



HAL
open science

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

Ahmed El Moukhtari, Mariem Ksiaa, Walid Zorrig, Cécile Cabassa, Chedly Abdelly, Mohamed Farissi, Arnould Savoure

► To cite this version:

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-03765797>

Submitted on 31 Aug 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

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

2

3 Ahmed EL MOUKHTARI^{1,2}, Mariem KSIAA^{1,3}, Walid ZORRIG³, Cécile CABASSA¹, Chedly ABDELLY³,
4 Mohamed FARISSI², Arnould SAVOURE^{1*}

5 ¹*Sorbonne Université, UPEC, CNRS, IRD, INRA, Institute of Ecology and Environmental Sciences of Paris (iEES),*
6 *F-75005, Paris, France*

7 ²*Laboratory of Biotechnology & Sustainable Development of Natural Resources, Polydisciplinary Faculty, Sultan*
8 *Moulay Slimane University, Beni Mellal, Morocco*

9 ³*Laboratory of Extremophile Plants, Centre of Biotechnology of Borj-Cedria, BP 901, Hammam-Lif, 2050, Tunisia*

10 *Corresponding author: Prof. Arnould SAVOURE,

11 *Sorbonne Université, UPEC, CNRS, IRD, INRA, Institute of Ecology and Environmental Sciences of Paris (iEES),*
12 *F-75005, Paris, France*

13 E-mail: arnould.savoure@sorbonne-universite.fr

14 Telephone : +33 1 44272672

15

16 Short title: Silicon and seed germination

17

18 **Acknowledgments**

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

23

24 **Abstract**

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

34

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

36

37

38

39

40

41 **Introduction**

42 Seed germination is the crucial stage when individual progeny of plant sexual reproduction become established
43 (Waterworth et al. 2019) and the environment of the future growth and development of the plant is determined
44 (Hubbard et al. 2012; Ali and Elozeiri 2017). Germination is naturally very sensitive to abiotic stresses, including
45 those caused by heavy metals, salinity, and drought (Dehnavi et al. 2020; Farissi et al. 2011; Ghavami and Ramin
46 2007; Seneviratne et al. 2017; Xiao et al. 2016). Abiotic stresses either delay or entirely prevent seed germination
47 through osmotic stress and/or ionic toxicity (Debez et al. 2018; Haghghi et al. 2012; Farissi et al. 2011). Some
48 abiotic stresses also increase reactive oxygen species (ROS), such as hydrogen peroxide (H₂O₂) and superoxide
49 anion (O₂⁻) in seeds (Bailly 2019), that may be produced during desiccation, germination, and aging (Pulido et al.
50 2009). In imbibed seeds, it has been reported that the metabolic activity in the different cell compartments such as
51 NADPH oxidase activity in the plasma membrane, respiratory activity in mitochondria, purine catabolism in
52 peroxisomes and lipid metabolism in glyoxysomes contribute to ROS production (Bailly 2004; Gomes and Garcia
53 2013). ROS disturb cellular metabolism by causing the peroxidation of proteins, lipids, and nucleic acids leading
54 to seed deterioration and germination failure (Parvin et al. 2019). The exposure of seeds to salinity, drought, or
55 heavy metals therefore induces modifications in protein structure, which diminishes hydrolytic enzyme activities
56 so mobilization of seed reserves is compromised (Farissi et al. 2011; Hameed et al. 2021; Kranner and Colville
57 2011; Liu et al. 2018; Muscolo et al. 2014; Seneviratne et al. 2017).

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

72
73

74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99

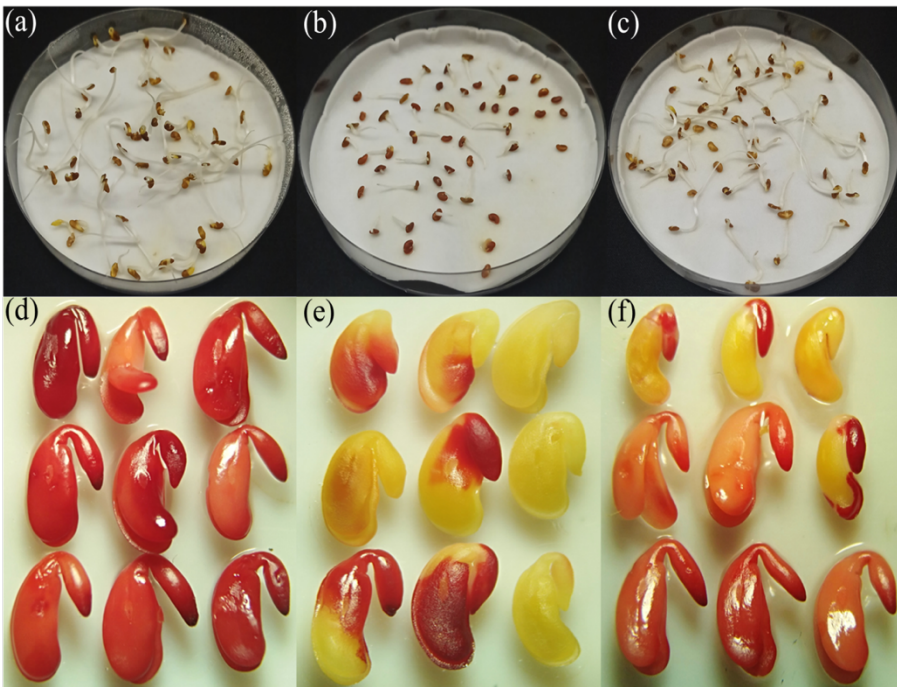


Fig. 1 Germination (a, b, and c) and embryo viability (d, e, and f) of seeds of the Moroccan *Medicago sativa* L. Demnate 201 variety treated with water (a, d), with 200 mM NaCl (b, e), or with 200 mM NaCl and 3 mM silicon in the form of CaSiO₃ (c, f). The germination rates were (a) 100%, (b) 51%, and (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

125 germination (e.g. Stejskalová et al. 2015). For example, seeds of the GA biosynthesis *A. thaliana* mutant *gal-3*
126 only germinate if exogenous GA is applied (Hauvermale and Steber 2020). A key step in the germination process
127 is the rupture of seed coat by the emerging radicle and GA stimulates radicle growth by mediating the activation
128 of cell division in the embryonic root apical meristem (Ravindran and Kumar 2019). In tomato and Arabidopsis,
129 GA promotes embryo growth and weakens the structures surrounding the embryo (Yamaguchi and Kamiya 2001).
130 GA also stimulates the synthesis and translation of specific mRNAs, particularly those encoding α -amylase, a
131 hydrolytic enzyme required for the digestion of seed reserves needed for germination (Ali and Elozeiri 2017;
132 Muralikrishna and Nirmala 2005).

133

134 **Overview of the effects of abiotic stresses on seed germination**

135 **Drought stress**

136 Water is a major factor necessary for the imbibition and germination of seeds (Bradford 2017). Drought decreases
137 external water potential, limiting the seed's ability to take up water and impairing germination (Balestrazzi et al.
138 2011; Campos et al. 2020). This effect has been observed in numerous Fabaceae species, including *Medicago*
139 *sativa* (Han et al. 2017; Wang et al. 2009), *Glycine max* (Wijewardana et al. 2018, 2019), and *Lens culinaris*
140 (Aniat-ul-Haq and Agnihotri 2010). Water stress was found to reduce several positive seed germination traits in
141 some crop species of the Poaceae, Solanaceae, Asteraceae and Brassicaceae families. For example, germination
142 percentage, germination rate, and vigor index are lowered by water stress in *Triticum aestivum* (Kizilgeci et al.
143 2017), *Hordeum vulgare* (Barati et al. 2015), *Oryza sativa* (Ali et al. 2020), *Solanum lycopersicum* (Galviz-Fajardo
144 et al. 2020), *Helianthus annuus* (Toscano et al. 2017) and *Brassica napus* (Xiong et al. 2018). According to Llanes
145 et al. (2015), drought stress can influence seed germination by changing endogenous plant growth regulator levels.
146 For example, water deficit mediated by PEG treatment triggered an increase in ABA and a decrease in GA in
147 *Trifolium repens*, impairing seed germination (Hassan et al. 2021). When less GA is available under water
148 shortage, reserve mobilization is compromised, because the synthesis of various hydrolytic enzymes is not
149 stimulated (Bewley 2001). In fact, Muscolo et al. (2014) and Hameed et al. (2021) reported that water deficiency
150 significantly impaired the activities of α - amylase, β -amylase and proteases in the endosperm of lentil and wheat
151 seeds, respectively, which consequently hampered seed reserve mobilization. In *Medicago truncatula* water deficit
152 also alters embryo respiration and seed viability (Balestrazzi et al. 2011). In drought-stressed wheat, a decrease in
153 germination rate appeared to result from the induction of oxidative stress, where a higher level of
154 malonyldialdehyde (MDA) was noted together with an increase in H_2O_2 and O_2^- (Guo et al. 2017).

155

156 **Salinity stress**

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

165 Salinity inhibits seed germination through various metabolic changes. In addition to the effects of osmotic
166 stress, salinity may induce ionic toxicity due to an excess of Na⁺ and Cl⁻ (de Oliveira et al. 2013). Salinity
167 drastically decreased the activities of α - and β -amylase in *Amaranthus caudatus* (BiaŁecka and Kępczyński 2009),
168 with negative consequences on seed reserve mobilization (Farissi et al. 2011). A similar effect was observed in *O.*
169 *sativa*, where salinity reduced the expression of the α -amylase gene and the activity of the enzyme (Liu et al.
170 2018). Similarly, catabolism of starch and lipids during *Cucumis sativus* seed germination was inhibited and
171 delayed under salinity (Zhang et al. 2017). In *Pancreaticum maritimum* seeds, salinity affects cell division and causes
172 DNA fragmentation, micronucleus formation, and chromosomal abnormalities (Mohamed et al. 2018). Salt can
173 also disturb the homeostasis of phytohormones leading to failure of seed germination (Miransari and Smith 2014).
174 Moreover, either through osmotic stress and/or ionic toxicity, salinity mediates an over-accumulation of ROS,
175 leading to damage of nucleic acids, lipids, proteins, and carbohydrates which limits seed germination (Ibrahim
176 2016).

177

178 **Heavy metals**

179 Heavy metals have been shown to negatively influence seed germination and seedling growth of various plant
180 species (El Rasafi et al. 2020; Seneviratne et al. 2017). There have been numerous descriptions of cadmium (Cd)
181 delaying or completely inhibiting germination. For example, wheat grain germination was reduced by 47% at 0.12
182 mM Cd (Guilherme et al. 2015), while no *O. sativa* grains germinated at 1 mM Cd (Ahsan et al. 2007). Mercury
183 (Hg), another toxic metal, is known to suppress seed germination and seedling growth. In *Vigna radiata*, 7 mM
184 Hg reduced seed germination, seedling elongation, and dry weight accumulation by 42%, 70%, and 47%,
185 respectively, compared to the control (Muhammad et al. 2015). Copper (Cu) also has a harmful impact on seed
186 germination, even at low concentrations. For example, 10 μ M Cu reduced seed germination of *H. vulgare*, *T.*
187 *aestivum*, and *O. sativa* by more than 7%, 39%, and 63%, respectively (Mahmood et al. 2007). When *M. sativa*
188 seeds were sown on solid media, 24% fewer seeds germinated when treated with 40 ppm nickel (Ni) (Aydinalp
189 and Marinova 2009). Lead (Pb) inhibits seed germination in various plant species, including *L. culinaris*
190 (Cokkizgin and Cokkizgin 2010). When 4.5 mM Pb was applied to lentil seeds, the germination percentage and
191 vigor index were 67% and 83% lower than controls without Pb, respectively, and the mean germination time was
192 17% longer. Seed germination inhibition by other metalloids has been reported, including aluminum (Al)
193 (Rodrigues et al. 2019), arsenic (As) (Mridha et al. 2021), and chromium (Cr) (Khan et al. 2020).

