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Review

Silicon Nutrition in Plants under Water-Deficit Conditions: Overview and Prospects

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Abstract: Drought is one of the major constraints for sustainable crop production worldwide, especially in arid and semiarid regions. The global warming and climate change scenario has worsened the dilemma of water scarcity, creating an immediate threat to food security. Conserving water resources and exploiting various strategies that enable plants to withstand water deficits need to be urgently addressed. Drought adversely affects plant growth by modulating a range of physio-chemical, metabolic, and molecular processes inside the plant body, which ultimately reduces crop productivity. Besides developing drought-tolerant cultivars, better nutrient management could be a promising strategy to enhance drought tolerance in crop plants. Silicon, a quasi-essential element, is known to play a vital role in improving crop performance under a range of biotic and abiotic stresses. This review discusses the potential of Si application in attenuating the adverse effects of water-deficit stress. Silicon enhances plant growth by improving seed germination, cell membrane stability, carbon assimilation, plant–water relations and osmotic adjustment (by accumulating soluble sugars, proline and glycine betaine). It triggers the activity of antioxidants, promotes the biosynthesis of phytohormones, enhances nutrient acquisition and regulates the activity of vital enzymes in plants under drought stress. Silicon also induces anatomical changes in the plant cell wall through the deposition of polymerized amorphous silica (SiO_2-nH_2O), thereby improving stem and leaf erectness and reducing lodging. Further, Si-mediated physiological, biochemical and molecular mechanisms associated with drought tolerance in plants and future research prospects have been elucidated.

Keywords: climate change; carbon fixation; drought; phytoliths; silicon transporters; antioxidants; water economy

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1. Introduction

Drought stress is a worldwide dilemma that adversely affects agricultural productivity, thus creating a food security threat [1,2]. The increase in the severity and frequency of droughts on the geological time scale is one of the pronounced consequences of climate change [3]. The impact of droughts is more prevalent in developing countries where per capita water availability has generally been less than 1000 m^3 [4]. Drought stress negatively influences plant growth and development through a range of morphological and physio-biochemical alterations [5] (Figure 1). It hampers crop growth and yield by negatively influencing phenology, water and nutrient relations, respiration, assimilate partitioning and photosynthesis in plants [6]. Drought-induced crop yield losses have been estimated at about 75% of the global harvested area [7]. Under the current scenario, there is dire need to improve drought tolerance in crop plants to feed growing populations around the globe. Long-term sustainable approaches to counteract this challenge aim to improve and conserve water resources, develop drought-tolerant varieties of agronomically important crops and exploit plant nutrition strategies to enhance crop performance under drought [8,9].

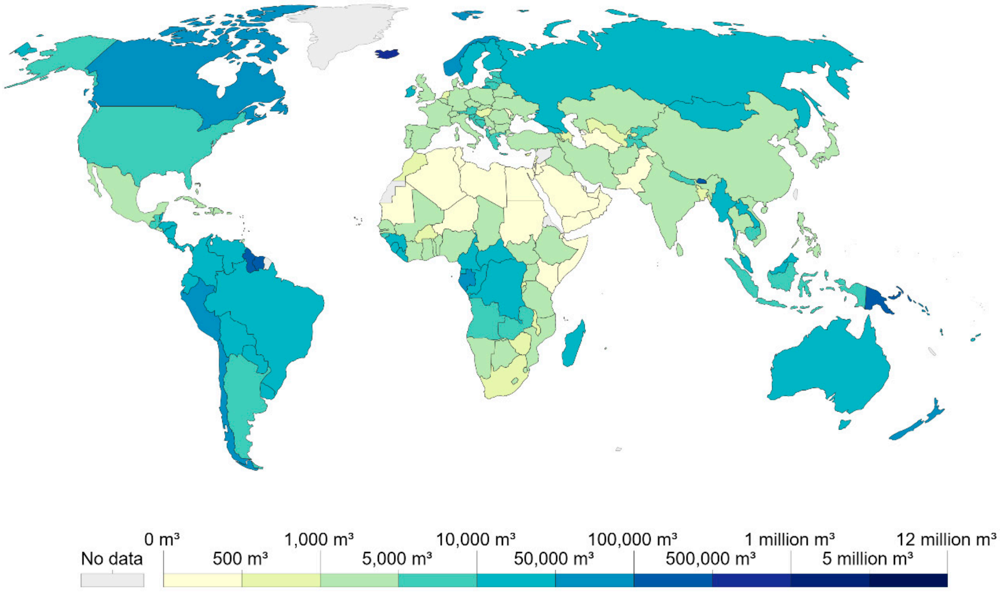

Figure 1. Available freshwater resources in the world (The World Bank, 2014).

Silicon (Si) is widely accepted as a beneficial element for multiple crop species, particularly in stressful environments [1,10,11]. However, genetic variations exist among crop species in terms of silica uptake and accumulation, and the subsequent stress tolerance mechanisms [12]. Plants of the *gramineae* family usually accumulate more Si in their tissues than other species. For instance, rice, as a typical accumulator, accumulates Si in quantities of up to 10% of shoot-dry biomass [13]. High-silica-accumulating plants differ to a great extent in their structure, mechanical strength, chemical composition, enzymatic activity, and stress tolerance from low-Si accumulators [14]. Si remains an underrated nutrient, and its role in plant growth and physiology was not recognized until the dawn of the 20th century. The possible reason for overlooking the beneficial effects on plants might be its unreactive nature in soil–plant systems. Further, it is abundantly present as a major inorganic constituent in plants with no visible symptoms of deficiency or toxicity [15]. In Japan, Si has been acknowledged as an 'agronomically essential element', and silicate fertilizers are being applied to paddy soils [12]. Silicon can be a sustainable, rapid and cost-effective method for improving crop yield under drought stress. The current review article comprehensively covers the constructive role of Si nutrition in mitigating the detrimental effects of water deficit in crop plants, its physiological and biochemical roles in plant metabolism and morphological responses under water-deficit conditions. Furthermore, physiological and biochemical mechanisms describing Si nutrition-based responses and behavioral adaptation to cope with drought stress are also discussed in detail and supported with particular case studies from the literature on Si nutrition in plants under water-deficit conditions.

