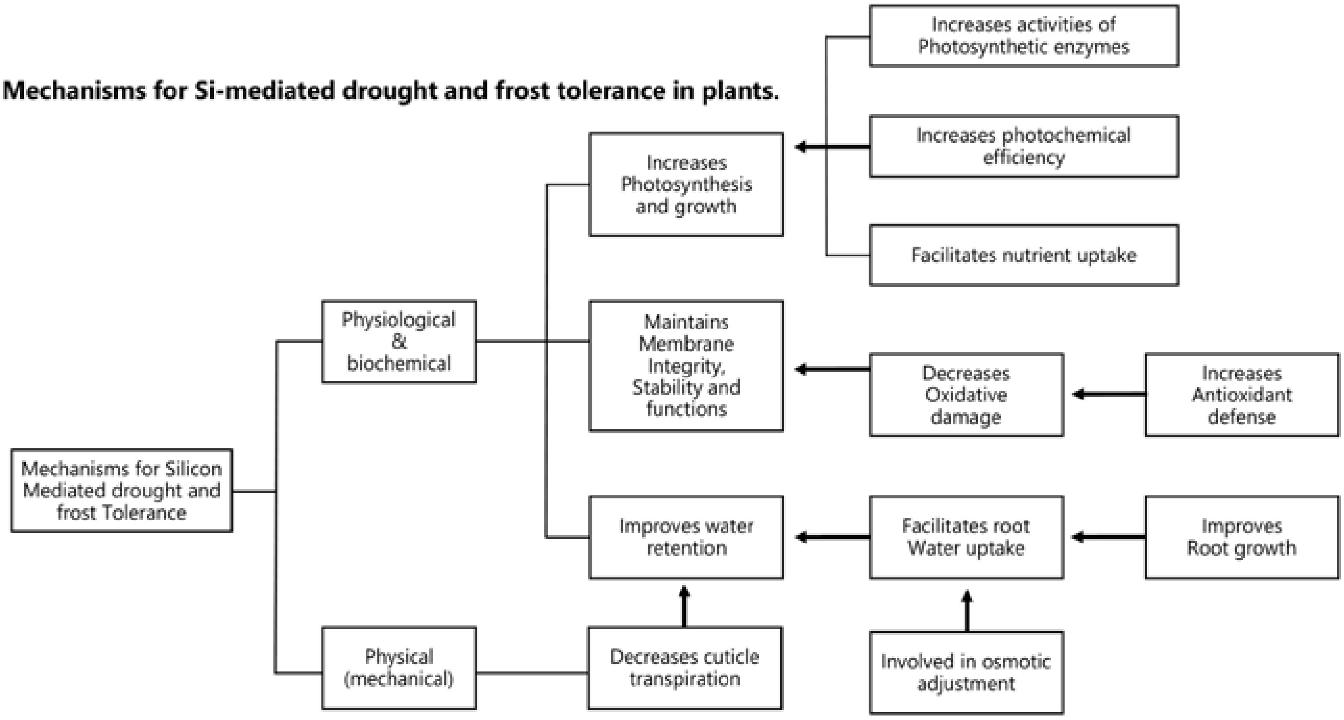
DROUGHT AND LOW TEMPERATURE STRESS

A highly economical ‘refined not mined’ alternative to entrenched agricultural products such as Gypsum with the added benefit of Silicon and other trace elements.

Silicon-Mediated Tolerance to drought and low temperature stress

Drought and low temperature are two of the major adverse climatic factors that restrain plant growth and sustainable agricultural development. Silicon (Si) application can alleviate various abiotic stresses including drought and low temperature. The mechanisms for Si-mediated increases of tolerance to drought and low-temperature stresses include physiological, biochemical and physical aspects. These include promoting photosynthetic enzymatic activities, photochemical efficiency and photosynthetic rates: maintaining nutrient balance: improving water retention by decreasing water loss from leaves and increasing water uptake by the roots; and scavenging reactive oxygen species by improving the capabilities of antioxidant defense.



