Silicon for Plant Stress Signalling and Defense Responses: Physiological and Molecular Prospective

Aashin Sharma[1]* and Narender K. Sankhyan[2]

[1]Ph. D. Scholar, [2]Head cum Principal Scientist, Department of Soil Science, CSK HPKV, Palampur, HP, India-176062

Corresponding Author
Aashin Sharma
Email: aashinsharma20@gmail.com

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ABSTRACT

The increase in world's population is accompanied with increase in demand for food. Climate change worsens the situation by making plants more prone to abiotic and biotic stresses. The defense responses produced by plants against various stresses are controlled by the stress responsive genes which in turn are regulated by a number of elements. One such inorganic element that plays an important role in upregulating the expression of stress responsive genes is silicon (Si). The beneficial effects of Si on plant growth are attributed to physical, biochemical and molecular aspects. Application of silicon increases the antioxidant enzymes activities, relative leaf water content, improves ionic homeostasis etc. Si increases the activity of defense-related enzymes, antimicrobial compounds production and regulates systemic signalling pathways. Thus silicon has the ability to improve overall plant performance under stress conditions by working at physiological and molecular levels.

INTRODUCTION

The increase in demand for foodgrain is exerting a lot of pressure on our natural resources especially soil as 95 per cent of our food comes directly or indirectly from it. Over the past few years decline in land under agriculture and rise in hunger has also been reported by many organizations. Global warming makes plant more prone to a number of abiotic and biotic stresses. Hence there is a need to understand how plants respond to various stresses at the molecular level in order to develop strategies to combat them.

Types of plant stress:

The word homeostasis has been taken from two Greek words. "Homeos" means similar and "stasis" means stable giving us the meaning of staying the same. Homeostasis is the characteristic of a living system to maintain a stable internal environment. Any factor that causes a disturbance in homeostasis leads to plant stress. Based on the types of stressors stress has been classified as: Abiotic and biotic stress. Abiotic stresses occurs in plants when they are exposed to high or low temperature, deficit of moisture, radiations etc. and biotic stress takes place due to the negative impact of fungus, bacteria, virus or any other pathogen.

Effects on plants exposed to abiotic and biotic stresses:

When plants are exposed to drought conditions they give a floppy appearance, stomata gets closed and reactive oxygen species (ROS) production takes place. Under salinity stress due to the increased osmotic pressure exosmosis takes place. Temperature stress has been classified as low and high temperature stresses. Photosynthesis process is very sensitive to exposure to high temperatures as at high temperature destabilization of enzymes takes place that plays an important role in this process. Chilling and freezing injuries takes place in cold stress conditions. Protein denaturation takes place when plants are exposed to harmful radiations which leads to photoinhibition.

There can be a number of biotic stressors like bacteria, fungi, nematodes etc. Reactive oxygen species (ROS) are produced at an exponential rate upon exposure to stress which affects stability of various biomolecules (lipids, enzymes, DNA etc.) and leads to oxidative damage, reduced photosynthetic and cell proliferation rates.

Plant stress signalling and defense reponses:

Due to sessile nature of plants they cannot escape stress. Plant stress signalling acts an interconnecting link between sensing the stimulus and producing an optimum response. There are three steps in signalling – Reception, transduction and response. Plant produces a number of defense responses. For drought avoidance wax is deposited in cuticle, leaf surface area in decreased, deep root system is developed etc. For drought tolerance osmotic adjustment is done by accumulation of osmoprotectants like proline, glycine betaine etc. ABA accumulation also takes place. In salinity stress responses osmoregulation and compatible solutes accumulation leads to resistance to water stress. Salt exclusion and compartmentation leads to resistance to salt toxicity. Under heat stress response heat shock proteins (HSPs) are produced. For heat avoidance transpirational cooling and for tolerance stem reserve mobilization is done. In cold stress response membrane lipid unsaturation, supercooling is done and cold response proteins (antifreeze proteins) are produced.

Defense responses to biotic stresses are classified as structural (lignification, suberization, tyloses, papillae formation) and biochemical (defense related enzymes, antimicrobial compounds are produced and systemic signalling is regulated) defenses. The defense responses produced by plants against various stresses are controlled by the stress responsive genes which in turn are regulated by a number of organic and inorganic elements. One such inorganic element that plays an important role in upregulating the expression of stress responsive genes is silicon (Si).