2. Silicon: Uptake, Translocation and Deposition in Plants

Silicon is the second most abundant element after oxygen, representing a mean share of 28.8% on a dry weight basis [10]. In soils, Si is present in various alumino-silicate forms, and its concentration usually ranges from 0.5 to 4%. The occurrence of pure Si crystals is very rare in nature. It is found as Si oxides such as quartz, sandstone, opal, flint and Earth's silicates [16]. Most of Si sources/forms are water insoluble and thus are not available to plants. Plant roots uptake Si as monosilicic acid (H_4SiO_4), an uncharged molecule produced by the dissolution of Si-rich minerals at pH below 9 [17]. The concentration of monosilicic acid in soil solution ranges from 0.1 to 0.6 mM, which is about two-fold higher than that of phosphorus [14,18].

Silicon is taken up by plant roots through active, passive and exclusive mechanisms based on the differential ability of plant species to uptake and accumulate Si [19]. Plant roots actively uptake Si at a faster rate than water. Monocotyledonous plants such as rice, wheat, barley, ryegrass and some cyperaceous plants actively uptake Si [20,21]. Silicon is passively absorbed by plants at a rate equivalent to water without causing significant changes in Si concentration in soil solution. This uptake mode dominates in dicotyledonous species such as soybean, strawberry, melon and cucumber [16,22]. An exclusive mechanism of Si uptake that is associated with the rise in Si concentration in nutrient solution has been found in beans and tomatoes [23].

Numerous transporters responsible for Si active uptake have been identified in several monocots, including wheat, rice, maize and barley [24,25], and some dicots, including soybean and pumpkin, regulating optimum Si concentration in plant tissues. The mechanism of Si uptake, translocation and deposition in cereals are illustrated in Figure 2. Silicon uptake through root cells takes place via low-Si (Lsi) influx and efflux transporters Lsi1 and Lsi2, respectively [26]. The Lsi transporters are thought responsible for the passive transport of Si from outer solution to plant cells across the plasma membrane. Homologs of Lsi transporters have also been identified in rice (OsLsi6) and barley (HvLsi6), showing their expression both in roots and shoots [27]. Lsi2 facilitates the transport of Si from the root cortex to the stele as silica against the concentration gradient across the membrane. Initially, Lsi2 was identified in rice; then, its homologs were identified in maize (ZmLsi2) and barley (HvLsi2) [24,27]. Initially, Si is taken up through Lsi transporters localized in the cortical cells of maize and barley roots and in the exodermal cells of rice roots (Figure 2). Si is transported via the symplastic pathway to endodermal cells and then imported into the xylem through ZmLsi2 and HvLsi2. Si is taken up in rice by OsLsi1, located at the distal end of exodermal cells, from where it is transported from sclerenchyma to aerenchyma cells via Lsi2. The Si deposited in the endodermis is transported to the xylem via the Lsi1 influx transporter (Figure 2). Later, silicic acid is loaded into the xylem via transpiration stream, and Si transporters for xylem loading need to be investigated; however, Lsi6 for xylem un-loading has been identified on the adaxial side of parenchyma cells of leaf blades of the xylem [28].

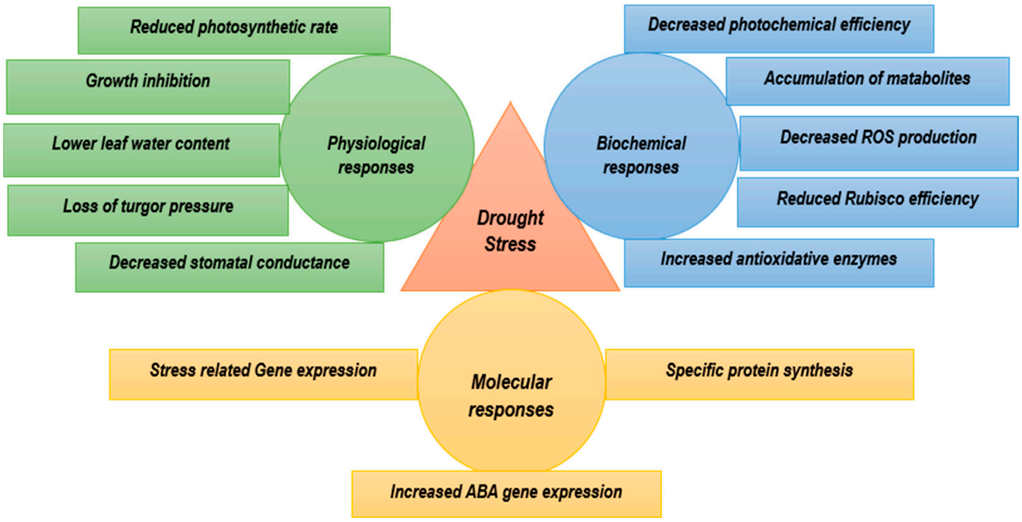

Figure 2. Physiological, biochemical and molecular responses in crop plants with water-deficit tolerance.

Considerable variations exist among plant species in Si accumulation in the shoots, ranging from 0.1 to 10% on a dry weight basis [13]. The differential behavior of plants in Si accumulation is due to the ability to uptake Si from soil solution via plant roots and subsequently transport it to above-ground plant tissues [23]. Within the plant root, Si is loaded into the xylem vessel either through the apoplastic or symplastic pathway. In many crop species, more than 90% of acquired Si is remobilized to shoots through the xylem by transpiration flow [25,29]. It is polymerized/precipitated throughout the plant mainly at transpiration sites as amorphous silica (SiO_2-nH_2O), also known as silica gel, opal, or phytoliths in higher plants [25,30]. The polymerization of Si in the form of phytoliths occurs when the concentration of silicic acid ($Si(OH)_4$) approaches the critical level of 100 mg kg^{-1}. The precipitation of phytoliths may largely occur in the epidermal parts of shoots and in the cell wall of the root endodermis [31]. In leaves, a layer of Si deposition develops over time around the stomata, mostly on the lower surface of leaves [32]. Phytolith synthesis, structure, composition and deposition density differ among crop species and genotypes [33].

3. Role of Silicon in Plant Biology

As a beneficial nutrient, Si is reported to improve plant growth and development under abiotic and biotic stresses [34,35]. Nonetheless, here, we discuss the multifarious roles of Si in physiological and metabolic pathways in plants under drought stress [1,36]. Silicon-mediated improvement in plant drought tolerance is illustrated in Figure 3. Si performs various functions by being polymerized as silicic acid, leading to the formation of solid, amorphous, hydrated silica, and by being instrumental in the formation of organic defense compounds through the alteration of gene expression. Evidence strongly suggests a critical role of Si in plant growth and development, challenging its notion of non-essential elements [37,38]. Silicon has a significant role in primary metabolism in Si-hyperaccumulating plant species [35]. Silicon deposition in the cell wall interacts with pectins and polyphenols, thereby promoting its strength and rigidity [39].

