seed priming with 0.05 mM Ca_2SiO_4 increased the germination percentage and germination rate index of *Lactuca sativa* exposed to 50 mM salinity stress. According to Pereira et al. (2021), Si priming affects seed metabolism at both physiological and molecular levels. The authors demonstrated that primed seeds showed an improved antioxidant response and upregulation of stress alleviation genes. The positive impact of seed priming with Si was also reported in *O. sativa* under As stress (Khan and Gupta 2018).

Si has also been used as a coating agent (Rufino et al. 2017). This method is generally used to protect seeds against biotic stress (Pedrini et al. 2017). For example, Nguyen et al. (2016) showed that coating soybean seeds with Ag/SiO_2 nano-composites provided antifungal activity against *Fusarium oxysporium* and *Rhizoctonia solani*. The authors also showed that seed coating with Si was able to increase soybean seed germination to 100% in the presence of *F. oxysporium* and to between 98% to 100% in the presence of *R. solani*. Additionally, under normal non-stressed conditions, Corlett et al. (2014) demonstrated that Si-coated barley seeds exhibited a greater emergence speed index than that of the non-coated control without affecting the physiological quality of the seed. The authors hypothesized that seed coating with Si would be a promising way to protect barley seeds against pathogens without affecting the rate of seedling emergence nor the physiological quality of the seed. When seeds of *Z. mays* were coated with 20 mg H_2SiO_3 kg^{-1}, the established plants showed better growth and yield in terms of plant height, cob length and diameter, thousand-grain weight, and grain yield, more photosynthetic pigments, and enhanced enzymatic and non-enzymatic antioxidant activities under 120 mM NaCl stress compared to those from uncoated seeds (ur Rehman et al. 2020).

Conclusions and perspectives

In this review, we intended to bring together evidence of how Si mediates seed germination under abiotic stresses. The literature shows that the application of Si improves seed germination, reduces germination time, and synchronizes germination under abiotic stressors. Si likely ameliorates seed germination under abiotic stresses through different modes of action, passing by ion and water uptake, reserve mobilization, phytohormone balance, reduction in oxidative stress by enhancing the activities of antioxidant defense system, and upregulation of gene expression (Fig. 4).

Previous investigations showed that Si is beneficial to plant abiotic stress tolerance (Debona et al. 2017; El Moukhtari et al. 2021; Rizwan et al. 2015), but the mechanisms of Si action are still unclear. Some authors hypothesized that Si can protect plant by forming a mechanical barrier (Coskun et al. 2019). Others suggested that soluble Si can be taken up by the roots and act as a secondary messenger to modulate defense responses (Coskun et al. 2019; Fauteux et al. 2005; Van Bockhaven et al. 2013). However, these hypotheses assume plants absorb Si from the soil solution. In roots, Si is taken up from the soil solution by an influx transporter encoded by *Lsi1* (for review see Ma and Yamaji 2015). However, to date, little is known about active Si transporters in seeds. Therefore, more studies are needed to identify and characterize Si transporter activity in seeds to understand better the mechanisms underlying the role of Si during seed germination.

Seed germination is a complex process governed by the expression of specific sets of genes (Rajjou et al. 2012). Several works have shown that Si has amazing beneficial effects on seed germination under various abiotic stresses (Biju et al. 2017; Delavar et al. 2017; Lamsaadi et al. 2022). How Si treatment works in reducing the detrimental effect of abiotic stress during seed germination is, however, still not well understood and further researches are needed. Transcriptomic, proteomic and metabolomic analyses have been widely applied to explore mechanisms involved in plant adaptation to abiotic stresses (Hao et al. 2021). These approaches will be essential to identify targets of Si. This is a prerequisite to potentially manipulate genes in order to improve plant tolerance to adverse environmental conditions and at different developmental stages, including germination. Therefore, new studies are required to identify and characterize molecular mechanisms involved in Si perception by cells to trigger better germination and development under adverse conditions.

Several studies showed the beneficial concentration-dependent effects of various compounds of Si, including $CaSiO_3$, $NaSiO_3$, K_2SiO_3, and silicon nanoparticles, on seed germination (El Moukhtari et al. 2021; Rizwan et al. 2015; Siddiqui et al. 2020). However, according to Voogt and Sonneveld (2001), silicate salts, like $NaSiO_3$ and K_2SiO_3, used as sources of Si in growth media, are highly alkaline and if not carefully handled, may cause precipitation issues. Furthermore, many authors have reported that plants absorb Si from soil or nutrient solutions only in the form of $Si(OH)_4$ (Coskun et al. 2019). Therefore, it would be interesting to conduct more studies using different Si forms at varying doses to determine the optimal Si form and concentration that farmers could use to improve seed germination under abiotic stress.