194 How heavy metal stress prevents seed germination is a complex biochemical process. Heavy metals can block
195 aquaporins by binding to a cysteine residue close to the pore of the protein (Daniels et al. 1994) thereby impeding
196 water uptake by seed cells and limiting seed imbibition (Cardoso et al. 2015; Lefèvre et al. 2009). Similar effects
197 have been observed in *Pisum sativum* under HgCl₂ and ZnCl₂ stresses (Kshetrimayum et al. 2017). Furthermore,
198 enzymes participating in reserve mobilization, such as α - and β -amylases, proteases, leucine amino peptidases as
199 well as cysteine-, aspartic-, and metallo-proteases, are altered by heavy metals, resulting in lower enzyme activity
200 that has a negative effect on germination (Seneviratne et al. 2017). Heavy metal stress may also alter endogenous
201 phytohormone homeostasis in seeds (Seneviratne et al. 2017). In *Cicer arietinum*, the negative effect of Pb or zinc
202 (Zn) stress on seed germination was due to an increase in ABA and a decrease in GA content (Atici et al. 2005).
203 Heavy metals can also reduce seed germination by inducing oxidative stress, reducing cell viability, and altering
204 embryo growth (Gonzalez-Mendoza et al. 2009; Li et al. 2005; Sethy and Ghosh 2013).

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

209 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	<i>Glycine max</i>	Lower germination indexes Shorter hypocotyl and root More abnormal seedlings	Machado Neto et al. (2004)
	PEG	15%	<i>Brassica napus</i>	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%	<i>Gossypium hirsutum</i>	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%	<i>Hordeum vulgare</i>	Lower germination indexes Fewer primary roots Shorter maximum root length Shorter shoots	Barati et al. (2015)
	PEG	0.5-2.5 MPa	<i>Juglans regia</i>	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%	<i>Lens culinaris</i>	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	<i>Lens culinaris</i>	Lower germination percentage Reduced seedling survival Shorter root and shoot	Aniat-ul-Haq and Agnihotri (2010)
	PEG	35%	<i>Medicago sativa</i>	Lower germination indexes More ROS accumulation More lipid peroxidation Increased activity of antioxidant enzymes	Wang et al. (2009)
	PEG	20%	<i>Oryza sativa</i>	Lower germination indexes Less water in seeds More ROS accumulation More lipid peroxidation More ABA Upregulated <i>OsNCED3</i> expression Upregulated SOD and CAT related gene expression	Liu et al. (2019)
	PEG	-0.3, -0.6 and -0.9 MPa	<i>Oryza sativa</i>	Lower germination indexes Shorter plumules Shorter roots Shorter seedlings	Ali et al. (2020)
	PEG	17%	<i>Trifolium repens</i>	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	<i>Triticum aestivum</i>	Lower germination indexes Lower amylase and esterase activity More ROS accumulation More lipid peroxidation	Zhang et al. (2010)
	AlCl ₃	2 mmol L ⁻¹	<i>Oryza sativa</i>	Lower germination indexes Lower GA/ABA ratio Downregulation of the expression of ABA catabolism genes (<i>OsABA8ox1</i> and <i>OsABA8ox2</i>) Lower α - and β -amylase activity More lipid peroxidation Increased antioxidant enzyme activity	Xu et al. (2017)

	Cd	100-500 μM	<i>Brassica napus</i>	Induced ROS accumulation Induced lipid peroxidation Ultrastructural changes in cells of germinating seeds	Ali et al. (2015)
	CdCl ₂	5 mM	<i>Phaseolus vulgaris</i>	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	<i>Trigonella foenum-graecum</i>	Lower germination indexes	Espanany et al. (2015)
	CdCl ₂	1-5 mM	<i>Triticum aestivum</i>	Lower germination indexes Shorter coleoptile and radicles Lower amylase activity Induced lipid peroxidation	Hu et al. (2015)
	CuSO ₄	100-500 μM	<i>Hordeum vulgare</i>	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	<i>Arabidopsis thaliana</i>	Lower germination indexes Less embryo viability Increased seed coat permeability	de Silva et al. (2021)
	Cr (VI)	100 μM	<i>Triticum aestivum</i>	Lower germination indexes Lower α -amylase activity Fewer free amino acids Induced ROS accumulation Induced lipid peroxidation	Lei et al. (2021)
	K ₂ Cr ₂ O ₇	30-300 mg L ⁻¹	<i>Lepidium sativum</i>	Lower germination indexes	Pavel et al. (2013)
	PbCl ₂	0.5-4.5 mM	<i>Lens culinaris</i>	Lower germination indexes Shorter plumules and radicles	Cokkizgin and Cokkizgin (2010)
	Pb (NO ₃) ₂	0.05-1 g L ⁻¹	<i>Triticum aestivum</i>	Induced lipid peroxidation, Increased proline accumulation Lower α -amylase activity Increased antioxidant enzyme activities	Lamhamdi et al. (2011)
Salinity	NaCl	150-300 mM	<i>Arabidopsis thaliana</i>	Lower germination indexes Induced ROS accumulation Induced lipid peroxidation	Luo et al. (2021)

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

NaCl	120 mM	<i>Oryza sativa</i>	Lower germination indexes Less bioactive GA Lower α -amylase activity Downregulated α -amylase gene expression	Liu et al. (2018)
NaCl	50-200 mM	<i>Pancreatum maritimum</i>	Lower germination indexes Affects cell division DNA fragmentation, micronucleus formation, and chromosomal abnormalities	Mohamed et al. (2018)
Na ₂ CO ₃	50 mM	<i>Oryza sativa</i>	Lower germination indexes Less bioactive GA Lower α -amylase content	Li et al. (2019)
NaHCO ₃	90 mmol L ⁻¹	<i>Cucumis sativus</i>	Lower germination indexes Shorter hypocotyl and radicles Lower α - and β -amylase activity Increased lipid peroxidation	Sun and Luo (2014)

210 PEG, polyethelene glycol; GA, gibberellic acid; ABA, abscisic acid; Na₂CO₃, sodium carbonate; NaHCO₃, sodium hydrogen carbonate; Pb (NO₃)₂, lead (II) nitrate; PbCl₂, lead

211 chloride; Cr(VI), chromium hexavalent; Cr³⁺, chromium; CuSO₄, copper sulfate; CdCl₂, cadmium chloride; Cd, cadmium; AlCl₃, aluminum chloride.

212

213 **Si improves seed germination under abiotic stresses**

214 Si has repeatedly been found to have a positive effect on seed germination under abiotic stress (e.g. Rizwan et al.
215 2015; Siddiqui et al. 2020), and several of the reports are listed in Table 2. Elemental Si increases seed germination
216 percentage, germination index, and seedling vigor of *C. sativus* exposed to stress caused by 200 mM NaCl (Gou
217 et al. 2020). Investigations by Almutairi (2016) indicate that 1 mM nano-silicon increased germination percentage
218 and germination rate of *S. lycopersicum* seeds under different NaCl concentrations (150-200 mM). In a different
219 study by Zhang et al. (2015), germination rate, germination index, and vitality indexes of *Glycyrrhiza uralensis*
220 seeds grown under salt stress (150 mM NaCl) were all improved upon Si treatment. In *Trigonella foenum-graecum*
221 seeds germinating under NaCl induced salinity stress, the application of CaSiO_3 improved the germination
222 percentage, germination speed, velocity index, germination energy, peak value and vitality index, all in a shorter
223 mean germination time (Lamsaadi et al. 2022). Alsaeedi et al. (2017) showed that Si in the form of nano-silica
224 restricted Na^+ uptake by *Phaseolus vulgaris* seeds resulting in a final germination percentage and germination rate
225 that were 19.7% and 22.6% higher, respectively, than Na^+ -stressed *P. vulgaris* seeds not supplied with Si. Toxicity
226 of NaCl on germination of *T. aestivum* (Azeem et al. 2015), *Zea mays* (Naguib and Abdalla 2019), and *L. sativa*
227 (Alves et al. 2020) was alleviated by Si application.

228 Si added as an exogenous compound was also beneficial as it improved seed germination under other abiotic
229 stresses, such as drought and heavy metal stress (Arif et al. 2021). Under drought stress, Ayed et al. (2021) reported
230 that Si in the form of sodium metasilicate ($\text{Na}_2\text{SiO}_3\cdot\text{H}_2\text{O}$) increased germination percentage, germination, and
231 seedling vigor indexes of *T. turgidum* by 22%, 62%, and 39%, respectively. Furthermore, under 100 μM Cd stress,
232 SiO_2 supplements improved *Phyllostachys edulis* seed germination (Emamverdian et al. 2021). In *O. sativa*, 5 mM
233 silicic acid increased germination percentage under 150 μM As stress from 56% to 78% (Khan and Gupta 2018).
234 In seed germination experiments with *Z. mays*, the toxic effects of Al were alleviated by exogenous application of
235 Si (Delavar et al. 2017). Si in the form of Na_2SiO_3 can also augment seed germination in *C. sativus* under 3-
236 phenylpropionic acid induced stress (Bu et al. 2018) and in *C. melo* under autotoxicity stress (Zhang et al. 2020).
237 The studies above indicate that Si has an amelioratory effect on the germination of seeds grown under various
238 abiotic stressors.

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

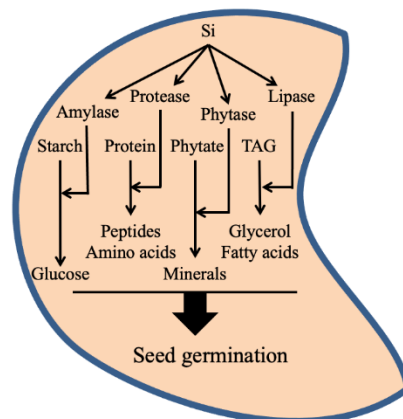
Plant species	Si			Stress		Mode of action	References
	Form	Technique	Concentration	Type	Level		
<i>Cucumis melo</i>	Na ₂ SiO ₃	Soaking	2 mM	MPWE	20 mg L ⁻¹	Germination traits Reserve mobilization Gene expression Antioxidant activities Membrane integrity	Zhang et al. (2020)
<i>Cucumis sativus</i>	Na ₂ SiO ₃	Soaking	2 mM	3-PPA	2 mM	Germination traits Reserve mobilization Gene expression	Bu et al. (2018)
<i>Cucumis sativus</i>	Na ₂ SiO 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)
<i>Lactuca sativa</i>	Ca ₂ SiO ₄	Priming	0.05-0.1 mM	NaCl	50 mM	Germination traits Antioxidant activities Membrane stability	Alves et al. (2020)
<i>Lathyrus odoratus</i>	nano-Si	Priming	20 mg L ⁻¹	NaCl	21.60 dS m ⁻¹	Germination traits	El-Serafy et al. (2021)
<i>Lens culinaris</i>	Na ₂ SiO ₃	Soaking	2 mM	PEG	18%	Germination traits Reserve mobilization Antioxidant activities ROS detoxification Membrane stability	Biju et al. (2017)
<i>Oryza sativa</i>	H ₄ SiO ₂ ⁻	Priming	5 mM	As	150 uM	Germination traits Antioxidant activities Gene expression	Khan and Gupta (2018)
<i>Oryza sativa</i>	SiO ₂	Priming	350 mg L ⁻¹	PEG	-0.9 Mpa	Germination traits Antioxidant activities Membrane stability	Gana Ali et al. (2021)
<i>Phaseolus vulgaris</i>	nano-Si	Soaking	300 mg L ⁻¹	Na ⁺	1-5 g L ⁻¹	Germination traits Nutrient homeostasis	Alsaeedi et al. (2017)

<i>Phyllostachys edulis</i>	nano-Si	Soaking	200 μ M	Cd	100 μ M	Germination traits	Emamverdian et al. (2021)
<i>Solanum lycopersicum</i>	Na ₂ SiO ₃	Soaking	0.5 mM	PEG	10%	Germination traits Antioxidant activities ROS detoxification Membrane integrity	Shi et al. (2014)
<i>Solanum lycopersicum</i>	nano-Si	Soaking	0.5-3 mM	NaCl	150-200 mM	Germination traits Gene expression	Almutairi (2016)
<i>Trigonella foenum-graecum</i>	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)
<i>Triticum aestivum</i>	K ₂ SiO ₃	Priming	1.5 mM	NaCl	up to 20 dS m ⁻¹	Germination traits	Feghhenabi et al. (2020)
<i>Triticum turgidum</i>	Na ₂ SiO ₃	Priming	15-20 mg L ⁻¹	PEG	150 g L ⁻¹	Germination traits	Ayed et al. (2021)
<i>Zea mays</i>	Na ₂ SiO ₃	Soaking	2 mM	NaCl	75 mM	Germination traits Phytohormones Reserve mobilization	Delavar et al. (2017)
<i>Zea mays</i>	Na ₂ SiO ₃	Soaking	2 mM	Al	10 mM	Germination traits Phytohormones Reserve mobilization	Delavar et al. (2017)
<i>Zea mays</i>	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)