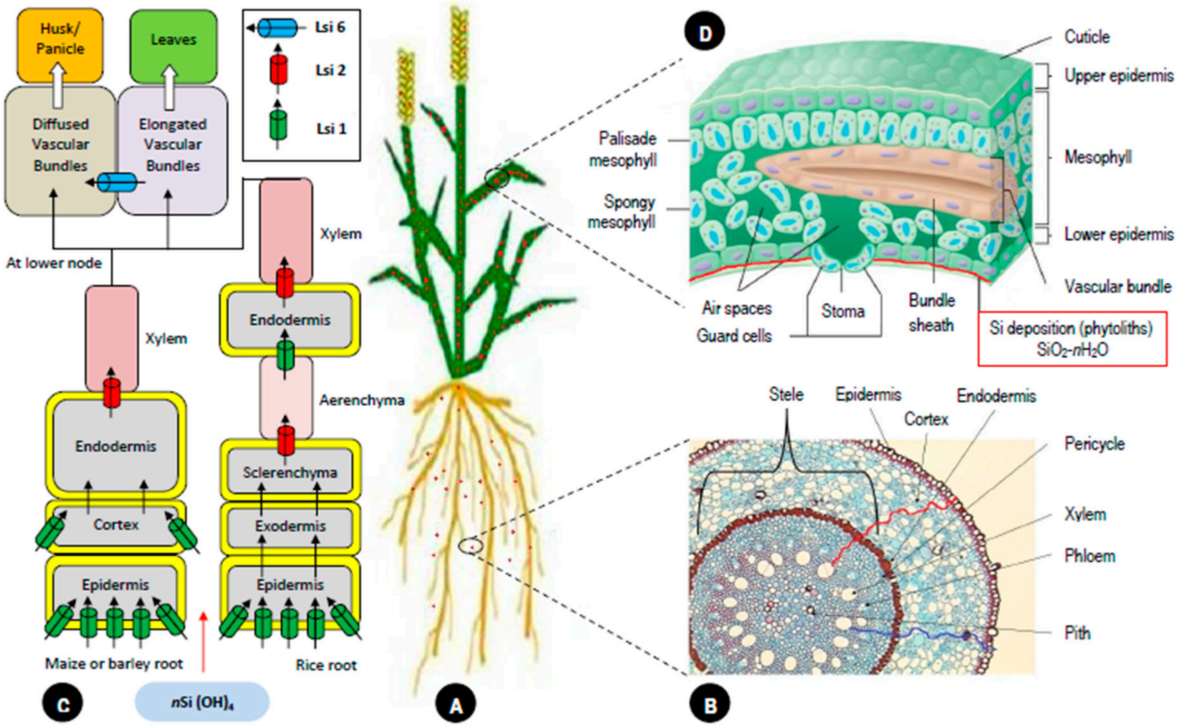

Figure 3. Mechanisms of Si uptake, translocation and deposition in higher plants: (**A**) Accumulation of SiO_2 (red symbols) at leaf margins as Si moves from soil solution towards plant leaves. (**B**) Apoplastic

and symplastic pathways of Si movement in plant roots. The apoplastic pathway (red line) involves cell wall spaces as well as intercellular spaces, while the symplastic pathway (blue line) includes the plasmodesmata and cytoplasm. (**C**) Loading of monosilicic acid (nSi $(OH)_4$) mediated by various transporters into xylem and subsequent translocation through stem into leaves. Lsi 1 is a low-Si influx transporter located in cortex of maize and barley roots, while it is found in exodermis and aerenchyma cells of rice roots. Lsi 2 is also a low-Si influx transporter present in endodermis of rice, maize and barley roots. Lsi 6 is a low-Si influx transporter involved in xylem unloading and is localized in xylem of leaf sheaths and leaf blades of rice, maize and barley. (**D**) Si deposition (red) between cuticle and epidermal cell of plant leaf in the form of amorphous silica (SiO_2-nH_2O) as phytoliths, mainly at transpiration sites.

4. Silicon Nutrition and Plant Drought Tolerance

Si fertilization modifies cellular metabolism and extenuates the physiological disorders in plants exposed to drought stress. It boosts crop tolerance by improving plant water uptake and transport, maintaining tissue water balance, leaf and stem erectness, photosynthetic activity and the structure of the xylem at high transpiration rates [20,40]. Although the impact of Si nutrition on plant morphology is the result of several physiological and metabolic processes, interestingly, Si was reported to affect the root anatomy in rice plants under unstressed conditions, which was found to be due to the up-regulation of specific protein-encoding genes [41]. Silicon presence in leaves also showed enhanced leaf retention and delayed leaf senescence due to the up-regulation of cytokinin synthesis in both Si-accumulating and non-Si-accumulating plant species [38]. Several plant metabolic processes lead to by-products that are responsible for cellular oxidative stress. The presence of Si in the plant body is almost vital to alleviate such physiological stresses [7,35]. Silicon is, therefore, reported to be closely associated with the processes of photosynthesis and respiration [42].

Silicon nutrition influences multiple morphological, physiological, biochemical and molecular attributes of plants to alleviate drought stress under water-deficit conditions, as well as in the case of secondary symptoms of water deficit in plants facing other abiotic and biotic stresses, i.e., salinity, heavy metals, heat, insect–pest attacks, etc. This review encompasses the positive effects of Si on plant growth and biomass production in plants exposed to drought stress. Enhanced plant growth by means of Si application might be due to improved seed germination, plant–water relations, better cell membrane stability, increased acquisition of mineral nutrients, carbon fixation and assimilation, osmotic adjustment, antioxidant regulation, alterations in phytohormones and cellular enzymes, and gene expression up-regulation in plants subjected to drought stress.