Mechanisms for Si-mediated drought and frost tolerance in plants.

Photosynthesis and Plant Growth

Under environmental stresses, photosynthesis is inhibited Ashraf and Harris (2013[1]) and exogenous Si has been found to revert this inhibition and therefore restore normal plant growth under drought and low-temperature conditions. Gong et al. (2005[2]) observed that, under drought conditions, Si-supplied wheat seedlings had higher net CO_2 assimilation rate as compared to untreated plants. A similar phenomenon was observed in other drought-stressed plants such as sorghum (Sorghum bicolor) (Hattori et al. 2005[3]; Liu et al. 2014[4]) and rice (Oryza sativa) Chen et al. 2011[5]). Under freezing conditions (<-5oC), Zhu et al. (2006[6]) found that the application of Si could increase the net photosynthetic rate of wheat (Triticum aestivum), with the improvement being more obvious in the low-temperature sensitive cultivar.

Stomatal and Non-stomatal Limitations of Photosynthesis

The inhibition of photosynthesis under drought stress has been attributed to both stomatal and non-stomatal limitations Yoranov et al. (2000[7]). Stomatal closure is the first response of plants subjected to serious water deficit, and it is generally considered to be the main limiting factor for photosynthesis (Reddy et al. 2004[8]; Farooq et al. 2009[9]). The stomatal closure appears to be the first line of defense against desiccation since it is much faster than changes in root growth, leaf area, chloroplast ultrastructure and pigment proteins Yordanov et al. (2000[10]). Although stomatal closure usually occurs under adverse environmental conditions, in some stress conditions, non-stomatal limitation, i.e. decreased capacity of C fixation by chloroplast, may inhibit photosynthesis. Gong et al. (2005[2]) observed that drought stress depressed the wheat photosynthetic rate but that the addition of Si application reinstated a normal rate. Similar results were also obtained in drought-stressed sorghum Hattori et al. (2005[3]). Zhu et al. (2006[6]) investigated the photosynthetic gas exchange of wheat leaves under freezing conditions and observed that the introduction of Si in the culture solution significantly increased the net photosynthesis of the stressed wheat seedings.

Similar results were also obtained in drought-stressed sorghum (Hattori et al. 2005[3]). Zhu et al. (2006[6]) investigated the photosynthetic gas exchange of wheat leaves under freezing conditions and observed that the introduction of Si in the culture solution significantly increased the net photosynthesis of the stressed wheat seedlings. They found that although the leaf stomatal conductance was decreased under freezing stress and was increased by Si introduction, the intercellular CO2 concentration was not changed (in the tolerant cultivar), or it was even increased (in the sensitive cultivar) under freezing stress without applied Si, while Si addition slightly decreased the concentration of intercellular CO2 of the stressed plants. These results suggest that the photosynthesis inhibition and Si-mediated improvement under freezing stress could both chiefly be attributed to non-stomatal factor.

Chlorophyll plays an important role in the photosynthesis and is responsible for light harvesting. Lobato et al. (2009[11]) found that the addition of Si could maintain the level of chlorophyll in capsicum (Capsicum annuum) under water-deficit stress, suggesting that Si could alleviate water stress-induced damage in the photosynthetic systems and therefore the improvement of photosynthesis.

Similar results were also observed in drought-stressed rice (Chen et al. 2011[5]). In freezing conditions, Zhu et al. (2006[6]) observed that Si addition not only increased the chlorophyll content but also increased the ratio of chlorophyll a/b which indicates the extent of thylakoid stacking Aro et al. (1993[12]).