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

241 **Si treatment enhances seed reserve mobilization under abiotic stress**

242 Si application improves the germination of seeds under abiotic stress conditions by modulating reserve
243 mobilization (Fig. 2). For example, in drought-stressed germinating seeds of *Eleusine coracana*, Mundada et al.
244 (2021) recently found that Si increased the breakdown of glucose to acetyl CoA via pyruvate, which was diverted
245 to lipid biosynthesis instead of the tricarboxylic acid cycle. This is good evidence that Si has a role in lipid
246 metabolism. Additionally, Si augmented the activity of α -amylase, β -amylase, and α -glucosidase in osmotically
247 stressed seeds of *L. culinaris* (Biju et al. 2017). Similar findings were reported in *C. sativus* (Ning et al. 2020). In
248 wheat, seed priming with Si nanoparticles increased amylase activity under drought stress (Rai-Kalal et al. 2021).
249 Similarly, in *C. sativus* under salt stress, application of 0.3 mM sodium silicate alleviated the negative effects of
250 200 mM NaCl and significantly increased α -amylase activity (Gou et al. 2020). Recently, Lamsaadi et al. (2022)
251 observed that the enhanced seed germination rate of Si-treated *Trigonella foenum-graecum* seeds under salt stress
252 was due to better reserve mobilization and embryo viability. Seed priming with nano-silica improved embryo
253 respiration by increasing aldolase and isocitrate lyase activities (Naguib and Abdalla 2019). Under Al stress, the
254 activity of amylase was 45% higher in Al-stressed seed with NaSiO₃ compared to Al-stressed seed without the
255 addition of Si (Delavar et al. 2017). In a study of *C. melo* seeds, the application of Si increased α -, β - and total-
256 amylase activities under autotoxicity stress (Zhang et al., 2020). The same was observed under 3-phenylpropionic
257 acid induced stress in *C. sativus*, where Si supplementation improved α -, β - and total-amylase activities, and finally
258 seed germination (Bu et al. 2018). Exogenous Si may therefore alleviate the negative effects of abiotic stresses on
259 seed germination by promoting reserve mobilization, but more detailed studies, including testing for embryo
260 viability and monitoring gene expression and the activity of other enzymes related to reserve mobilization, are
261 required.

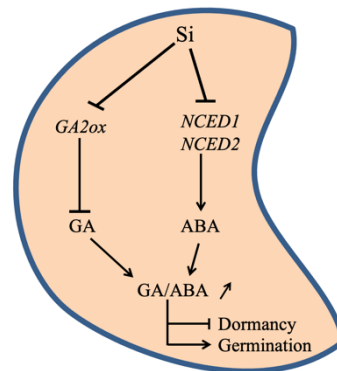


272 Fig. 2 Proposed effects of Si on seed reserve mobilization during seed germination under abiotic stresses. TAG,
273 triacylglycerol

282 **Exogenous Si mediates seed germination by modulating phytohormone balance**

283 The effects of Si on phytohormone synthesis in stressed plants during vegetative growth have been reviewed by
284 El Moukhtari et al. (2021) and Rizwan et al. (2015). Only a few reports show a link between Si treatment and plant
285 hormone metabolism during seed germination (Fig. 3). A recent study demonstrated that seed priming with nano-
286 silica increased *Z. mays* seed germination under 150 mM NaCl stress, and this was correlated with a higher
287 GA/ABA ratio (Naguib and Abdalla 2019). The authors also revealed that changes in hormone metabolism were

288 sufficient to explain the effect of Si on seed germination, particularly under unfavorable conditions. Another
 289 interesting study demonstrated that under 75 mM NaCl or 10 mM Al stress, *Z. mays* seeds that were soaked in 2
 290 mM Na₂SiO₃ solution contained more GA and less ABA compared to the control, leading to a higher germination
 291 rate (Delavar et al. 2017). According to Gou et al. (2020), the increased GA in NaCl-treated *C. sativus* treated with
 292 Si was the result of downregulated expression of GA catabolism gene *GA2ox*, while the decreased ABA was the
 293 result of downregulated expression of ABA anabolism genes such as *NCED1* and *NCED2*. The combined effect
 294 was to raise the GA/ABA ratio to the level needed for dormancy release and germination. In PEG-stressed seeds
 295 of *E. coracana*, the application of Si modulates jasmonic acid (JA) synthesis during germination, especially under
 296 stressed conditions (Mundada et al. 2021). These results provide evidence that Si is effective in improving seed
 297 germination through the modulation of GA, ABA, and JA metabolism. Further investigations are necessary to
 298 understand the mode of action of Si and any signaling crosstalk in modulating phytohormones in seeds during
 299 abiotic stress.



300
301
302
303
304
305
306
307
308
309
310
311
312
313
314
315
316
317
318
319

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

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

322 During environmental stresses, the generation of ROS is enhanced (Nadarajah 2020). At high levels, ROS causes
 323 proteins, lipids, and nucleic acid peroxidation, hence causing cell damage and death (Hasanuzzaman et al. 2020).
 324 Maintaining membrane integrity and functionality during environmental change is a challenge for sessile plants
 325 (Rogowska and Szakiel 2020). Antioxidative defense systems, including both enzymatic and non-enzymatic
 326 antioxidants, play a major role preventing ROS build-up in cells (Kasote et al. 2015). Si has been reported to lower
 327 ROS activity and restore damaged plant membranes during seed germination by enhancing the antioxidant system
 328 (Debona et al. 2017; Mostofa et al. 2021). In drought-stressed *S. lycopersicum* (Shi et al. 2014) and *L. culinaris*
 329 (Biju et al. 2017), Na₂SiO₃ increased the activity of ascorbate peroxidase (APX), peroxidase (POX), catalase
 330 (CAT), and superoxide dismutase (SOD), consequently decreasing how much H₂O₂, O₂⁻, and malondialdehyde
 331 were generated, with less lipid peroxidation as a result. Parallel evidence using the Evans Blue method is that
 332 under 200 mM NaCl *C. sativus* seed membrane integrity was improved by Si-treatment (Gou et al. 2020). The
 333 latter effect was linked to the ability of Si to limit ROS generation by modulating the activity of SOD, POX, CAT
 334 and APX. Likewise, *Trigonella foenum graecum* seeds supplied with 3 mM CaSiO₃ and exposed to 200 mM NaCl

335 solution showed increased SOD and polyphenol oxidase (PPO) activities, and a greater content of total polyphenol,
336 flavonoids, glycine betaine and proline, while displaying lowered levels of H₂O₂, O₂⁻, MDA and electrolyte leakage
337 (Lamsaadi et al. 2022). Similar findings were reported by Naguib and Abdalla (2019), who showed that the
338 decreases in both lipid peroxidation and ROS accumulation in salt-stressed *Z. mays* seeds were associated with the
339 higher activities of SOD, POX, and PPO in response to nano-silica applied as a priming agent. Again as a priming
340 agent, Si stimulated the activities of antioxidant enzymes, particularly CAT, decreasing lipid peroxidation in Cd-
341 stressed lettuce seeds (Pereira et al. 2021). Si supplementation to *C. melo* seeds triggered an increased SOD, CAT
342 and POD activities and a reduced MDA content under autotoxicity stress (Zhang et al. 2020). It is clear from the
343 above studies that Si improves seed germination under multiple abiotic constraints by enhancing enzymatic and
344 non-enzymatic antioxidant activities and thus maintaining the integrity and stability of membranes. Currently
345 studies related to the molecular mechanisms and the metabolic pathways of Si-mediated stress tolerance are still
346 limited.

347

348 Si modulates gene expression during seed germination

349 The complex process of seed germination is governed by the expression of specific sets of genes (Rajjou et al.
350 2012). Si has been reported to regulate transcript levels of various abiotic stress-related genes during seed
351 germination. The example of 0.3 mM Na₂SiO₃ downregulating the expression of *NCED1* and *NCED2* encoding
352 nine-cis-epoxycarotenoid dioxygenases involved in ABA synthesis and *GA2ox* encoding gibberellin 2-oxidase,
353 which deactivates bioactive Gas, was already cited (Gou et al. 2020). In another case, as ABA is known to activate
354 *Mitogen-activated protein kinase (MAPK)* expression, which are genes involved in signal transduction pathways
355 (Lu et al. 2002), the lower levels of ABA due to Si treatment (Delavar et al. 2017) may be the reason *MAPK2* and
356 *MAPK3* are downregulated in Si-treated salt-stressed *S. lycopersicum* (Almutairi 2016). ABA was also shown to
357 regulate the expression of *Ethylene response factor (ERF)*, a key transcription factor in abiotic stress signaling
358 (Müller and Munné-Bosch 2015). In *S. lycopersicum*, the application of Si downregulates the expression of
359 *Ethylene response factor 5 (ERF5)*, and this was associated with lower levels of ABA (Almutairi 2016). Moreover,
360 *ERF* controls *Respiratory burst oxidase (RBOH)* (Yao et al. 2017), and the reduction of *ERF5* expression in salt-
361 stressed *S. lycopersicum* in response to Si treatment downregulates *RBOH1* (Almutairi 2016).

362 The accumulation of compatible osmolytes, including proline, is one of the most common strategies to
363 overcome adverse environmental conditions (El Moukhtari et al. 2020). This response is mediated by several
364 genes, including *delta-1-Pyrroline5-carboxylate synthetase (P5CS)* involved in proline biosynthesis (Szabadoz
365 and Savouré 2010). In a study by Almutairi (2016), the application of Si increased the expression of *P5CS* in *S.*
366 *lycopersicum* during NaCl-induced salinity stress. This suggests that Si may be involved in mediating osmotic
367 adjustment in germinating seeds during osmotic stress. Another mechanism of plant resistance to salt stress is to
368 decrease Na⁺ uptake and accumulation (Bargaz et al. 2015) through the action of the Na⁺/H⁺ antiporters of the
369 plasma membrane (Rizwan et al. 2015). To investigate how Si controls Na⁺ uptake by the seeds, Almutairi (2016)
370 studied the effect of Si on the expressions of *Na⁺/H⁺ antiporter 6 (NHX6)* in salt-stressed seeds of *S. lycopersicum*.
371 The results showed that Si under salt stress up-regulated this gene expression, preventing Na⁺ uptake by the seeds.
372 Abscisic Acid-Responsive Element-Binding Protein (AREB) is required for the establishment of *Arabidopsis*
373 seedlings (Sharma et al. 2011). During salinity stress, Si-treatment upregulated *AREB* expression in *S.*
374 *lycopersicum* as compared to controls (Almutairi 2016). Acid phosphatase and esterases belonging to a group of

375 hydrolytic enzymes that catalyze the hydrolysis of the seed reserve are required for the germination process
376 (Kantharaju and Murth 2014; Senna et al. 2006). In Cd-stressed lettuce, the use of Si as a priming agent triggered
377 the expression of genes associated with esterase and acid phosphatase (Pereira et al. 2021). The upregulation of
378 *Low silicon 2 (OsLSi2)* and *OsLSi6* genes and the downregulation of the *OsLSi1* gene, which all encode Si-
379 transporters, were reported in *O. sativa* supplemented with Si under 150 μ M As stress (Khan and Gupta 2018).
380 These findings indicate that *O. sativa* seeds may take Si up from the soil via OsLsi2 and/or OsLSi6 transporters.
381 Moreover, seven days after rice seed imbibition, Si upregulated the expression of genes encoding Nitrate reductase
382 (*NR*), Nitrite reductase (*NiR*), Glutamine synthetase (*GS*), Glutamate synthase (*GOGAT*), high affinity Nitrate
383 transporter protein (*NRT2*), high affinity Ammonium transporter protein (*AMT1*), high affinity Phosphate
384 transporters 1 and 2 (*PHT1*, *PHT2*), Acid phosphatases (*APase*), Potassium channel protein (*KAT1*) and Potassium
385 transporter protein (*HAK10*) during As induced stress (Khan and Gupta 2018). In *C. sativus*, expression of *AMY*
386 and *BMY* genes encoding α -amylase and β -amylase, respectively, were upregulated after 36h of stress from 10%
387 PEG in the presence of Si, indicating that Si contributes to reserve mobilization of the embryo (Ning et al. 2020).
388 In line with this, the positive effects of 2 mM Si on *C. sativus* under toxicity induced by 2 mM 3-phenylpropionic
389 acid were attributed to the higher *AMY* and *BMY* transcript levels (Bu et al. 2018).