Dehghanipoodeh et al. (2018) illustrated the impact of Si on the productivity of strawberries subjected to drought conditions. The outcomes exhibited that enhancing the levels of water stress resulted in a reduction in the majority of the quantitative traits, for instance, specific leaf area, chlorophyll content, net photosynthetic rate and stomatal conductance. Thus, Si treatments significantly attenuated water-deficit stress and enhanced most of the studied parameters; they also considerably reduced the transpiration rate and increased chlorophyll content and water use efficiency. This idea was further strengthened by Amin et al. (2014), who reported that impaired plant growth caused by drought stress profoundly escalated with Si treatment. Si supply significantly increased plant growth in terms of plant height, leaf area, primary root length, shoot and root dry matter, water relations and gas exchange parameters in maize hybrids under a water-deficit regime. Moreover, drought-stressed maize plants exposed to Si treatment produced 21.68% more plant dry weight than plants not supplied with Si nutrition. These improvements in plant growth and dry matter accumulation might be attributed to better osmotic adjustment, photosynthetic rate, and reduced transpiration. Salem et al. (2022) evaluated the efficacy of various Si forms to minimize the drought-induced decrease in yield and the modifications in nutrient buildup within plants. As compared with the control, a significant improvement in all agronomic traits of wheat with various Si forms decreased zinc and manganese uptake and increased Si accumulation. Overall, the induction of plant resistance to drought stress by Si might be attributed to the polymerization of insoluble Si and the formation of phytoliths in the cell wall and in the vicinity of vascular bundles, decreasing water loss by regulating transpiration (Mecfel et al., 2007). Details of these mechanisms are discussed below.

4.1. Seed Germination

Seed germination is directly related to water availability and is inhibited under drought stress, resulting in poor crop stands [43]. Various studies report Si-induced improvement in seed germination under drought stress [44–47]. Starch breakdown is an important step during seed germination that provides energy to the growing embryo. This process is catalyzed by hydrolytic enzymes such as α-amylase, the activity of which decreases under drought stress [48]. Moreover, Si-induced enhanced seed viability and vigor have been reported in hydroponically grown alfalfa under drought [44]. Seed priming with sodium silicate improved seed germination percentage in wheat [47], and with calcium silicate in pepper, it increased the root surface area under drought [49]. Similarly, Si-induced improvement in seed germination and seedling growth rate has been reported in soybean [50], cowpea [51] and maize [46] under drought stress.

However, the mechanism of Si-mediated improvement in seed germination is still not fully understood. Seed germination is regulated by plant hormones. Abscisic acid and gibberellin acid are the two major plant hormones that direct seed germination and dormancy [52]. However, information about the possible regulation of Si on their levels or metabolism is lacking. Only few a studies have illustrated the Si-dependent regulation of phytohormone production and suggested that Si might decrease the ABA level and maintain a high gibberellin level in germinating seeds, thus improving overall germination [35].

4.2. Cell Membrane Stability (CMS)

Cell membrane stability is used as a physiological index for drought tolerance [53]. Silicon maintains the structural and functional integrity of cellular membranes in plants under drought stress (Figure 4; [54]). Improved membrane stability is associated with reduced oxidative damage. This decline is associated with the increase-induced enhanced activity of various antioxidant enzymes, e.g., superoxide dismutase (SOD) and catalase (CAT), which help to maintain membrane stability in stressful environments [55,56]. Silicon polymerizes in cells and forms phytoliths [35], which deposit in the cell wall of leaf epidermal cells to reduce electrolyte leakage (EL) [57,58] and lipid peroxidation [59]. Silicon fertilization reduces EL in maize [59] and cucumber [60] under drought. Foliar application of Si increased the membrane stability index and the chlorophyll stability index in wheat at different field capacity levels [54].

4.3. Carbon Fixation and Assimilation

Drought stress considerably affects the photosynthetic rate by reducing chlorophyll contents [36,61,62], damaging the photosynthetic apparatus and stomatal function [63]. Silicon application increases photosynthetic performance owing to the increase in chlorophyll contents and photosynthetic rate in wheat [1,54], rice [64,65], soybean [58], sorghum [55,66], pepper [67], white lupine [68] and Chinese licorice [69] under drought stress. Foliar application of Si increases the chlorophyll stability index and carboxylation efficiency by decreasing intercellular CO_2 concentration in wheat plants [54] under drought. Improved plant growth in response to Si application has been associated with increased photosynthetic attributes [70], ribulose bisphosphate carboxylase (Rubisco) activity [71,72] and gas exchange attributes, including net CO_2 assimilation rate and stomatal conductance [73]. Silicon-enriched application of nanoparticles such as silica and titanium improved photosynthesis in several plant species. Silicon increases leaf chlorophyll contents and lowers H_2O_2 contents and lipid peroxidation in water-stressed wheat [1] and maize [74]. Nonetheless, Si application provides protection against oxidative damage to chloroplast through the activation of the antioxidant defense system and membrane stability by reducing lipid peroxidation under drought [55,56,75].

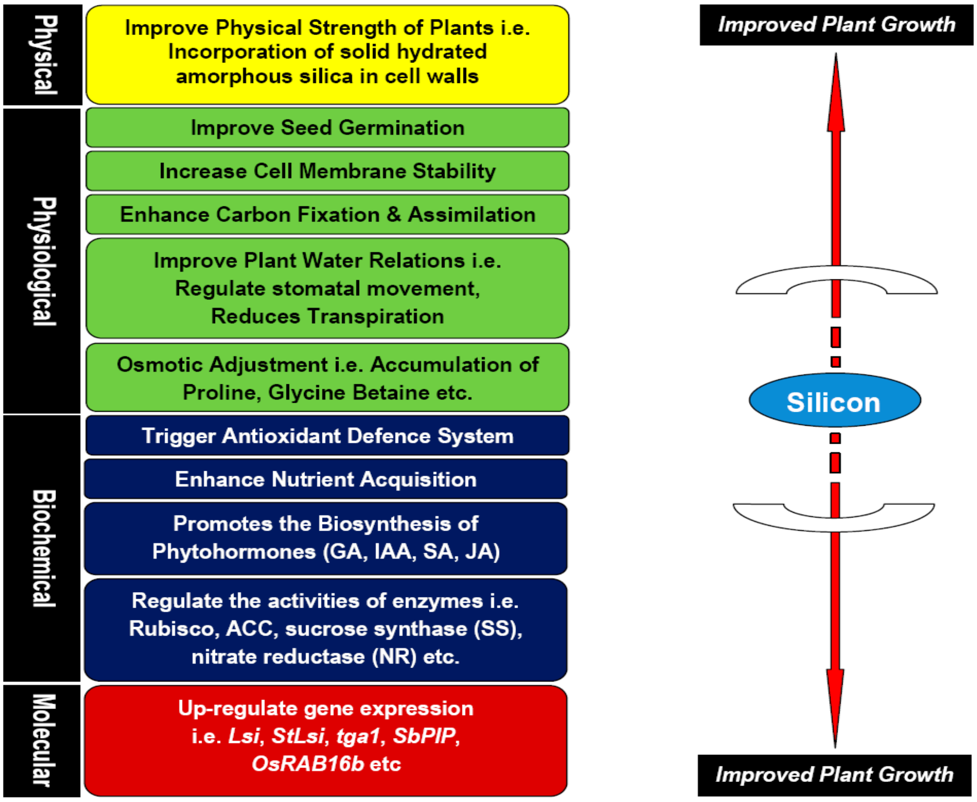

Figure 4. Various mechanisms of Si-mediated water-deficit tolerance in plants.