It has been shown that there is an inverse linear relationship between the ratio of chlorophyll a/b and extent of photoinhibition Aro et al. (1993[12]). Therefore, Si-mediated increase in chlorophyll content and chlorophyll a/b ratio indicates a higher stacking extent of thylakoid and less photoinhibition under stress conditions. Moreover, since chlorophyll a is more sensitive to reactive oxygen species (ROS) than chlorophyll b (Powles 1984[13]), the increase in chlorophyll content and ratio of chlorophyll a/b by Si may reflect a decreased oxidative damage under freezing stress. The decrease in oxidative damage may be attributed to Si-mediated increase in activities of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Gong et al. 2005[2] ; Liang et al. 2008[14]).pathogens resulting in improved plant health.

Nutrient Uptake and Plant Growth

The improvement of plant growth by the application of Si under environmental stress is not only related to increased photosynthesis but may be related to nutrient uptake and use. Water-deficit and other environmental stresses restrict the uptake of nutrients by roots and their transport to shoots and thereby reduce the availability of nutrients (Chen et al. 1983[7] ; Farooq et al. 2009[9]).

Si may play an important role in maintaining the balance of the uptake, transport and distribution of mineral nutrients in stressed

plants and therefore improve plant growth in adverse

environmental conditions. The beneficial effects of Si on the growth of roots under stress conditions have been observed in some studies.

In drought stress conditions, Hattori et al. (2005[3]) observed a lower shoot/root ratio and higher root dry mass accumulation in Si-applied sorghum, which suggests that Si facilitated root growth under drought stress. Ahmed et al. (2011[15]) found that the addition of Si was mainly beneficial to the growth of sorghum roots, with more biomass being allocated to the root system and therefore increased drought tolerance of plants. The growth stimulation of roots by Si may be related to root elongation, thereby enhancing the extensibility of cell walls in the growing zone, as observed in sorghum by Hattori et al. (2003[16]).

Silicon-Mediated Water Retention (Transpiration)

In adverse conditions such as drought and freezing stress, the water potential and water content of plants are sub- stantially decreased (Siddique et al. 2001[20] ; Verslues et al. 2006[21] ; Farooq et al. 2009[9] ; Liang et al. 2008[14]).

The addition of Si can improve the water status of plants under drought or freezing conditions. Transpiration rate can influence plant water relations (Farooq et al. 2009[9]). Plants transpire mainly through leaves, via the cuticle and stomata. The positive role of Si in plant growth and water retention has long been associated with Si-mediated alleviation of environmental stresses. In the early days, it was suggested that the formation of a silica–cuticle double layer on leaf epidermal tissue might contribute to the reduction in leaf transpiration (Yoshida 1965[22]; Wong et al. 1972[23]; Matoh et al. 1991[24]). In maize, Gao et al. (2006[25]) observed that the transpirational rate and conductance from the leaf cuticle were not changed by Si, while the transpirational rate and conductance from the stomata were significantly decreased.

The results suggest that Si was involved in the regulation of stomatal movement. Hence, the Si-triggered decrease in transpiration is one of the mechanisms for Si-mediated increase of tolerance. It is worth noting that whether the decrease of transpiration is from the cuticle or stomata may be related to plant species or culture conditions. stress conditions. Moreover, since chlorophyll a is more sensitive to reactive oxygen species (ROS) than chlorophyll b (Powles 1984[13]), the increase in chlorophyll content and ratio of chlorophyll a/b by Si may reflect a decreased oxidative damage under freezing stress. The decrease in oxidative damage may be attributed to Si-mediated increase in activities of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Gong et al. 2005[2] ; Liang et al. 2008[14]). pathogens resulting in improved plant health.

Root Water Uptake

The complex relationship between transpiration and Si suggests that there might be some mechanism besides transpiration that contributes to Si-mediated tolerance to environmental stresses.