390

391 **Si uptake by germinating seeds**

392 Si has been reported to be taken up by plants in three different modes: active, passive, and rejective (Rizwan et al.
393 2015; Zhu and Gong 2014). Si assimilation by plants from soil was reported to be facilitated by the specialized Si-
394 transporters Lsi1 and Lsi2 (Coskun et al. 2021). *Lsi1* was first discovered in *O. sativa* by Ma et al. (2006), where
395 the suppression of its expression resulted in less Si uptake. Soon after another gene named *Lsi2* was identified in
396 a rice mutant which accumulates less Si than the wild type and does not display any deleterious symptoms when
397 grown in the presence of germanium, a toxic analog of Si (Ma et al. 2007). Other Si transporters, Lsi3 and Lsi6,
398 have since been documented (Ahire et al. 2021). Most of the studies have investigated the uptake of Si by plants
399 during vegetative stages, showing particularly that Si transporters are localized in roots. However, there is little
400 information on the presence and role of functional Si-transporters in seeds. Strong evidence comes from a report
401 by Khan and Gupta (2018) who demonstrated that Si supplementation to *O. sativa* seeds germinating under As
402 stress upregulated the expression of *Lsi1*, *Lsi2* together and *Lsi6* (analog to *Lsi1*). These findings indicate that
403 seeds express Si-transporter genes potentially allowing Si uptake.

404

405 **Investigation of Si application for improvement of seed germination**

406 Numerous reports have documented a beneficial effect of Si on seed germination of several plant species,
407 particularly under unfavorable conditions (Ayed et al. 2021; Pereira et al. 2021; Sun et al. 2021). Si has the
408 potential to induce various physiological changes inside seeds, but the effects on seed germination may depend on
409 how Si is applied. To date, the most widespread method is to soak seeds in a solution with an optimal concentration
410 of Si (Haghighi et al. 2012; Zhang et al. 2020). For example, the germination percentage of *L. culinus* seeds under
411 18% PEG stress was higher if they were soaked in 2 mM Na_2SiO_3 (Biju et al. 2017). The authors suggested that
412 the induction of seed reserve mobilization mediated the improved seed germination. Under salinity stress, the
413 improved germination percentage observed for *G. uralensis* seeds soaked in low Si concentrations was mediated
414 by better membrane integrity and antioxidant systems (Zhang et al. 2015). Soaking *C. sativus* seeds in 0.3 mM

415 NaSiO₃ increased seed germination under 200 mM NaCl by triggering the expression of some genes related to
416 dormancy release and seed germination (Gou et al., 2020). Soaking seeds with Si was also reported to increase
417 seed germination by modulating plant hormone metabolism, especially ABA and GA (Delavar et al. 2017).

418 Priming seeds with Si is another method (Khan and Gupta 2018) that is widely used to synchronize the
419 germination of individual seeds in a population, resulting in enhanced, faster, and more vigorous germination
420 (Marthandan et al. 2020; Sharma et al. 2014). With this method, Si generally enhances the metabolic processes in
421 the seed, which makes it efficient in responding more quickly to abiotic stress (Abdel Latef and Tran 2016; Hameed
422 et al. 2013). For example, *Triticum turgidum* seeds primed with sodium metasilicates showed improved
423 germination parameters, including germination percentage, germination index, and seedling vigor index under
424 drought stress compared to unprimed seeds (Ayed et al. 2021). Consistent with this, Alves et al. (2020) observed
425 that seed priming with 0.05 mM Ca₂SiO₄ increased the germination percentage and germination rate index of
426 *Lactuca sativa* exposed to 50 mM salinity stress. According to Pereira et al. (2021), Si priming affects seed
427 metabolism at both physiological and molecular levels. The authors demonstrated that primed seeds showed an
428 improved antioxidant response and upregulation of stress alleviation genes. The positive impact of seed priming
429 with Si was also reported in *O. sativa* under As stress (Khan and Gupta 2018).

430 Si has also been used as a coating agent (Rufino et al. 2017). This method is generally used to protect seeds
431 against biotic stress (Pedrini et al. 2017). For example, Nguyen et al. (2016) showed that coating soybean seeds
432 with Ag/SiO₂ nano-composites provided antifungal activity against *Fusarium oxysporium* and *Rhizoctonia solani*.
433 The authors also showed that seed coating with Si was able to increase soybean seed germination to 100% in the
434 presence of *F. oxysporium* and to between 98% to 100% in the presence of *R. solani*. Additionally, under normal
435 non-stressed conditions, Corlett et al. (2014) demonstrated that Si-coated barley seeds exhibited a greater
436 emergence speed index than that of the non-coated control without affecting the physiological quality of the seed.
437 The authors hypothesized that seed coating with Si would be a promising way to protect barley seeds against
438 pathogens without affecting the rate of seedling emergence nor the physiological quality of the seed. When seeds
439 of *Z. mays* were coated with 20 mg H₂SiO₃ kg⁻¹, the established plants showed better growth and yield in terms of
440 plant height, cob length and diameter, thousand-grain weight, and grain yield, more photosynthetic pigments, and
441 enhanced enzymatic and non-enzymatic antioxidant activities under 120 mM NaCl stress compared to those from
442 uncoated seeds (ur Rehman et al. 2020).

443

444 **Conclusions and perspectives**

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

451 Previous investigations showed that Si is beneficial to plant abiotic stress tolerance (Debona et al. 2017; El
452 Moukhtari et al. 2021; Rizwan et al. 2015), but the mechanisms of Si action are still unclear. Some authors
453 hypothesized that Si can protect plant by forming a mechanical barrier (Coskun et al. 2019). Others suggested that
454 soluble Si can be taken up by the roots and act as a secondary messenger to modulate defense responses (Coskun

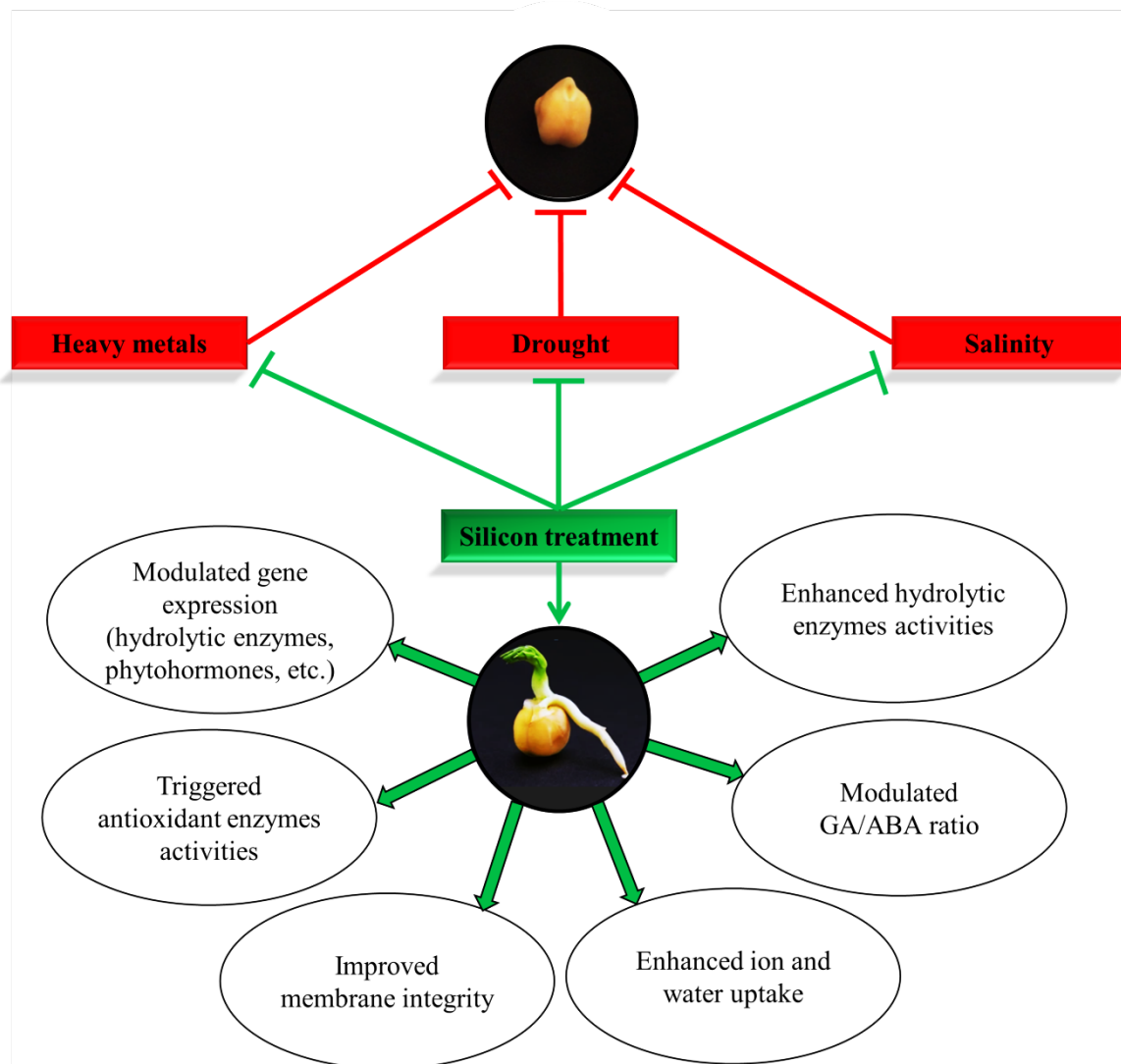
455 et al. 2019; Fauteux et al. 2005; Van Bockhaven et al. 2013). However, these hypotheses assume plants absorb Si
456 from the soil solution. In roots, Si is taken up from the soil solution by an influx transporter encoded by *Lsi1* (for
457 review see Ma and Yamaji 2015). However, to date, little is known about active Si transporters in seeds. Therefore,
458 more studies are needed to identify and characterize Si transporter activity in seeds to understand better the
459 mechanisms underlying the role of Si during seed germination.

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

470 Several studies showed the beneficial concentration-dependent effects of various compounds of Si, including
471 CaSiO_3 , NaSiO_3 , K_2SiO_3 , and silicon nanoparticles, on seed germination (El Moukhtari et al. 2021; Rizwan et al.
472 2015; Siddiqui et al. 2020). However, according to Voogt and Sonneveld (2001), silicate salts, like NaSiO_3 and
473 K_2SiO_3 , used as sources of Si in growth media, are highly alkaline and if not carefully handled, may cause
474 precipitation issues. Furthermore, many authors have reported that plants absorb Si from soil or nutrient solutions
475 only in the form of Si(OH)_4 (Coskun et al. 2019). Therefore, it would be interesting to conduct more studies using
476 different Si forms at varying doses to determine the optimal Si form and concentration that farmers could use to
477 improve seed germination under abiotic stress.

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

481



482
 483 **Fig. 4** Schematic summarizing the modes of action of silicon during seed germination under different abiotic
 484 stresses. Silicon upregulates hydrolytic enzyme activities, modulates phytohormone homeostasis, enhances ion
 485 and water uptake, induces antioxidant enzyme activities and improves membrane integrity, and upregulates the
 486 expression of abiotic stress tolerance genes. GA, gibberellic acid; ABA, abscisic acid
 487

488

489 **Statements and Declarations**

490 **Author Contributions**

491 Conceptualization: A.E.M and A.S.; Literature review: A.E.M.; Original draft: A.E.M. and M.K.; Review editing:
 492 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
 493 authors read and approved the final manuscript.