4.4. Plant–Water Relations

Plants transpire water through stomata for gaseous exchange with the environment. The leaf epidermis is covered with cuticular wax to prevent excessive water loss and for photo-protection [76]. Silicon application improves plant–water relations with significant reductions in transpiration rate and water flow in the xylem [10,54,77]. Si is reported to precipitate in epidermal cells of the stem, leaves and cuticle and diminishes unnecessary loss of water in plants under drought stress [78]. The polymerization of Si (2.5 µm) between the cuticle and endodermal cells reduces the transpiration rate by 30% in rice [79]. Si deposition in guard cells also significantly reduces transpiration by improving plant water uptake and transportation to the stem and leaves under drought conditions [40,80]. This Si-induced plant–water relation has been associated with improved intrinsic water use efficiency [6,81] under drought [54]. This has been reported in rice [65], wheat [82,83], maize [84], sorghum [85], chickpea [86], cucumber [87] and sunflower [88,89]. In fact, the possible reason behind this is increased thickness due to the deposition of a silica double layer in leaf and epidermal tissues [90]. Drought-tolerant sorghum cultivars accumulate large amounts of Si in their endodermal tissues [91]. In fact, silica crystal deposition in guard cells not only increases the cellular water potential but also physically hinders cuticle transpiration [92]. An increase of 33% in leaf water content has been reported with Si application in Kentucky grass [93]. In addition, the escape of water molecules is reduced due to the accumulation/polymerization of polar mono-silicic acid in leaf and epidermal cells of the cell wall, forming H-bonds between SiO_2-nH_2O and H_2O [31,94,95].

4.5. Osmotic Adjustment (OA)

Under limited water availability, osmotic adjustment is an effective mechanism to maintain higher cellular water contents (Figure 4; [96,97]). Plants accumulate various osmotically active compounds into the cytosol, which reduces cell osmotic potential and maintains turgor, thus contributing towards plant drought tolerance [5]. Silicon application improves plant growth by modifying osmolyte concentration and accumulating non-protein amino acid proline, which is frequently associated with osmotic adjustment [98]. Silicon-induced accumulation of proline has been reported in maize [81], potato [98], pepper [67], wheat [97,99] and sweet Basil [100] under drought stress. The accumulation of proline and other osmolytes, such as soluble sugars and proteins, amino acids, minerals and glycine betaine, reduces the osmotic potential of roots, depicting an active osmotic adjustment that helps plants to adjust cellular concentrations and thus perform better in growth and grain yield [97,101,102].

4.6. Phytohormone Metabolism

Phytohormones affect plant growth and development by affecting cell metabolism and associated mechanisms. Numerous studies have reported Si-induced regulation of the levels of plant growth hormones, their pre-cursors and associated enzyme activity under drought stress [55,67,73,103,104]. The application of Si increases salicylic acid (SA) and bioactive gibberellins (GA_1 and GA_4), while it reduces jasmonic acid (JA) levels in shoots of soybean under drought [103]. Si-enhanced plant drought resistance in pepper has been related to modified phytohormones and increased nitrogen metabolism, including higher nitrate reductase activity [67]. Increased photosynthetic rate in wheat with Si application has been associated with improved activity of phosphoenol pyruvate carboxylase (PEPcase) and slightly reduced activity of ribulose-1,5-bisphosphate carboxylase (Rubisco) [73]. Silicon affects the sucrose contents in tomato owed to increased sucrose synthase (SS) and sucrose phosphate synthase (SPS) activity under drought [105]. Similarly, altered levels of 1-aminocyclopropane-1-1carboxylic acid (ACC) and polyamine production in response to Si fertilization improve drought resistance in sorghum [55]. Silicon also triggers multiple hormones and enzyme activity associated with carbon and nitrogen metabolism for inducing drought resistance in plants [7,106].

4.7. Antioxidant Defense Mechanism

Reactive oxygen species (ROS) are generated within cells as by-products of various biochemical reactions under drought stress, and their effects are often neutralized by various enzymatic and non-enzymatic mechanisms [107]. Under drought conditions, ROS accumulation within cells causes oxidative damage to different macromolecular structures, such as biological membranes, proteins, lipids and nucleic acids [1,54,100]. These ROS damages are reduced by water- and lipid-soluble scavenging molecules and antioxidant enzymes [6,108]. In plants, the antioxidant defense mechanism includes both enzymatic and non-enzymatic components. Enzymatic components comprise catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), glutathione reductase (GR) and ascorbate peroxidase (APX), while non-enzymatic components consist of glutathione (GSH), ascorbic acid (AsA), carotenoids, tochopherols and cysteine [73]. Silicon application reduces oxidative damage in crop plants by up-regulating the activity of enzymes associated with the antioxidant defense system under drought (Figure 4; [1,7,43]). The production of ROS in chloroplasts causes lipid peroxidation and damages cellular membranes under drought. The application of Si enhances the activity of SOD, CAT, APX and POD enzymes in order to reduce H_2O_2 contents and lipid peroxidation by regulating glutathione reductase (GSH) and ascorbate (ASC) contents and the expression of genes associated with antioxidant enzymes [1,94]. This lowers photo-oxidative damage to membranes and consequently improves drought tolerance in wheat [102], sunflower [89], white lupine [68], chickpea [109] and tomato [43]. Nonetheless, the Si-induced activation of the antioxidant defense system varies among species and even genotypes, as well as plant growth stages, under drought [81,110].