Root water uptake is an important process that maintains the water balance in plants. Si may affect root growth and therefore regulate water relations. Chen et al. (2011[5]) found that application of Si enhanced the root growth of rice under drought conditions. They observed that the total root length, root surface area, root volume and root activity were all increased in Si-applied stressed plants. Si -mediated enhancement in root growth has also been observed in sorghum under drought (Yin et al. 2014[26]). Yin et al. (2014[26]) suggested that the growth enhancement of roots was related to the modulation of root plasticity, which were regulated by Si-mediated increase in polyamine levels and decrease in ethylene levels. The improved root growth can enhance water absorption, which helps to increase plant tolerance to drought stress. In root water uptake, aquaporins are major facilitators of water transport in plants (Maurel et al. 2008[27]). Aquaporins can be subdivided into five sub- families, i.e. the plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), small basic intrinsic proteins (SIPs), nodulin26-like intrinsic proteins (NIPs) and the uncharacterized X intrinsic proteins (XIPs) Bienert et al. (2011). Among these aquaporins, PIPs and TIPs represent the core pathway of water transport between and within cells Maurel et al. (2008[27]). Fairly recently, Liu et al. (2014[4]) found that application of Si could increase the root hydraulic conductance and induce the upregulation of PIP gene expressions in the roots of sorghum seedlings under water deficit stress, suggesting the involvement of Si in the regulation of water uptake under water stress.

Silicon-Mediated Membrane Integrity, Stability and Functions

Cell membrane systems, including plasma membrane and endomembrane system, are primary targets of environmental stresses Agarie et al. (1998[28]). In adverse conditions, the maintenance of integrity of cell membranes is crucial for the survival of plants. Leakage of electrolytes from the cell has long been used as an indicator of membrane damage. The application of Si has been shown to decrease the leakage of electrolytes in drought-/water-stressed plants, such as rice, soybean and wheat Agarie et al. (1998[28]; Pei et al. 2010[19]; Shen et al. 2010[29]), indicating the protective role of Si against membrane damage. Ding (2006[30]) investigated the effect of Si on the change of cell structure in drought-stressed wheat leaves. She observed that in the absence of Si, a clear plasmolysis phenomenon occurred. In the chloroplast, the thylakoids became swollen, and the matrix lamella appeared degraded; when Si was fed to the plants, this resulted in a reduction of plasmolysis and improved the chloroplast structure. The improvement of leaf cell ultrastructure was also observed in Si-treated rice plants grown under drought conditions (Ming 2012[31]). Fluidity is a basic and essential characteristic for the function of cell membranes. Huang and Yang (1996[32]) suggested that proper fluidity in mitochondrial membrane was important to maintain its optimal structure. Membrane fluidity is influenced by several factors such as interactions of proteins and lipids (Huang and Yang 1996[32]) and lipid composition Zhang et al. (2002[33]).

Silicon-Mediated Antioxidant Response

ROS (Reactive Oxygen Species) induced oxidation of functional molecules (lipids, protein, etc.) is one of the most damaging processes in living organisms Yordanov et al. (2000[10]); Gill and Tuteja 2010[35]). Numerous studies have shown that Si-mediated plant tolerance against abiotic stress such as salt stress and heavy metal stress is associated with decreased oxidative damage of functional molecules in the cell In drought conditions, Gong et al. (2005[2]) also observed that application of Si increased the chlorophyll and protein contents in wheat. The double bond index of fatty acids, which reflects its unsaturation, was decreased under drought, while it was significantly increased by feeding Si to the plants Gong et al. (2005[2]). Moreover, they found that drought stress increased the level of oxidized proteins, which was depressed in Si-fed plants. These results suggest that supply of Si can decrease oxidative damage of lipids and proteins under drought stress. Si-mediated decrease of lipid peroxidation damage under water stress has also been observed in other plants, such as chickpea, sunflower, soybean and rice (Gunes et al. 2007[36] , 2008[18] ; Shen et al. 2010[29]; Ming et al. 2012a[37]). Under freezing conditions, the increased production of malondialdehyde, the end product of membrane lipid peroxidation, could be depressed by added Si, as observed in barley (Liang et al. 2008[14]). Si-mediated decrease in oxidative damage is attributed to its regulation on the antioxidant defense and decreased level of ROS in plants. Liang et al. (2008[14]) found that, under freezing conditions, addition of Si increased the activities of SOD (Superoxide dismutase) and CAT (Catalase) as well as contents of glutathione (GSH) and ascorbic acid in wheat. They also observed a Si-mediated decrease in H_2O_2 level in the freezing-stressed plants.