494

495 **Competing Interests**

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

498

- Abdel Latef AA, Tran L-SP (2016) Impacts of priming with silicon on the growth and tolerance of maize plants to alkaline stress. *Front Plant Sci* 7:243. <https://doi.org/10.3389/FPLS.2016.00243>
- Ahire M, Mundada P, Nikam T, Bapat V, Suprasanna P (2021) Multifaceted roles of silicon in mitigating environmental stresses in plants. *Plant Physiol Biochem* 169:291–310. <https://doi.org/10.1016/j.plaphy.2021.11.010>
- Ahsan N, Lee SH, Lee DG, Lee H, Lee SW, Bahk JD, Lee BH (2007) Physiological and protein profiles alternation of germinating rice seedlings exposed to acute cadmium toxicity. *C R Biol* 330:735–746. <https://doi.org/10.1016/J.CRVI.2007.08.001>
- Ali B, Deng X, Hu X, Gill RA, Ali S, Wang S, Zhou W (2015) Deteriorative effects of cadmium stress on antioxidant system and cellular structure in germinating seeds of *Brassica napus* L. *J Agr Sci Tech* 17: 63–74
- Ali AS, Elozeiri AA (2017) Metabolic processes during seed germination. In: *Advances in Seed Biology*. pp 141–166
- Ali LG, Nulit R, Ibrahim MH, Yien CYS (2020) Enhancement of germination and early seedling growth of rice (*Oryza sativa*) var. FARO44 by seed priming under normal and drought stressed conditions. *J Plant Nutr* 43:1579–1593. <https://doi.org/10.1080/01904167.2020.1739298>
- Almutairi ZM (2016) Effect of nano-silicon application on the expression of salt tolerance genes in germinating tomato (*Solanum lycopersicum* L.) seedlings under salt stress. *Plant Omics* 9:106–114
- Alsaeedi AH, El-Ramady H, Alshaal T, El-Garawani M, Elhawat N, Almohsen M (2017) Engineered silica nanoparticles alleviate the detrimental effects of Na⁺ stress on germination and growth of common bean (*Phaseolus vulgaris*). *Environ Sci Pollut Res* 24:21917–21928. <https://doi.org/10.1007/s11356-017-9847-y>
- Alves R de C, Nicolau MCM, Checchio MV, Sousa Junior GS, de Oliveira FA, Prado RM, Gratão PL (2020) Salt stress alleviation by seed priming with silicon in lettuce seedlings: An approach based on enhancing antioxidant responses. *Bragantia* 79:19–29. <https://doi.org/10.1590/1678-4499.20190360>
- Aniat-ul-Haq R, Agnihotri R (2010) Effect of osmotic stress (PEG) on germination and seedling survival of lentil (*Lens culinaris* Medik.). *Res J Agric Sci* 1:201–204
- Arif Y, Singh P, Bajguz A, Alam P, Hayat S (2021) Silicon mediated abiotic stress tolerance in plants using physio-biochemical, omic approach and cross-talk with phytohormones. *Plant Physiol Biochem* 166:278–289. <https://doi.org/10.1016/J.PLAPHY.2021.06.002>
- Ashraf MY, Afaf R, Qureshi MS, Sarwar G, Naqvi MH (2002) Salinity induced changes in α -amylase and protease activities and associated metabolism in cotton varieties during germination and early seedling growth stages. *Acta Physiol Plant* 24: 37-44. <https://doi.org/10.1007/s11738-002-0019-3>
- Atici Ö, Açar G, Battal P (2005) Changes in phytohormone contents in chickpea seeds germinating under lead or zinc stress. *Biol Plant* 49:215–222. <https://doi.org/10.1007/s10535-005-5222-9>
- Aydinalp C, Marinova S (2009) The effects of heavy metals on seed germination and plant growth on alfalfa plant (*Medicago sativa*). *Bulg J Agric Sci* 15:347–350
- Ayed S, Othmani A, Bouhaouel I, Rasâa N, Othmani S, Amara HS (2021) Effect of silicon (Si) seed priming on germination and effectiveness of its foliar supplies on durum wheat (*Triticum turgidum* L. ssp. durum) genotypes under semi-arid environment. *Silicon* 1–11. <https://doi.org/10.1007/s12633-021-00963-2>
- Azeem M, Iqbal N, Kausar S, Javed MT, Akram MS, Sajid MA (2015) Efficacy of silicon priming and fertigation to modulate seedling's vigor and ion homeostasis of wheat (*Triticum aestivum* L.) under saline environment. *Environ Sci Pollut Res* 22:14367–14371. <https://doi.org/10.1007/S11356-015-4983-8>
- Bai Y, Xiao S, Zhang Z, Zhang Y, Sun H, Zhang K, Wang X, Bai Z, Li C, Liu L (2020) Melatonin improves the germination rate of cotton seeds under drought stress by opening pores in the seed coat. *PeerJ* 8: e9450. <https://doi.org/10.7717/peerj.9450>
- Bailly C (2004) Active oxygen species and antioxidants in seed biology. *Seed Sci Res* 14:93–107. <https://doi.org/10.1079/SSR2004159>
- Bailly C (2019) The signalling role of ROS in the regulation of seed germination and dormancy. *Biochem J* 476:3019–3032. <https://doi.org/10.1042/BCJ20190159>
- Balestrazzi A, Confalonieri M, Macovei A, Carbonera D (2011) Seed imbibition in *Medicago truncatula* Gaertn.: Expression profiles of DNA repair genes in relation to PEG-mediated stress. *J Plant Physiol* 168:706–713. <https://doi.org/10.1016/J.JPLPH.2010.10.008>
- Barati M, Majidi MM, Mirlohi A, Pirnajmodini F, Sharif-Moghaddam N (2015) Response of cultivated and wild Barley germplasm to drought stress at different developmental stages. *Crop Sci* 55:2668–2681. <https://doi.org/10.2135/cropsci2015.04.0229>
- Bargaz A, Zaman-Allah M, Farissi M, Lazali M, Drevon JJ, Maougal RT, Georg C (2015) Physiological and molecular aspects of tolerance to environmental constraints in grain and forage legumes. *Int J Mol Sci* 16: 18976-19008. <https://doi.org/10.3390/ijms160818976>
- Baskin JM, Baskin CC (2004) A classification system for seed dormancy. *Seed Sci Res* 14:1–16.

- 559 <https://doi.org/10.1079/ssr2003150>
- 560 Bewley JD (2001) Seed germination and reserve mobilization. *Encycl Life Sci* 1–7.
- 561 <https://doi.org/10.1038/npg.els.0002047>
- 562 BiaŁecka B, Kępczyński J (2009) Effect of ethephon and gibberellin A3 on *Amaranthus caudatus* seed
563 germination and alpha-and beta-amylase activity under salinity stress. *Acta Biol Cracoviensia Ser Bot*
564 2:119–125
- 565 Biju S, Fuentes S, Gupta D (2017) Silicon improves seed germination and alleviates drought stress in lentil crops
566 by regulating osmolytes, hydrolytic enzymes and antioxidant defense system. *Plant Physiol Biochem*
567 119:250–264. <https://doi.org/10.1016/J.PLAPHY.2017.09.001>
- 568 Boesewinkel F, Bouman F (1984) Embryology of angiosperms. In: Media. SS& B (ed) *Embryology of*
569 *angiosperms*
- 570 Bradford KJ (2017) Water relations in seed germination. *Seed Dev Germination* 351–396.
571 <https://doi.org/10.1201/9780203740071-13>
- 572 Bu R, Xiao X, Liao W, Hu Y, Li J, Lv J, Wang R, Xie J (2018) Exogenous Si alleviation of autotoxicity in
573 cucumber (*Cucumis sativus* L.) seed germination is correlated with changes in carbohydrate metabolism. *J*
574 *Plant Growth Regul* 37:784–793. <https://doi.org/10.1007/s00344-017-9773-8>
- 575 Calone R, Sanoubar R, Noli E, Barbanti L (2020) Assessing *Salicornia europaea* tolerance to salinity at seed
576 germination stage. *Agriculture* 10:29. <https://doi.org/10.3390/AGRICULTURE10020029>
- 577 Campos H, Trejo C, Pena-Validiva CB, Gracia-Nava R, Conde-Martinez VF, Cruz-Ortega R (2020) Water
578 availability effects on germination, membrane stability and initial root growth of *Agave lechuguilla* and *A.*
579 *salmiana*. *flora* 268:151606. <https://doi.org/10.1016/j.flora.2020.151606>
- 580 Cardoso AA, Euclides De Lima E Borges E, Aparecida De Souza G, Jovelina Da Silva C, Maria De Oliveira Pires
581 R, Fernandes DC, Dias S (2015) Seed imbibition and germination of *Plathymenia reticulata* Benth.
582 (Fabaceae) affected by mercury: Possible role of aquaporins. *Acta Bot Brasilica* 29:285–291.
583 <https://doi.org/10.1590/0102-33062014abb0038>
- 584 Carles C, Bies-Etheve N, Aspart L, Léon-Kloosterziel KM, Koornneef M, Echeverria M, Delseny M (2002)
585 Regulation of *Arabidopsis thaliana* Em genes: role of ABI5. *Plant J* 30: 373–383.
586 <https://doi.org/10.1046/j.1365-313X.2002.01295.x>
- 587 Chen L, Lu B, Liu L, Duan W, Jiang D, Li J, Zhang K, Sun H, Zhang Y, Li C, Bai Z (2021) Melatonin promotes
588 seed germination under salt stress by regulating ABA and GA3 in cotton (*Gossypium hirsutum* L.). *Plant*
589 *Physiol Biochem* 162: 506–516. <https://doi.org/10.1016/j.plaphy.2021.03.029>
- 590 Cokkizgin A, Cokkizgin H (2010) Effects of lead (PbCl₂) stress on germination of lentil (*Lens culinaris* Medic.)
591 lines. *African J Biotechnol* 9:8608–8612. <https://doi.org/10.4314/ajb.v9i50>.
- 592 Corlett FMF, Rufino C de A, Vieira JF, Tavares LC, Tunes LVM, Barros ACSA (2014) The influence of seed
593 coating on the vigor and early seedling growth of barley. *Cienc e Investig Agrar* 41:129–135.
594 <https://doi.org/10.4067/S0718-16202014000100013>
- 595 Coskun D, Deshmukh R, Shivaraj S, Isenring P, Bélanger R (2021) Lsi2: A black box in plant silicon transport.
596 *Plant Soil* 466:1–20. <https://doi.org/10.1007/s11104-021-05061-1>
- 597 Coskun D, Deshmukh R, Sonah H, Menzies JG, Reynolds O, Ma JF, Kronzucker HJ, Bélanger RR (2019) The
598 controversies of silicon's role in plant biology. *New Phytol* 221:67–85. <https://doi.org/10.1111/nph.15343>
- 599 Daniels MJ, Mirkov TE, Chrispeels MJ (1994) The plasma membrane of *Arabidopsis thaliana* contains a mercury-
600 insensitive aquaporin that is a homolog of the tonoplast water channel protein TIP. *Plant Physiol* 106:1325–
601 1333. <https://doi.org/10.1104/PP.106.4.1325>
- 602 de Oliveira AB, Mendes Alencar NL, Gomes-Filho E (2013) Comparison between the water and salt stress effects
603 on plant growth and development. *Responses Org to Water Stress*. <https://doi.org/10.5772/54223>
- 604 de Silva NDG, Boutin C, Lukina AO, Western TL, Molina I, Rowland O (2021) Seed coat suberin forms a barrier
605 against chromium (Cr³⁺) during early seed germination in *Arabidopsis thaliana*. *Environ Exp Bot* 191:
606 104632. <https://doi.org/10.1016/j.envexpbot.2021.104632>
- 607 Debez A, Belghith I, Pich A, Taamalli W, Abdelly C, Braun HP (2018) High salinity impacts germination of the
608 halophyte *Cakile maritima* but primes seeds for rapid germination upon stress release. *Physiol Plant*
609 164:134–144. <https://doi.org/10.1111/ppl.12679>
- 610 Debez A, Ben Hamed K, Grignon C, Abdelly C (2004) Salinity effects on germination, growth, and seed
611 production of the halophyte *Cakile maritima*. *Plant Soil* 262:179–189.
612 <https://doi.org/10.1023/B:PLSO.0000037034.47247.67>
- 613 Debona D, Rodrigues FA, Datnoff LE (2017) Silicon's role in abiotic and biotic plant stresses. *Annu Rev Plant*
614 *Biol* 55:85–107. <https://doi.org/10.1146/ANNUREV-PHYTO-080516-035312>
- 615 Dehnavi AR, Zahedi M, Ludwiczak A, Perez SC, Piernik A (2020) Effect of salinity on seed germination and
616 seedling development of sorghum (*Sorghum bicolor* (L.) Moench) genotypes. *Agronomy* 10:859.
617 <https://doi.org/10.3390/agronomy10060859>
- 618 Delavar K, Ghanati F, Zare-Maivan H, Behmanesh M (2017) Effects of silicon on the growth of maize seedlings