4.8. Acquisition of Mineral Nutrients

Drought stress significantly reduces the uptake of essential nutrients required for optimum plant growth and development [111]. Silicon fertilization enhances the uptake of macronutrients (phosphorus, potassium, calcium and magnesium) and micronutrients (iron, copper and manganese) in maize [81], alfalfa [112], wheat [83], rice [113], sunflower [88], grass species [57,111] and cucumber [114] (Figure 4). The silicon-mediated increased uptake of these mineral nutrients improves growth and biomass in crop plants. One possible mechanism behind the stimulated effect of Si on nutrient uptake might be membrane-activated H^+-ATPase activity and the Si-induced regulation of osmotic potential due to ion solubilization [115]. Higher nutrient contents in roots and the up-regulation of aquaporin gene expression in response to exogenously applied Si have been reported in sorghum [116,117] and cucumber [118]. These mechanisms ultimately enhance plant water uptake and nutrient absorption [119].

5. Molecular Basis of Si-Induced Drought Tolerance

One important aspect for better understanding and clarifying the role of Si in alleviating drought stress is to study this nutrient at the gene level in plants. Two different types of Si transporters (Low Si 1 (Lsi1) and 2 (Lsi2)) have been identified to be involved in the uptake and distribution of Si (Ma et al., 2015). In rice, the low Si rice 1 (Lsi1) gene is responsible for Si transport and its accumulation in rice shoots [120], and its suppression results in diminished Si uptake [28]. The Lsi1 gene is localized on the plasma membrane along the distal sides of both endodermal and exodermal cells. Another low Si transporter gene 2 (Lsi2) has been characterized [27] to be localized on the proximal side of endodermal and ectodermal cells. This transporter has a unique mechanism of Si transport in plants, as it has both an influx transporter on one side and an efflux transporter on the other side of the cell, thus permitting the transcellular transport of nutrients in a more efficient way. Likewise, in soybean, two Si influx transporter genes (*GmNIP2-2* and *GmNIP2-1*) have been characterized and quantified for Si uptake permeability [121]. In potato, *StLsi1 a*, a putative Si transporter, has been identified as having homology with the pumpkin Si transporter [36]. *StLsi1* is localized in leaves and roots, with higher expression rates in roots. Likely, Lsi2-like Si transporters have been identified and characterized in maize and barley [24] and are only localized in endodermal cells of the plasma membrane. It reveals a distinct feature of Si uptake, including their cell-type specificity and the lack of polarity of their localization in Lsi2 compared with that in rice.

Influx transporter gene *CsLsi1* has been isolated and characterized in cucumber root hairs [122] and shows >55% and >90% homology with pumpkin and rice *Lsi1* transporter genes, respectively. An efflux Si transporter, *CsLsi2*, located on the plasma membrane has been identified and characterized, and its uptake is an energy-dependent process [123]. Nonetheless, a candidate gene whose mutation causes a deficiency in Si uptake has been identified and may allow the uptake mechanism to be understood [15]. Moreover, a collection of 'reverse genetic' gene knockouts are available for *Arabidopsis*; therefore, it could be interesting to screen these mutants to identify genes involved in Si biology [124].

Phytolith deposition could be correlated with the presence of mutant locus Hard rind (Hr) in dicot Cucurbita [125] and with the teosinte glume architecture 1 (tga1) locus in monocot maize [126]. In both species, phytolith deposition was linked to a locus that is involved in lignification. Moreover, silicic acid shows strong affinity for the organic polyhydroxyl compound, which precipitates during the synthesis of lignin [127,128]. In rice, the presence of higher-density transporters for xylem loading and radial transport is responsible for high Si accumulation [129]. Most dicots are unable to accumulate Si in large amounts from soil to shoots. However, a gene responsible for xylem loading in rice has been mapped on chromosome 2 and may be cloned from rice to other crop plants to enhance plant resistance against multiple stresses [87]. Ref. [55] studied the effect of Si application in sorghum plants and reported that enhanced resistance is achieved by up-regulating genes associated with the biosynthesis of conjugated polyamines. Similarly, Ref. [130] reported that Si up-regulates the gene expression of root SbPIP aquaporins, which regulates root hydraulic conductance and improves drought resistance in sorghum. Si application in rice considerably increased the expression of drought-specific genes, i.e., OsRAB16b, OsRDCP1 and OsCMO, coding dehydrin and choline monooxygenase [131].

The effects of Si fertilization on the transcript level of putative transporters, its uptake and tuber quality in potatoes have been studied under drought stress conditions [36]. A putative transporter for Si transport in roots and leaves, StLsi1, has been isolated with conserved amino acid domains, and Si fertilization increased its transcript level about five-fold under drought and two-fold under normal conditions. Additionally, high-Si-concentration-induced anatomical and compositional changes that enhance suberization and lignification have been observed to delay skin maturation in tubers.

Thus, the identification and characterization of Si transporters and their subsequent incorporation using DNA recombinant technology is predicted to be a promising strategy in the future for producing crops with high resistance to drought stress. However, Si-mediated plant antioxidant defense systems result in better morpho-physiological and biochemical attributes even under limited water-availability conditions (Table 1).

Table 1. Plant responses to Si nutrition under water-deficit conditions.

Crop	**Drought Level**	**Source and Rate**	**Method of Application**	**Experimental Conditions**	**Major Findings**	**Reference**
Phoenix dactylifera L.	PEG-8000 (15%)	3.6 mM Si Ca_2SiO_4	Nutrient medium	In vitro (MS media)	Improved physiological (Chlorophyll contents) and biochemical attributes, and antioxidant activity	[132]
Triticum aestivum L.	60% of FC	4 mM Si (K_2SiO_4)	Foliar spray at anthesis	Pot	Improved biochemical attributes and accumulation of nutrients	[133]
	−0.3 MPa	150 mg L^{-1} Si (Na_2SiO_3. H_2O)	Nutrient medium	Hydroponics	Higher chlorophyll content, relative water content, and shoot and root length	[134]
	100 and 40% of FC	6 mM Si ($Na_2Si_3O_7$)	Foliar application	Field	Enhanced activity of key antioxidant enzymes, accumulation of osmolytes, and reduction in H_2O_2 and MDA levels	[54]
	40% WHC	50 mM Si	Foliar application	Pot	Significant increase in photosynthetic pigments, photosynthesis rate, stomatal conductance, leaf turgor pressure, and enzymatic antioxidants	[135]
	Irrigation frequencies (2, 3 and 4)	0–12 kg ha^{-1} (K_2SiO_3)	Soil	Field	Improved growth and yield; higher tissue K^+ ion contents	[136]
	60% of FC	1 mM $Na_2SiO_3.5H_2O$ solution per pot	Fertigation	Pot	Higher activity of antioxidant enzymes such as APX, POD and CAT	[137]
	PEG-6000 (20%)	1.0 mM Si (K_2SiO_4)	Soil	Hydroponics	Increased total soluble protein contents and SOD activity, and reduced electrolyte leakage	[138]
	75, 50 and 25% of FC	30 kg Si ha^{-1}	Soil	Field	Reduced electrolyte leakage and increased SOD activity, and grain K^+ and Si concentrations	[57]
	Withholding irrigation	0.28 g Si kg^{-1} soil	Soil	Field	Improved tissue water status and leaf stomatal conductance; increased phosphoenol pyruvate carboxylase (PEPCase) activity	[83]
	Withholding water for 12 days in 26-day-old seedlings	7.14 mmol Si kg^{-1} soil	Soil	Pot	Greater leaf water ratio (LWR) and lower specific leaf area (SLA)	[90]