References

1. Ashraf M, Harris PJC. Photosynthesis under stressful environments: an overview. Photosynthetica.2013;51:163–90.
2. Gong HJ, Zhu XY, Chen KM, Wang S, Zhang CL. Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Sci. 2005;169:313–21.
3. Hattori T, Inanaga S, Araki H, An P, Morita S, Luxová M, Lux A. Application of silicon enhanced drought tolerance in Sorghum bicolour. Physiol Plant. 2005;123:459–66.
4. Liu P, Yin L, Deng X, Wang S, Tanaka K, Zhang S. Aquaporin-mediated increase in root hydraulic conductance is involved in silicon-induced improved root water uptake under osmotic stress in Sorghum bicolor L. J Exp Bot. 2014;65:4747–56.
5. Chen W, Yao XQ, Cai KZ, Chen J. Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. Biol Trace Elem Res. 2011;142:67–76.
6. Zhu J, Liang Y-C, Ding Y-F, Li Z-J. Effect of silicon on photosynthesis and its related physiological parameters in two winter wheat cultivars under cold stress. Sci Agric Sin. 2006;39:1780–8 (In Chinese with English abstract).
7. Yordanov I, Velikova V, Tsonev T. Plant responses to drought, acclimation, and stress tolerance. Photosynthetica. 2000;38:171–86.
8. Reddy AR, Chaitanya KV, Vivekanandanb M. Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J Plant Physiol. 2004;161:1189–202.
9. Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. Plant drought stress: effects, mechanisms and management. Agron Sustain Dev. 2009;29:185–212.
10. Yordanov I, Velikova V, Tsonev T. Plant responses to drought, acclimation, and stress tolerance. Photosynthetica. 2000;38:171–86.
11. Lobato AKS, Coimbra GK, Neto MAM, Costa RCL, Filho BGS, Neto CFO, Luz LM, Barreto AGT, Pereira BWF, Alves GAR, Monteiro BS, Marochio CA. Protective action of silicon on water relations and photosynthetic pigments in pepper plants induced to water defi cit. Res J Biol Sci. 2009;4:617–23.
12. Aro E-M, McCaffery S, Anderson JM. Photoinhibition and D1 protein degradation in peas acclimated to different growth irradiances. Plant Physiol. 1993;103:835–43.
13. Powles SB. Photoinhibition of photosynthesis induced by visible light. Annu Rev Plant Physiol Plant Mol Biol. 1984;35:15–44.
14. Liang YC, Zhu J, Li ZJ, Chu GX, Ding YF, Zhang J, Sun WC. Role of silicon in enhancing resistance to freezing stress in two contrasting winter wheat cultivars. Environ Exp Bot. 2008;64:286–94.
15. Ahmed M, Hassen FU, Qadeer U, Aslam MA. Silicon application and drought tolerance mechanism of sorghum. Afr J Agric Res. 2011;6:594–607.
16. Hattori T, Inanaga S, Tanimoto E, Lux A, Luxova M, Sugimoto Y. Silicon-induced changes in viscoelastic properties of sorghum root cell walls. Plant Cell Physiol. 2003;44:743–9.
17. Gong HJ, Chen KM, Chen GC, Wang SM, Zhang CL. Effects of silicon on growth of wheat under drought. J Plant Nutr. 2003;26:1055–63.
18. Gunes A, Pilbeam DJ, Inal A, Coban S. Influence of silicon on sunflower cultivars under drought stress. I: Growth, antioxidant mechanisms, and lipid peroxidation. Common Soil Sci Plant Anal. 2008;39:1885–903.
19. Pei ZF, Ming DF, Liu D, Wan GL, Geng XX, Gong HJ, Zhou WJ. Silicon improves the toleranceto water-deficit stress induced by polyethylene glycol in wheat (Triticum aestivum L.) seedlings. J Plant Growth Regul. 2010;29:106–15.