Silicon for plant stress signalling and defense reponses:

Si, a quasi essential element, constitutes 27.7 per cent of the earth's crust making it the second abundant element after oxygen. It was discovered by John Berzelius in 1823 and is predominantly present in the soil as silica (SiO_2) which is a tectosilicate, highly stable and resistant to weathering so the plant available form of Si i.e. monosilicic acid [H_4SiO_4 or $Si(OH)_4$] is present at very low concentrations. Silicon exists in soil in three forms i.e. solid, adsorbed and liquid forms. Bulk of the silicon is present in crystalline form as primary and secondary silicates. Since silicon is not present in soil in plant available form, fertilization is done by using various sources of Si. The most commonly used fertilizers are potassium and sodium silicate. Industrial by-products like slag and plant based materials like biochar and rice hull ash can also be used. Based on the content of Si in shoots on dry weight basis plants have been categorized as high accumulator having >1.5% Si content e.g. rice, sugarcane, bamboo etc., intermediate accumulator having 0.5-1.5% Si content e.g wheat, maize, sunflower, cucumber etc. Non accumulators have silicon content <0.5% e.g. tomato, beans etc. This difference in accumulation of silicon is based on the presence or absence of certain transporters that play an important role in uptake of monosilicic acid. Lsi1 and Lsi2 are the infux (facilitate passive uptake) and efflux (facilitate secondary active uptake) transporters respectively. When water gets transpired silicon gets polymerized and condensed to form an amorphous from called as phytolith or opal.

After silicon reaches inside the cell through various transporters it leads to the overexpression of genes which are responsible for synthesis of proline, glycine betaine, catalase, peroxidise, superoxide dismutase, late embryogenesis stress proteins, polyamines that play an important role in scavenging of ROS, maintain stability of membrane. Downregulation of sodium transporters and increase in the activity, number of K^+/H^+-ATPase pumps upon silicon application leads to maintenance ionic homeostasis when plants are exposed to salt stress. Silicon increases the activity of defense-related enzymes (polyphenol oxidase, glucanase, peroxidase and phenylalanine ammonia-lyase), antimicrobial compounds production [phenolics, flavonoids, phytoalexins and pathogenesis-related (PR) proteins] and regulates systemic signalling pathways mediated by salicylic acid, jasmonic acid and ethylene.

1. **Silicon for alleviating drought stress:** Under drought stress with the application of silicon photosynthetic rate, transpiration rate, antioxidant enzyme activities increases which decreases the oxidative damage and leads to better germination of seeds and plant growth. Application of sodium silicate significantly increases the chlorophyll content, relative leaf water content as compared to the treatment where no silicon is applied under drought stress conditions (Bijanzadeh et al. 2022). Upregulation of relative expression of transcription factors NAC5 and DREB2A which are involved in drought-responsive gene expression also takes place with application of silicon.

2. **Silicon for alleviating salinity stress:** Silicon application significantly lowers the Na^+ / K^+, improves ionic homeostasis, decreases electrolyte leakage potential, increases net photosynthetic rates when plants are challenged with salt stress and induces tolerance to salinity. Silicon blocks the apoplastic pathway which is important for the uptake of sodium ion which leads to its decreased concentration inside the cell

and facilitates the active uptake of potassium ion through pumps. This results in decreasing the Na^+ / K^+ and promotes better growth of plants (Ali et al. 2021).

3. **Silicon for alleviating heat stress:** Under heat stress conditions the application of silicon leads to enhanced proline and soluble protein content which promotes osmoregulation and makes plants tolerant to stress. Thermotolerance is induced in tomato seedlings through upregulation of genes encoding for antioxidant enzymes (superoxide dismutase and catalase) and heat shock proteins transcription factors (HSFs) with the application of silicon (Khan et al. 2021).

4. **Silicon for alleviating UV radiation damage:** Silicon enhances tolerance to UV-B radiations by significantly increasing anthocyanins and flavonoids content in wheat seedlings. Anthocyanins and flavanoids scavenge ROS and decreases the transmittance of UV photons inside the leaf tissue.

5. **Silicon for alleviating biotic stress**: Silicon application decreases disease index, disease incidence, increases phenylalanine ammonia-lyase and polyphenol oxidase activities. It gets deposited in leaf tissues, increases the rigidity and decreases the digestibility of foliage which prevents the development of pathogen larvae and disrupts the cycle. Higher glucanase and chitanase activity with the application of silicon induces resistance against smut disease in sugarcane. Glucanase and chitanase are important antifungal or PR proteins which prevents the spread of fungus (Deng et al. 2020). Many researchers have also reported the upregulation of disease resistant genes upon the application of silicon.

CONCLUSIONS:

Silicon has the ability to improve overall plant performance under stress conditions by improving various morphological, biochemical and physiological defense responses. At the molecular level, silicon is involved in the regulation of number of stress responsive genes. The application of silicon fertilizers can help to attain better crop growth under stress conditions. However, modern transcriptomic and proteomic studies are required to elucidate the mode of action of silicon. There is a need to focus on the role of silicon in promoting plant growth in field conditions rather than the controlled laboratory environments.

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