Table 1. *Cont.*

Crop	Drought Level	Source and Rate	Method of Application	Experimental Conditions	Major Findings	Reference
Zea mays L.	Deficit irrigation (DI20% = 80% of full irrigation)	4 mM Si (Na_2SiO_3)	Foliar application	Field	Enhanced physiological performance, water use efficiency, and productivity of maize under water deficit	[139]
	60% of FC	0, 4 and 6 mM Si (Na_2SiO_3)	Seed priming	Pot	Increased shoot and root length, and photosynthetic pigments; enhanced activity of antioxidant enzymes (SOD, POD and CAT) and reduced MDA and H_2O_2 contents	[74]
	100 and 60% of FC	150 mg Ca_2SiO_4 kg^{-1} soil	Foliar	Pot	Improved growth, dry matter, plant–water relations and gas exchange attributes	[84]
	Naturally rain-fed conditions	700 kg Ca_2SiO_4 ha^{-1}	Soil	Field	Increased kernel number per ear; improved relative water content and stomatal density, and reduced canopy temperature	[46]
	50% of FC	1–2 mM Si (Na_2SiO_3)	Soil	Pot	Improved physiological attributes, i.e., chlorophyll and relative water contents; higher tissue Ca and K contents	[81]
	PEG-6000	2 mmol L^{-1} (H_4SiO_4)	Nutrient medium	Hydroponics	Higher WUE; lower transpiration rate	[140]
Solanum lycopersicum L.	1.0% PEG	0.6 mM Si (Na_2SiO_3)	Nutrient medium	Hydroponics	Improved energy dissipation in mitochondria and chloroplasts via Si-mediated alternative oxidase and malate/oxaloacetate shuttle, and reduced ROS accumulation	[141]
	(PEG-6000) 10% (*w*/*v*)	2.5 mmol L^{-1} Si (K_2SiO_3)	Nutrient medium	Hydroponics	Promoted photosynthesis by modulating some photosynthesis-related genes and regulating the photochemical process	[142]
	1.0% PEG	0.6 mM Si (Na_2SiO_3)	Nutrient solution	Greenhouse	Improved hydraulic conductivity in radial direction, which enhanced water uptake of tomato roots; high solute accumulation, such as proline, soluble sugar and soluble protein; enhanced antioxidant activity (SOD and CAT) and reduced O_2^- production rate, and H_2O_2 and MDA contents	[143]
	(PEG-6000) 10% (*w*/*v*)	2.5 mmol L^{-1} Si (K_2SiO_3)	Nutrient medium	Hydroponics	Enhanced root hydraulic conductance and water uptake, and decreased membrane oxidative damage	[144]
	PEG-6000 (10%)	0.5 mM Si	Nutrient medium	Hydroponics	Increased seed germination and antioxidant enzymes activity, i.e., SOD, CAT, APX and POD	[43]
Oryza Sativa L.	70, 80, 90, 100 and 120% of the soil saturation point	0, 2.1, 4.2, 6.3 and 8.4 mg Si per pot. (K-Silicate)	Foliar spray	pot	Increased plant height, rice straw, root yield and grain yield; increased concentrations of N, P, K and Si in straw	[145]
	100, 75 and 50% of FC	0, 75, 150, 300 and 600 kg Si ha^{-1}	Soil	Pot	Increased grain yield (34–45%) and highest number of panicles per plant	[146]
	80, 70 and 60% of FC	0, 200, 400 and 600 kg Si ha^{-1}. (Calcium. Silicate)	Soil	Field	Increased grain yield and plant height, and reduced number of stalks	[147]

Table 1. *Cont.*

Crop	Drought Level	Source and Rate	Method of Application	Experimental Conditions	Major Findings	Reference
Sorghum bicolor L.	−138 KPa	2 mM Si (K_2SiO_3)	Soil	Pot	Increased growth of the root system, and improved photosynthesis	[148]
	PEG-6000 (−4.0, −6.0, −8.0 and −10.0 MPa)	3.0 mmol Si L^{-1}) (K_2SiO_3)	Solution application	Pot	Increased leaf water potential, leaf area index, SPAD chlorophyll, net assimilation and relative growth rate	[85]
	40 mm of irrigation	200 mL L^{-1} kg^{-1} soil	Soil	Pot	Improved plant–water relations and higher chlorophyll contents	[66]
Saccharum officinarum L.	100–95, 55–50 and 35–30% of FC	0, 100, 300 and 500 mg L^{-1} Si ($CaO{\cdot}SiO_2$)	Fertigation	Pot	Increased plant growth, photosynthetic efficiency and biomass/yield; promoted better adaptation of stomata to drought	[149]
	55% of FC	0 and 600 kg Si ha^{-1}	Soil	Field	Increased relative water content, dry weight of leaves, carotenoids content, leaf water potential (Ψw) and SPAD, and decreased electrolyte leakage in leaves	[150]
Glycine max L.	−0.5 MPa PEG-6000 (20%)	1.70 mM Si	Nutrient medium	Hydroponics	Improved photosynthesis and antioxidant activity (i.e., CAT, POD, SOD and H_2O_2); increased proline and relative water contents	[58]
	PEG-6000	100–200 mg Si L^{-1}	Nutrient medium	Hydroponics	Improved growth and hormonal homeostasis	[103]
Foeniculum vulgar L.	90, 75 and 60% of FC	0, 2.5, 5, 7.5 and 10 mM Si	Foliar application	Field	Increased concentrations of proline, soluble sugars, Na^+ and K^+ in seeds; improved LAI, seed yield and essential oil percentage	[151]
	40, 70 and 100% of FC	0, 2.5, 5, 7.5 and 10 mM	Foliar	Field	Enhanced ascorbate peroxidase activity and increased osmotic adjustment	[152]
Brassica napus L.	10 and 20% PEG	Si (1 mM SiO_2)	Hyponex solution	Semi-hydroponic	Significantly improved antioxidant enzymes, AsA-GSH pool, glyoxalase systems and proline	[153]
Vigna radiata L.	100, 75, 50 and 25% soil moisture	20, 40 and 60 ppm $MgSiO_3$	Fertigation	Pot	Increased total carbohydrate and protein contents	[154]
Nicotiana Rustica L.	100, 60 and 30% of FC	2 mM Si (Na_2SiO_3)	Solution application	Pots having Perlite	Increased soluble proteins, free α-amino acids and proline concentrations; enhanced activity of antioxidative enzymes and decreased H_2O_2 concentration	[155]
Vicia faba L.	4000, 3000 and 2000 m^3 water ha^{-1}	2.0 mM Si (K_2SiO_3)	Foliar application	Field	Improved growth, yields and water use efficiency by raising antioxidant activities and suppressing lipid peroxidation and electrolyte leakage	[156]
Fragaria x ananasa var. Paros	90, 75 and 35% WHC	3 mmol Si L^{-1} (Na_2SiO_3)	Nutrient solution	Hydroponics	Enhanced plant biomass production by increasing photosynthesis rate, water content and use efficiency, antioxidant enzyme defense and nutritional status	[157]
Cucumis melo L.	100, 75 and 50% of FC	0, 100, 200 and 400 kg Si ha^{-1} (H_4SiO_4)	Soil	Pot	Higher yield, flesh thickness and total soluble solids content	[158]
Poa pratensis L.	Withholding irrigation for 20 days	0, 200, 400 and 800 mg Si L^{-1} ($Na_2SiO_3{\cdot}9H_2O$)	Nutrient solution	Glasshouse (Vermiculite + loam soil)	Increased net photosynthesis, leaf water contents, leaf green color and turf quality	[93]