619 under normal, aluminum, and salinity stress conditions. *J Plant Nutr* 40:1475–1484.
620 <https://doi.org/10.1080/01904167.2016.1269344>

621 El-Hendawy S, Elshafei A, Al-Suhaibani N, Alotabi M, Hassan W, Dewir YH, Abdella K (2019) Assessment of
622 the salt tolerance of wheat genotypes during the germination stage based on germination ability parameters
623 and associated SSR markers. *J Plant Interact* 14: 151-163. <https://doi.org/10.1080/17429145.2019.1603406>

624 El-Serafy R, El-Sheshtawy A, Atteya AKG, Al-Hashimi A, Abbasi AM, Al-Ashkar I (2021) Seed priming with
625 silicon as a potential to increase salt stress tolerance in *Lathyrus odoratus*. *Plants* 10:2140.
626 <https://doi.org/https://doi.org/10.3390/plants10102140>

627 El Moukhtari A, Lamsaadi N, Oubenali A, Mouradi M, Savoure A, Farissi M (2021) Exogenous silicon application
628 promotes tolerance of legumes and their N₂ fixing symbiosis to salt stress. *Silicon* 1–18.
629 <https://doi.org/10.1007/s12633-021-01466-w>

630 El Moukhtari A, Cabassa-Hourton C, Farissi M, Savouré A (2020) How does proline treatment promote salt stress
631 tolerance during crop plant development?. *Front Plant Sci* 11: 1127. <https://doi.org/10.3389/fpls.2020.01127>

632 El Rasafi T, Oukarroum A, Haddioui A, Song H, Kwon EE, Bolan N, Tack FMG, Sebastian A, Prasad MNV,
633 Rinklebe J (2020) Cadmium stress in plants: A critical review of the effects, mechanisms, and tolerance
634 strategies. *Crit Rev Environ Sci Technol* 1–52. <https://doi.org/10.1080/10643389.2020.1835435>

635 Emamverdian A, Ding Y, Mokhberdoran F, Ahmad Z, Xie Y (2021) The effect of silicon nanoparticles on the
636 seed germination and seedling growth of moso bamboo (*Phyllostachys edulis*) under cadmium stress. *Polish*
637 *J Environ Stud* 30:3033–3042. <https://doi.org/10.15244/pjoes/129683>

638 Espanany A, Fallah S, Tadayyon A (2015) The effect of haloprimering and salicylic acid on the germination of
639 fenugreek (*Trigonella foenum-graecum*) under different cadmium concentrations. *Not Sci Biol* 7: 322–329.
640 <https://doi.org/10.15835/nsb739563>

641 Farissi M, Bouizgaren A, Faghire M, Bargaz A, Ghoulam C (2011) Agro-physiological responses of Moroccan
642 alfalfa (*Medicago sativa* L.) populations to salt stress during germination and early seedling stages. *Seed Sci*
643 *Technol* 39:389–401. <https://doi.org/10.15258/SST.2011.39.2.11>

644 Fauteux F, Rémus-Borel W, Menzies JG, Bélanger RR (2005) Silicon and plant disease resistance against
645 pathogenic fungi. *FEMS Microbiol Lett* 249:1–6. <https://doi.org/10.1016/j.femsle.2005.06.034>

646 Feghhenabi F, Hadi H, Khodaverdiloo H, van Genuchten MT (2020) Seed priming alleviated salinity stress during
647 germination and emergence of wheat (*Triticum aestivum* L.). *Agric Water Manag* 231:106022.
648 <https://doi.org/10.1016/J.AGWAT.2020.106022>

649 Finch-Savage WE, Footitt S (2017) Seed dormancy cycling and the regulation of dormancy mechanisms to time
650 germination in variable field environments. *J Exp Bot* 68:843–856. <https://doi.org/10.1093/jxb/erw477>

651 Finkelstein R, Reeves W, Ariizumi T, Steber C (2008) Molecular aspects of seed dormancy. *Annu Rev Plant Biol*
652 59:387–415. <https://doi.org/10.1146/annurev.arplant.59.032607.092740>

653 Galviz-Fajardo YC, Bortolin GS, Deuner S, Amarante LD, Reolon F, de Moraes DM (2020) Seed priming with
654 salicylic acid potentiates water restriction- induced effects in tomato seed germination and early seedling
655 growth. *J Seed Sci* 42:e202042031. <https://doi.org/10.2135/1984.physiologicalbasis.c4>

656 Gana Ali L, Nulit R, Hafiz Ibrahim M, Yong C (2021) Potassium nitrate and silicon dioxide priming improve
657 germination, seedling growth and protective enzymes of rice var. FARO44 under drought. *J Plant Nutr* 1–
658 14. <https://doi.org/10.1080/01904167.2021.1921201>

659 Ghavami N, Ramin AA (2007) Salinity and temperature effects on seed germination of milk thistle. *Commun Soil*
660 *Sci Plant Anal* 38:2681–2691. <https://doi.org/10.1080/00103620701662901>

661 Gomes MP, Garcia QS (2013) Reactive oxygen species and seed germination. *Biologia (Bratisl)* 68:351–357.
662 <https://doi.org/10.2478/s11756-013-0161-y>

663 Gonzalez-Mendoza D, Quiroz-Moreno A, Medrano REG, Grimaldo-Juarez O, Zapata-Perez O (2009) Cell
664 viability and leakage of electrolytes in *Avicennia germinans* exposed to heavy metals. *Zeitschrift fur*
665 *Naturforsch - Sect C J Biosci* 64:391–394. <https://doi.org/10.1515/znc-2009-5-615>

666 Gou T, Chen X, Han R, Liu J, Zhu Y, Gong H (2020) Silicon can improve seed germination and ameliorate
667 oxidative damage of bud seedlings in cucumber under salt stress. *Acta Physiol Plant* 42:12.
668 <https://doi.org/10.1007/s11738-019-3007-6>

669 Graeber K, Nakabayashi K, Miatton E, Leubner-Metzger G, Soppe WJJ (2012) Molecular mechanisms of seed
670 dormancy. *Plant, Cell Environ* 35:1769–1786. <https://doi.org/10.1111/j.1365-3040.2012.02542.x>

671 Guilherme M de F de S, de Oliveira HM, da Silva E (2015) Cadmium toxicity on seed germination and seedling
672 growth of wheat *Triticum aestivum*. *Biol Sci* 37:499–504. <https://doi.org/10.4025/actasciobiolsci.v37i4.28148>

673 Guo Q, Wang Y, Zhang H, Qu G, Wang T, Sun Q, Liang D (2017) Alleviation of adverse effects of drought stress
674 on wheat seed germination using atmospheric dielectric barrier discharge plasma treatment. *Sci Rep* 7:1–14.
675 <https://doi.org/10.1038/s41598-017-16944-8>

676 Haghghi M, Afifipour Z, Mozafarian M (2012) The alleviation effect of silicon on seed germination and seedling
677 growth of tomato under salinity stress. *Veg Crop Res Bull* 76:119–126. <https://doi.org/10.2478/v10032-012-0008-z>

678

- 679 Hameed A, Farooq T, Hameed A, Sheikh MA (2021) Sodium nitroprusside mediated priming memory invokes
680 water-deficit stress acclimation in wheat plants through physio-biochemical alterations. *Plant Physiol*
681 *Biochem* 160:329–340. <https://doi.org/10.1016/J.PLAPHY.2021.01.037>
- 682 Hameed A, Sheikh MA, Jamil A, Basra SMA (2013) Seed priming with sodium silicate enhances seed germination
683 and seedling growth in wheat (*Triticum aestivum* L.) under water deficit stress induced by polyethylene
684 glycol. *Pakistan J Life Soc Sci* 11:19–24
- 685 Han R, Gao G, Li Z, Dong Z, Guo Z (2017) Effects of exogenous 5-aminolevulinic acid on seed germination of
686 alfalfa (*Medicago varia* Martyn.) under drought stress. *Grassl Sci* 46:100–107.
687 <https://doi.org/10.1111/grs.12189>
- 688 Hao L, Shi S, Guo H, Zhang J, Li P, Feng Y (2021) Transcriptome analysis reveals differentially expressed MYB
689 transcription factors associated with silicon response in wheat. *Scientific reports* 11:1-9.
690 <https://doi.org/10.1038/s41598-021-83912-8>
- 691 Hasanuzzaman M, Bhuyan MHMB, Zulfiqar F, Raza A, Mohsin SM, Mahmud JA, Fujita M, Fotopoulos V (2020)
692 Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of
693 a universal defense regulator. *Antioxidants* 9:681. <https://doi.org/10.3390/ANTIOX9080681>
- 694 Hassan MJ, Geng W, Zeng W, Raza MA, Khan I, Iqbal MZ, Peng Y, Zhu Y, Li Z (2021) Diethyl aminoethyl
695 hexanoate priming ameliorates seed germination via involvement in hormonal changes, osmotic adjustment,
696 and dehydrins accumulation in white clover under drought stress. *Front Plant Sci* 12:709187.
697 <https://doi.org/10.3389/fpls.2021.709187>
- 698 Hauvermale AL, Steber CM (2020) GA signaling is essential for the embryo-to-seedling transition during
699 *Arabidopsis* seed germination, a ghost story. *Plant Signal Behav* 15: 1705028.
700 <https://doi.org/10.1080/15592324.2019.1705028>
- 701 Hu K-D, Bai G-S, Li W-J, Yan H, Hu L-Y, Li Y-H, Zhang H (2015) Sulfur dioxide promotes germination and
702 plays an antioxidant role in cadmium-stressed wheat seeds. *Plant Growth Regul* 75: 271–280.
703 <https://doi.org/10.1007/s10725-014-9951-7>
- 704 Hubbard M, Germida J, Vujanovic V (2012) Fungal endophytes improve wheat seed germination under heat and
705 drought stress. *Botany* 90:137–149. <https://doi.org/10.1139/B11-091>
- 706 Ibrahim EA (2016) Seed priming to alleviate salinity stress in germinating seeds. *J Plant Physiol* 192:38–46.
707 <https://doi.org/10.1016/J.JPLPH.2015.12.011>
- 708 Infante-Izquierdo MD, Castillo JM, Grewell BJ, Nieva FJJ, Muñoz-Rodríguez AF (2019) Differential effects of
709 increasing salinity on germination and seedling growth of native and exotic invasive cordgrasses. *Plants*
710 8:372. <https://doi.org/10.3390/PLANTS8100372>
- 711 Kalai T, Khamassi K, Teixeira da Silva JA, Gouia H, Bettaieb Ben-Kaab L (2014) Cadmium and copper stress
712 affect seedling growth and enzymatic activities in germinating barley seeds. *Arch Agron Soil Sci* 60: 765–
713 783. <https://doi.org/10.1080/03650340.2013.838001>
- 714 Kantharaju S, Murthy KS (2014) Characterization of esterases of *Tamarindus indica* seeds. *J Biosci Med* 2: 54-
715 62. <http://dx.doi.org/10.4236/jbm.2014.24009>
- 716 Kasote DM, Katyare SS, Hegde M V, Bae H (2015) Significance of antioxidant potential of plants and its relevance
717 to therapeutic applications. *Int J Biol Sci* 11:982–991. <https://doi.org/10.7150/ijbs.12096>
- 718 Khan E, Gupta M (2018) Arsenic–silicon priming of rice (*Oryza sativa* L.) seeds influence mineral nutrient uptake
719 and biochemical responses through modulation of Lsi-1, Lsi-2, Lsi-6 and nutrient transporter genes. *Sci Rep*
720 8:10301. <https://doi.org/10.1038/s41598-018-28712-3>
- 721 Khan MN, Alamri S, Al-Amri AA, Alsubaie QD, Al-Munqedi B, Ali HM, Singh VP, Siddiqui MH (2020) Effect
722 of nitric oxide on seed germination and seedling development of tomato under chromium toxicity. *J Plant*
723 *Growth Regul* 1–13. <https://doi.org/10.1007/s00344-020-10212-2>
- 724 Kizilgeci F, Tazebay N, Namili M, Albayrak O, Yildirim M (2017) The drought effect on seed germination and
725 seedling growth in bread wheat (*Triticum aestivum* L.). *Int J Agric Environ Food Sci* 1:33–37.
726 <https://doi.org/10.31015/jaefs.17005>
- 727 Kong X, Luo Z, Zhang Y, Li W, Dong H (2017) Soaking in H₂O₂ regulates ABA biosynthesis and GA catabolism
728 in germinating cotton seeds under salt stress. *Acta Physiol Plant* 39: 1-10. <https://doi.org/10.1007/s11738-016-2299-z>
- 729
- 730 Koornneef M, Bentsink L, Hilhorst H (2002) Seed dormancy and germination. *Curr Opin Plant Biol* 5:33–36.
731 <https://doi.org/10.5860/choice.26-5658>
- 732 Kraner I, Colville L (2011) Metals and seeds: Biochemical and molecular implications and their significance for
733 seed germination. *Environ Exp Bot* 72:93–105. <https://doi.org/10.1016/J.ENVEXPBOT.2010.05.005>
- 734 Kshetrimayum E, Sahoo DP, Mitra J, Kumar Panda S (2017) Regulation of seed germination and the role of
735 aquaporins under abiotic stress. *Int J Environ Agric Biotechnol* 2:238710.
736 <https://doi.org/10.22161/ijeab/2.2.7>
- 737 Lamhamdi M, Bakrim A, Aarab A, Lafont R, Sayah F (2011) Lead phytotoxicity on wheat (*Triticum aestivum* L.)
738 seed germination and seedlings growth. *C R Biol* 334: 118–126. <https://doi.org/10.1016/j.crv.2010.12.006>