20. Siddique MRB, Hamid A, Islam MS. Drought stress effects on water relations of wheat. Bot Bull Acad Sinica. 2001;41:35–9.
21. Yoshida S. Chemical aspect of silicon in physiology of the rice plant. Bull Natl Agric Sci B. 1965;15:1–58.
22. Wong YC, Heits A, Ville DJ. Foliar symptoms of silicon deficiency in the sugarcane plant. Proc Cong Int Soc Sugarcane Technol. 1972;14:766–76.
23. Matoh T, Murata S, Takahashi E. Effect of silicate application on photosynthesis of rice plants. Jpn J Soil Sci Plant Nutr. 1991;62:248–51 (in Japanese).
24. Gao X, Zou C, Wang L, Zhang F. Silicon decreases transpiration rate and conductance from stomata of maize plants. J Plant Nutr. 2006;29:1637–47.
25. Yin LN, Wang SW, Liu P, Wang WH, Cao D, Deng XP, Zhang SQ. Silicon-mediated changes in polyamine and 1-aminocyclopropane-1-carboxylic acid are involved in silicon-induced drought resistance in Sorghum bicolor L. Plant Physiol Biochem. 2014;80:268–77.
26. Maurel C, Verdoucq L, Luu DT, Santon V. plant aquaporins: membrane channels with multiple integrated functions. Annu Rev Plant Biol. 2008;59:595–624.
27. Agarie S, Hanaoka N, Ueno O, Miyazaki A, Kubota F, Agata W, Kaufman PB. Effects of silicon on tolerance to water deficit and heat stress in rice plants (Oryza sativa L.), motored by electrolyte leakage. Plant Prod Sci. 1998;1:96–103.
28. Shen X, Zhou Y, Duan L, Li Z, Eneji AE, Li J. Silicon effects on photosynthesis and antioxidant parameters of soybean seedlings under drought and ultraviolet-B radiation. J Plant Physiol. 2010;167:1248–52.
29. Ding YF. Mechanisms of silicon-enhancement of drought tolerance in wheat seedlings. MSc thesis, Nanjing Agricultural University; 2006.
30. Ming DF. Regulatory mechanisms of silicon on physiological and biochemical characteristics, ultrastructure and related gene expression of rice under water stress. PhD thesis, Zhejiang University; 2012.
31. Huang Y, Yang F. Physical state change of phospholipids mediated by Ma2+ modulates activity and conformation of reconstituted mitochondrial F0-F1-ATPase. In: Yang F, Wang F, editors. Membrane lipid-protein interaction and its application in medicine and agriculture. Jinan: Shandong Science Press; 1996. p. 1–17.
32. Zhang W, Chen Q, Liu Y. Relationship between H + -ATPase activity and fluidity of tonoplast in barley roots under NaCl stress. Acta Bot Sin. 2002;44:292–6. Zhu JK. Salt and drought stress signal transduction in plants. Annu Rev Plant Biol. 2002;53:247–73.
33. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem. 2010;48:909–30.
34. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem. 2010;48:909–30.
35. Gunes A, Pilbeam DJ, Inal A, Bagci EG, Coban S. Influence of silicon on antioxidant mechanisms and lipid peroxidation in chickpea (Cicer arietinum L.) cultivars under drought stress. J Plant Interact. 2007;2:105–13.
36. Ming DF, Yuan HM, Wang YH, Gong HJ, Zhou WJ. Effects of silicon on the physiological and biochemical characteristics of roots of rice seedlings under water stress. Sci Agric Sin.2012a;45:2510–9 (In Chinese with English abstract).