Table 1. *Cont.*

Crop	Drought Level	Source and Rate	Method of Application	Experimental Conditions	Major Findings	Reference
Ocimum basilicum L.	45 and 65% of FC	250 mg L^{-1} Si	Soil	Pot	Improved essential oil yield, antioxidant system and osmoregulation, and maintained organelle ultrastructure	[100]
Pistacia vera L.	70% of FC	2.73 mmol Si kg^{-1} soil (Na_2SiO_3)	Soil	Pot	Enhanced photochemical efficiency and photosynthetic gas exchange; improved maximum quantum yield of PSII, stomatal conductance and antioxidant defense capacity	[159]
Mangifera indica L.	−0.77-bar water potential	1.5 mM Si (K_2SiO_3)	Fertigation through drip irrigation	Field	Increased IAA, GA and CK, and decreased ABA levels; improved antioxidative enzyme activity and fruit quality	[160]

Notes: Field capacity (FC); water holding capacity (WHC); polyethylene glycol (PEG); hydrogen peroxide (H_2O_2); malondialdehyde (MDA); ascorbate peroxidase (APX); superoxide dismutase activity (SOD); peroxidase (POD); catalase (CAT); soil plant analysis development (SPAD); leaf area index (LAI); ascorbate–glutathione (AsA-GSH); indole-3-acetic acid (IAA); gibberellic acid (GA); cytokinin (CK); *abscisic acid (ABA).*

6. Conclusions and Perspectives

Drought is one of the principal abiotic stresses around the globe causing considerable losses of crop yields, particularly in the current climate change scenario. It has become very alarming with the passage of time and poses a serious threat to food security in the future, which may result in the worst famines and/or other disasters [111,132]. Traditional plant breeding, genetic engineering and agronomic approaches including plant nutrition could provide a sustainable solution to mitigate the detrimental effects of drought stress on plant growth, as the development of drought-tolerant crop cultivars is a laborious and time-consuming protocol that may cause certain other limitations regarding yield, quality and disease resistance and other related traits require to be considered while developing a new crop variety. On the other hand, the agronomic application of Si either in soil, on leaves or along with other fertilizers, i.e., urea, phosphates and potassium fertilizers, can be essentially performed in crops for sustainable yield. Silicon, as a beneficial element, enhances drought resistance in plants by improving morphological, physiological and biochemical attributes, each of which has positive effects on plant growth and development.

- The potential of Si in mitigating drought stress is poorly understood at the molecular level; the molecular physiology of the Si-induced regulation of osmotic adjustment, water and nutrient uptake, the biosynthesis of stress proteins and phytohormones, including K-regulated aquaporin expression, need investigation.
- Some members of the poaceae family, including maize and wheat, also accumulate Si but in lesser amounts than rice. Understanding mechanisms for Si uptake in these plants needs further identification of transporters. Likely, transporters involved in Si efflux in non-accumulating species are required.
- Advancements in molecular biology and biotechnology such as CRISPAR/Cas and DNA recombinant technologies have enabled the transfer of desired genes or the restriction/knockout of undesired genes to be achieved, which is not possible with traditional plant breeding techniques. Therefore, gene transfer from rice to other crop plants, especially dicots, should be exploited to enhance plant resistance against drought stress by genetically manipulating the Si uptake ability of other plants.
- Optimizing the rates and timing for Si foliar and soil application may increase its agronomic application, especially in water-soluble fertilizers.
- The sole application of Si as a fertilizer may increase input costs in terms of fertilizer price and labor costs for application and may affect the direct income of the farm. However, the enrichment of essential fertilizers such as urea and phosphate fertilizers

with Si in areas facing acute risk of abiotic stresses, particularly water deficit, may provide a sustainable solution for Si application to field crops.

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Abbreviations

Si, silicon; CMS, cell membrane stability; EL, electrolyte leakage; MSI, membrane stability index; LWR, leaf water ratio; SLA, specific leaf area; CSI, chlorophyll stability index; OA, osmotic adjustment; ROS, reactive oxygen species; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; POD, peroxidase; GR, glutathione reductase; MDA, malondialdehyde; WUE, water use efficiency; PWR, plant–water relation; ACC, 1-aminocyclopropane-1-1carboxylic acid; SA, salicylic acid; JS, jasmonic acid; IAA, indole acetic acid; GA, gibberellic acid; SS, sucrose synthase; SPS, sucrose phosphate synthase; tga1, teosinte glume architecture 1; StLsi, low silicon transporter; Lsi, low silicon; PEG, polyethylene glycol

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