In summary, the application of Si is a promising strategy to improve seed germination under abiotic stresses, but more specific research is needed in different crop species to show how Si acts in diverse agricultural contexts with optimal modes of application.

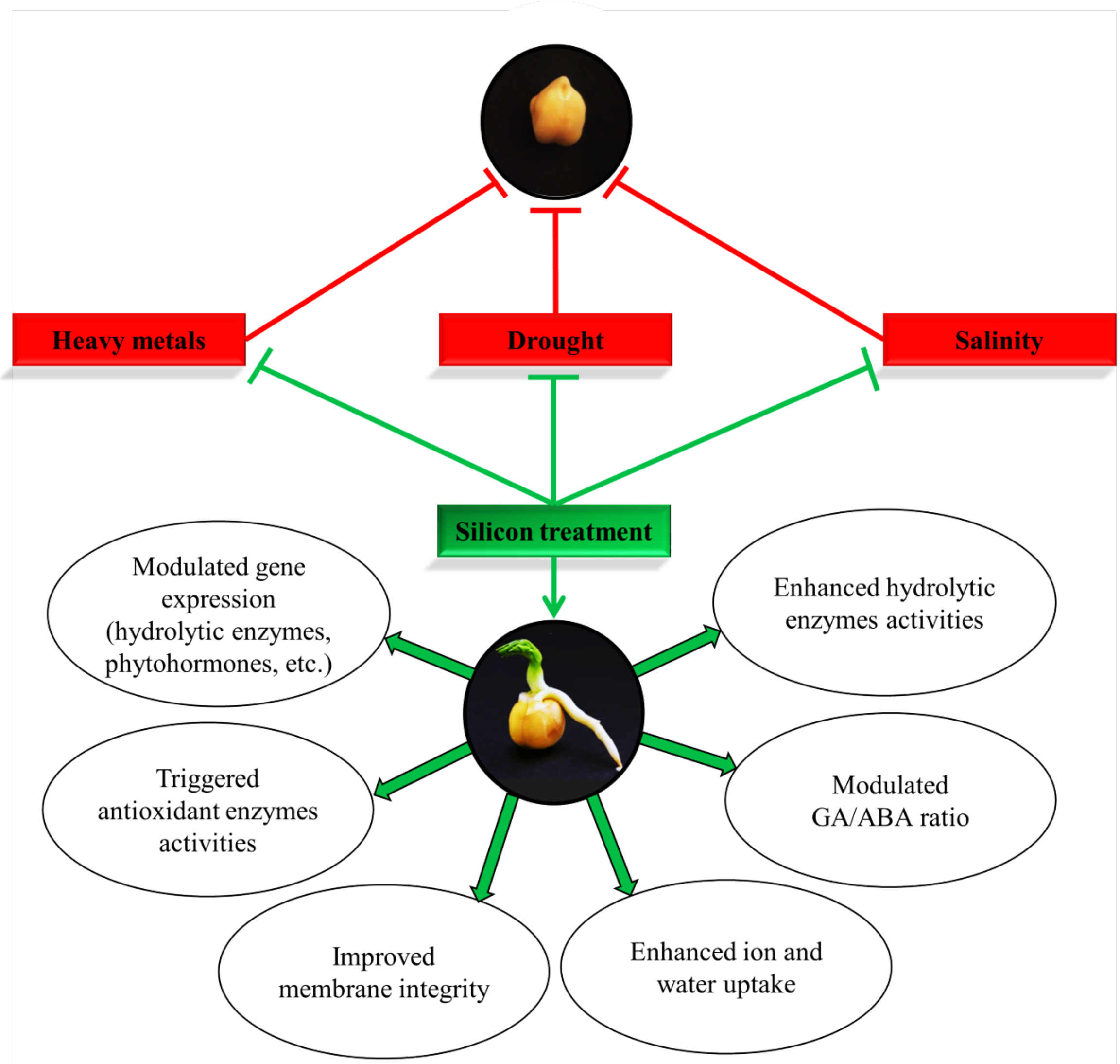

Fig. 4 Schematic summarizing the modes of action of silicon during seed germination under different abiotic stresses. Silicon upregulates hydrolytic enzyme activities, modulates phytohormone homeostasis, enhances ion and water uptake, induces antioxidant enzyme activities and improves membrane integrity, and upregulates the expression of abiotic stress tolerance genes. GA, gibberellic acid; ABA, abscisic acid

Statements and Declarations

Author Contributions

Conceptualization: A.E.M and A.S.; Literature review: A.E.M.; Original draft: A.E.M. and M.K.; Review editing: A.S., M.F., C.C., C.A., and W.Z.; Funding acquisition: A.S., M.F., and C.A.; Supervision: A.S. and M.F.; All authors read and approved the final manuscript.

Competing Interests

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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