- 739 Lamsaadi N, El Moukhtari A, Oubenali A, Farissi M (2022) Exogenous silicon improves salt tolerance of
740 Fenugreek (*Trigonella foenum-graecum* L.) during seed germination and early seedling stages. *Biologia*.
741 <https://doi.org/10.1007/s11756-022-01035-5>
- 742 Lefèvre I, Marchal G, Corréal E, Zanuzzi A, Lutts S (2009) Variation in response to heavy metals during vegetative
743 growth in *Dorycnium pentaphyllum* Scop. *Plant Growth Regul* 2009 591 59:1–11.
744 <https://doi.org/10.1007/S10725-009-9382-Z>
- 745 Lei K, Sun S, Zhong K, Li S, Hu H, Sun C, Zheng Q, Tian Z, Dai T, Sun J (2021) Seed soaking with melatonin
746 promotes seed germination under chromium stress via enhancing reserve mobilization and antioxidant
747 metabolism in wheat. *Ecotoxicol Environ Saf* 220: 112241. <https://doi.org/10.1016/j.ecoenv.2021.112241>
- 748 Li Q, Yang A, Zhang WH (2019) Higher endogenous bioactive gibberellins and α -amylase activity confer greater
749 tolerance of rice seed germination to saline-alkaline stress. *Environ Exp Bot* 162: 357-363.
750 <https://doi.org/10.1016/j.envexpbot.2019.03.015>
- 751 Li W, Khan MA, Yamaguchi S, Kamiya Y (2005) Effects of heavy metals on seed germination and early seedling
752 growth of *Arabidopsis thaliana*. *Plant Growth Regul* 46:45–50. <https://doi.org/10.1007/s10725-005-6324-2>
- 753 Li J, Zhao C, Zhang M, Yuan F, Chen M (2019) Exogenous melatonin improves seed germination in *Limonium*
754 *bicolor* under salt stress. *Plant Signal Behav* 14: 1659705. <https://doi.org/10.1080/15592324.2019.1659705>
- 755 Liu L, Xia W, Li H, Zeng H, Wei B, Han S, Yin C (2018) Salinity inhibits rice seed germination by reducing α -
756 amylase activity via decreased bioactive gibberellin content. *Front Plant Sci* 9:275.
757 <https://doi.org/10.3389/FPLS.2018.00275>
- 758 Liu J, Hasanuzzaman M, Wen H, Zhang J, Peng T, Sun H, Zhao Q (2019) High temperature and drought stress
759 cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice.
760 *Protoplasma* 256: 1217-1227. <https://doi.org/10.1016/j.scienta.2019.02.060>
- 761 Llanes A, Andrade A, Masciarelli O, Alemanno S, Luna V (2015) Drought and salinity alter endogenous hormonal
762 profiles at the seed germination phase. *Seed Sci Res* 26:1–13. <https://doi.org/10.1017/S0960258515000331>
- 763 Lotfi N, Soleimani A, Vahdati K, Çakmakçı R (2019) Comprehensive biochemical insights into the seed
764 germination of walnut under drought stress. *Sci Hortic* 250: 329-343
- 765 Lu C, Han MH, Guevara-Garcia A, Fedoroff NV (2002) Mitogen-activated protein kinase signaling in
766 postgermination arrest of development by abscisic acid. *Proc Natl Acad Sci* 99: 15812-15817.
767 <https://doi.org/10.1073/pnas.242607499>
- 768 Luo X, Dai Y, Zheng C, Yang Y, Chen W, Wang Q, Chandrasekaran U, Du J, Liu W, Shu K (2021) The ABI4-
769 RbohD/VTC2 regulatory module promotes reactive oxygen species (ROS) accumulation to decrease seed
770 germination under salinity stress. *New Phytol* 229: 950-962. <https://doi.org/10.1111/nph.16921>
- 771 Ma FJ, Yamaji N, Mitani N, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M (2007) An efflux transporter
772 of silicon in rice. *Nature* 448:209–212. <https://doi.org/10.1038/nature05964>
- 773 Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M (2006) A silicon
774 transporter in rice. *Nature* 440:688–691. <https://doi.org/10.1038/nature04590>
- 775 Ma JF, Yamaji N (2015) A cooperative system of silicon transport in plants. *Trends Plant Sci* 20:435–442.
776 <https://doi.org/10.1016/j.tplants.2015.04.007>
- 777 Machado Neto NB, Saturnino SM, Bomfim DC, Custódio CC (2004) Water stress induced by mannitol and sodium
778 chloride in soybean cultivars. *Braz Arch Biol Technol* 47: 521-529. <http://dx.doi.org/10.1590/S1516-89132004000400004>
- 779
- 780 Mahmood T, Islam KR, Muhammad S (2007) Toxic effects of heavy metals on early growth and tolerance of
781 cereal crops. *Pakistan J Bot* 39:451–462
- 782 Marthandan V, Geetha R, Kumutha K, Renganathan VG, Karthikeyan A, Ramalingam J (2020) Seed priming: A
783 feasible strategy to enhance drought tolerance in crop plants. *Int J Mol Sci* 21:8258.
784 <https://doi.org/10.3390/ijms21218258>
- 785 Miransari M, Smith DL (2014) Plant hormones and seed germination. *Environ Exp Bot* 99:110–121.
786 <https://doi.org/10.1016/J.ENVEXPBOT.2013.11.005>
- 787 Mohamed E, Kasem AMM, Farghali KA (2018) Seed germination of Egyptian *Pancratium maritimum* under
788 salinity with regard to cytology, antioxidant and reserve mobilization enzymes, and seed anatomy. *Flora*
789 242:120–127. <https://doi.org/10.1016/J.FLORA.2018.03.011>
- 790 Mostofa MG, Rahman MM, Ansary MMU, Keya SS, Abdelrahman M, Miah MG, Phan Tran LS (2021) Silicon
791 in mitigation of abiotic stress-induced oxidative damage in plants. *Crit Rev Biotechnol* 41:918–934.
792 <https://doi.org/10.1080/07388551.2021.1892582>
- 793 Mridha D, Paul I, De A, Ray I, Das A, Joardar M, Chowdhury NR, Bhadoria PBS, Roychowdhury T (2021) Rice
794 seed (IR64) priming with potassium humate for improvement of seed germination, seedling growth and
795 antioxidant defense system under arsenic stress. *Ecotoxicol Environ Saf* 219:112313.
796 <https://doi.org/10.1016/J.ECOENV.2021.112313>
- 797 Muhammad ZI, Maria KS, Mohammad A, Muhammad S, Zia-ur-Rehman F, Muhammad KABIR (2015) Effect
798 of mercury on seed germination and seedling growth of Mungbean (*Vigna radiata* (L.) Wilczek). *J Appl Sci*

799 Environ Manag 19: 191-199.

800 Müller M, Munné-Bosch S (2015) Ethylene response factors: a key regulatory hub in hormone and stress signaling.

801 Plant physiol 169: 32-41. <https://doi.org/10.1104/pp.15.00677>

802 Mundada PS, Barvkar VT, Umdale SD, Anil Kumar S, Nikam TD, Ahire ML (2021) An insight into the role of

803 silicon on retaliation to osmotic stress in finger millet (*Eleusine coracana* (L.) Gaertn). J Hazard Mater

804 403:124078. <https://doi.org/10.1016/J.JHAZMAT.2020.124078>

805 Muralikrishna G, Nirmala M (2005) Cereal α -amylases—an overview. Carbohydrate polymers 60 : 163-173.

806 <https://doi.org/10.1016/j.carbpol.2004.12.002>

807 Muscolo A, Sidari M, Anastasi U, Santonoceto C, Maggio A (2014) Effect of PEG-induced drought stress on seed

808 germination of four lentil genotypes. J Plant Interact 9:354-363.

809 <https://doi.org/10.1080/17429145.2013.835880>

810 Nadarajah KK (2020) ROS homeostasis in abiotic stress tolerance in plants. Int J Mol Sci 21:5208.

811 <https://doi.org/10.3390/ijms21155208>

812 Naguib DM, Abdalla H (2019) Metabolic status during germination of nano silica primed *Zea mays* seeds under

813 salinity stress. J Crop Sci Biotechnol 22:415-423. <https://doi.org/10.1007/s12892-019-0168-0>

814 Nakabayashi K, Leubner-Metzger G (2021) Seed dormancy and weed emergence: From simulating environmental

815 change to understanding trait plasticity, adaptive evolution, and population fitness. J Exp Bot 72:4181-4185.

816 <https://doi.org/10.1093/JXB/ERAB150>

817 Nasri N, Mahmoudi H, Baatour O, M'rah S, Kaddour R, Lachâal M (2012) Effect of exogenous gibberellic acid

818 on germination, seedling growth and phosphatase activities in lettuce under salt stress. Afr J Biotechnol 11:

819 11967-11971

820 Nguyen HC, Nguyen TT, Dao TH, Ngo QB, Pham HL, Nguyen TBN (2016) Preparation of Ag/SiO₂

821 nanocomposite and assessment of its antifungal effect on soybean plant (a Vietnamese species DT-26). Adv

822 Nat Sci Nanosci Nanotechnol 7:45014. <https://doi.org/10.1088/2043-6262/7/4/045014>

823 Ning J, Jian L, Jihua Y, Jianming X, Li J, Guobin Z, Zhi F (2020) Effect of exogenous silicon on seed germination

824 and expression of related genes in cucumber under osmotic stress. Acta Horti Sin 47:41

825 Parvin K, Nahar K, Hasanuzzaman M, Bhuyan MHMB, Fujita M (2019) Calcium-mediated growth regulation and

826 abiotic stress tolerance in plants. Nature, Springer

827 Pavel VL, Sobariu DL, Diaconu M, Stătescu F, Gavrilăscu M (2013) Effects of heavy metals on *Lepidium sativum*

828 germination and growth. Environ Eng Manag J 12: 727-733

829 Pedrini S, Merritt DJ, Stevens J, Dixon K (2017) Seed coating: Science or marketing spin? Trends Plant Sci

830 22:106-116. <https://doi.org/10.1016/J.TPLANTS.2016.11.002>

831 Pereira ADES, Oliveira HC, Fraceto LF, Santaella C (2021) Nanotechnology potential in seed priming for

832 sustainable agriculture. Nanomaterials 11:267. <https://doi.org/10.3390/nano11020267>

833 Pulido P, Cazalis R, Cejudo FJ (2009) An antioxidant redox system in the nucleus of wheat seed cells suffering

834 oxidative stress. Plant J 57:132-145. <https://doi.org/10.1111/J.1365-313X.2008.03675.X>

835 Rai-Kalal P, Tomar RS, Jajoo A, Rai-Kalal P, Tomar RS, Jajoo A (2021) Seed nanopriming by silicon oxide

836 improves drought stress alleviation potential in wheat plants. Funct Plant Biol 48:905-915.

837 <https://doi.org/10.1071/FP21079>

838 Rajjou L, Duval M, Gallardo K, Catusse J, Bally J, Job C, Job D (2012) Seed germination and vigor. Annu Rev

839 Plant Biol 63:507-533. <https://doi.org/10.1146/annurev-arplant-042811-105550>

840 Ravindran P, Kumar PP (2019) Regulation of seed germination: The involvement of multiple forces exerted via

841 gibberellic acid signaling. Mol Plant 12:24-26. <https://doi.org/10.1016/j.molp.2018.12.013>

842 Rizwan M, Ali S, Ibrahim M, Farid M, Adrees M, Bharwana SA, Zia-ur-Rehman M, Qayyum MF, Abbas F (2015)

843 Mechanisms of silicon-mediated alleviation of drought and salt stress in plants: A review. Environ Sci Pollut

844 Res 22:15416-15431. <https://doi.org/10.1007/S11356-015-5305-X>

845 Rodrigues AA, Filho SCV, Müller C, Rodrigues DA, Sales JF, Zuchi J, Costa AC, Rodrigues CL, Silva AA,

846 Barbosa DP (2019) Tolerance of *Eugenia dysenterica* to aluminum: Germination and plant growth. Plants

847 8:317. <https://doi.org/10.3390/PLANTS8090317>

848 Rogowska A, Szakiel A (2020) The role of sterols in plant response to abiotic stress. Phytochem Rev 19: 1525-

849 1538. <https://doi.org/10.1007/s11101-020-09708-2>

850 Rufino C de A, Tavares LC, Martín-Ramos P, Fernandes-Vieira J, Abreu Júnior JS, Silva FJA, Fernandes-Correa

851 M, Martín-Gil J (2017) Performance of soybean seedlings upon nutrient application by seed coating.

852 Brazilian Arch Biol Technol 60:1-11. <https://doi.org/10.1590/1678-4324-2017160128>

853 Sano N, Marion-Poll A (2021) ABA metabolism and homeostasis in seed dormancy and germination. Int J Mol

854 Sci 22:5069. <https://doi.org/10.3390/ijms22105069>

855 Seneviratne M, Rajakaruna N, Rizwan M, Madawala HMSP, Ok YS, Vithanage M (2017) Heavy metal-induced

856 oxidative stress on seed germination and seedling development: A critical review. Environ Geochem Health

857 41:1813-1831. <https://doi.org/10.1007/s10653-017-0005-8>

858 Senna R, Simonin V, Silva-Neto MAC, Fialho E (2006) Induction of acid phosphatase activity during germination

859 of maize (*Zea mays*) seeds. Plant Physiol Biochem 44: 467-473.
860 <https://doi.org/10.1016/j.plaphy.2006.03.008>

861 Sethy SK, Ghosh S (2013) Effect of heavy metals on germination of seeds. J Nat Sci Biol Med 4:272–275.
862 <https://doi.org/10.4103/0976-9668.116964>

863 Sfaxi-Bousbih A, Chaoui A, El Ferjani E (2010) Cadmium impairs mineral and carbohydrate mobilization during
864 the germination of bean seeds. Ecotoxicol Environ Saf 73: 1123–1129.
865 <https://doi.org/10.1016/j.ecoenv.2010.01.005>

866 Sharma AD, Rathore SVS, Srinivasan K, Tyagi RK (2014) Comparison of various seed priming methods for seed
867 germination, seedling vigour and fruit yield in okra (*Abelmoschus esculentus* L. Moench). Sci Hortic
868 (Amsterdam) 165:75–81. <https://doi.org/10.1016/J.SCIENTA.2013.10.044>

869 Sharma PD, Singh N, Ahuja PS, Reddy TV (2011) Abscisic acid response element-binding factor 1 is required for
870 establishment of *Arabidopsis* seedlings during winter. Mol Biol Rep 38: 5147-5159.
871 <https://doi.org/10.1007/s11033-010-0664-3>

872 Shi Y, Zhang Y, Yao H, Wu J, Sun H, Gong H (2014) Silicon improves seed germination and alleviates oxidative
873 stress of bud seedlings in tomato under water deficit stress. Plant Physiol Biochem 78:27–36.
874 <https://doi.org/10.1016/J.PLAPHY.2014.02.009>

875 Siddiqui H, Ahmed KBM, Sami F, Hayat S (2020) Silicon nanoparticles and plants: Current knowledge and future
876 perspectives. In: Sustainable Agriculture Reviews 41. Springer, Cham, pp 129–142

877 Stejskalová J, Kupka I, Miltner S (2015) Effect of gibberellic acid on germination capacity and emergence rate of
878 *Sycamore maple* (*Acer pseudoplatanus* L.) seeds. J For Sci 61:325–331. [https://doi.org/10.17221/22/2015-](https://doi.org/10.17221/22/2015-JFS)
879 [JFS](https://doi.org/10.17221/22/2015-JFS)

880 Sun YD, Luo WR (2014) Effects of exogenous hydrogen sulphide on seed germination and seedling growth of
881 cucumber (*Cucumis sativus*) under sodium bicarbonate stress. Seed Sci Technol 42: 126-131.
882 <https://doi.org/10.15258/sst.2014.42.2.02>

883 Sun Y, Xu J, Miao X, Lin X, Liu W, Ren H (2021) Effects of exogenous silicon on maize seed germination and
884 seedling growth. Sci Rep 11:1–13. <https://doi.org/10.1038/s41598-020-79723-y>

885 Szabados L, Savaure A (2010) Proline: a multifunctional amino acid. Trends Plant Sci 15: 89-97.
886 <https://doi.org/10.1016/j.tplants.2009.11.009>

887 Tai L, Wang H-J, Xu X-J, Sun W-H, Ju L, Liu W-T, Li W-Q, Sun J, Chen K-M (2021) Pre-harvest sprouting in
888 cereals: Genetic and biochemical mechanisms. J Exp Bot 72:2857–2876.
889 <https://doi.org/10.1093/JXB/ERAB024>

890 Toscano S, Romano D, Tribulato A, Patanè C (2017) Effects of drought stress on seed germination of ornamental
891 sunflowers. Acta Physiol Plant 39:184. <https://doi.org/10.1007/s11738-017-2484-8>

892 ur Rehman A, Qamar R, Rehman A, Wasaya A, Farooq O, Sarwar N, Iqbal MM, Ahmad S (2020) Silicon coating
893 on maize seed mitigates saline stress in yermosols of southern punjab. Silicon 1–11.
894 <https://doi.org/10.1007/s12633-020-00737-2>

895 Van Bockhaven J, De Vleeschauwer D, Höfte M (2013) Towards establishing broad-spectrum disease resistance
896 in plants: Silicon leads the way. J Exp Bot 64:1281–1293. <https://doi.org/10.1093/jxb/ers329>

897 Voogt W, Sonneveld C (2001) Silicon in horticultural crops grown in soilless culture. Stud Plant Sci 8:115–131.
898 [https://doi.org/10.1016/S0928-3420\(01\)80010-0](https://doi.org/10.1016/S0928-3420(01)80010-0)

899 Wang W-B, Kim Y-H, Lee H-S, Kim K-Y, Deng X-P, Kwak S-S (2009) Analysis of antioxidant enzyme activity
900 during germination of alfalfa under salt and drought stresses. Plant Physiol Biochem 47:570–577.
901 <https://doi.org/10.1016/j.plaphy.2009.02.009>

902 Waterworth WM, Bray CM, West CE (2019) Seeds and the art of genome maintenance. Front Plant Sci 10:706.
903 <https://doi.org/10.3389/fpls.2019.00706>

904 Wijewardana C, Alsajri FA, Reddy KR (2018) Soybean seed germination response to in vitro osmotic stress. Seed
905 Technol 39:143–154

906 Wijewardana C, Reddy RK, Krutz JL, Gao W, Bellaloui N (2019) Drought stress has transgenerational effects on
907 soybean seed germination and seedling vigor. PLoS One 14:e0214977.
908 <https://doi.org/10.1371/journal.pone.0214977>

909 Xiao Y, Sun J, Liu F, Xu T (2016) Effects of salinity and sulphide on seed germination of three coastal plants.
910 Flora - Morphol Distrib Funct Ecol Plants 218:86–91. <https://doi.org/10.1016/J.FLORA.2015.12.002>

911 Xiong J-L, Li J, Wang H-C, Zhang C-L, Naeem MA (2018) Fullerol improves seed germination, biomass
912 accumulation, photosynthesis and antioxidant system in *Brassica napus* L. under water stress. Plant Physiol
913 Biochem 129:130–140. <https://doi.org/10.1016/j.plaphy.2018.05.026>

914 Xu D, Cao H, Fang W, Pan J, Chen J, Zhang J, Shen W (2017) Linking hydrogen-enhanced rice aluminum
915 tolerance with the reestablishment of GA/ABA balance and miRNA-modulated gene expression: A case
916 study on germination. Ecotoxicol Environ Saf 145: 303–312. <https://doi.org/10.1016/j.ecoenv.2017.07.055>

917 Yamaguchi S, Kamiya Y (2001) Gibberellins and light-stimulated seed germination. J Plant Growth Regul 20:369–
918 376. <https://doi.org/10.1007/s003440010035>

919 Yan A, Chen Z (2020) The control of seed dormancy and germination by temperature, light and nitrate. *Bot Rev*
920 86:39–75. <https://doi.org/10.1007/s12229-020-09220-4>

921 Yao Y, He RJ, Xie QL, Zhao XH, Deng XM, He JB, Song L, He J, Marchant A, Chen X-Y, Wu AM (2017)
922 *Ethylene Response Factor 74 (ERF74)* plays an essential role in controlling a *respiratory burst oxidase*
923 *homolog D (RbohD)*-dependent mechanism in response to different stresses in *Arabidopsis*. *New Phytol* 213:
924 1667-1681. <https://doi.org/10.1111/nph.14278>

925 Zhang H, Tan Z-Q, Hu L-Y, Wang S-H, Luo J-P, Jones RL (2010) Hydrogen sulfide alleviates aluminum toxicity
926 in germinating wheat seedlings. *J Integr Plant Biol* 52: 556–567. <https://doi.org/10.1111/j.1744-7909.2010.00946.x>

927
928 Zhang N, Zhang H-J, Sun Q-Q, Cao Y-Y, Li X, Zhao B, Wu P, Guo Y-D (2017) Proteomic analysis reveals a role
929 of melatonin in promoting cucumber seed germination under high salinity by regulating energy production.
930 *Sci Reports* 7:1–15. <https://doi.org/10.1038/s41598-017-00566-1>

931 Zhang Q, Rue K, Wang S (2012) Salinity effect on seed germination and growth of two warm-season native grass
932 species. *HortScience* 47:527–530. <https://doi.org/10.21273/hortsci.47.4.527>

933 Zhang XH, Zhou D, Cui JJ, Ma HL, Lang DY, Wu XL, Wang ZS, Qiu HY, Li M (2015) Effect of silicon on seed
934 germination and the physiological characteristics of *Glycyrrhiza uralensis* under different levels of salinity.
935 *J Hortic Sci Biotechnol* 90:439–443. <https://doi.org/10.1080/14620316.2015.11513207>

936 Zhang Z, Fan J, Wu J, Zhang L, Wang J, Zhang B, Wang-Pruski G (2020) Alleviating effect of silicon on melon
937 seed germination under autotoxicity stress. *Ecotoxicol Environ Saf* 188:109901.
938 <https://doi.org/10.1016/J.ECOENV.2019.109901>

939 Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plants. *Agron Sustain Dev*
940 34:455–472. <https://doi.org/10.1007/s13593-013-0194-1>

941