



Review

Morpho-physiological dynamics of plants to heat stress and Si induced thermo-tolerance

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Abstract

Heat stress, resulting from global warming, is the foremost abiotic risk to crop development, yield and productivity. Heat stress adversely affects plant growth and development at every stage of their life cycle, from germination to reproductive development, fueling food insecurity. Therefore, sustainable and eco-friendly solutions are needed to make plants resilient to heat stress. Plants respond to heat stress by initiating a series of physiological, biochemical, and molecular response and adapt by activating many stress-responsive genes. Cuticles, helps the plants to reduce the absorption of solar radiation. Intensive transpiration in well hydrated plants also protect the plants from heat stress. Recent findings have established Silicon (Si) as an essential stress relieve element in plants, which protect it against numerous biotic and abiotic stresses. It is involved in root growth, transportation and uptake of essential nutrients, activities of key enzymes, carbon assimilation, enhance ROS scavenging, upregulate the linker histone, and modulates intercellular signaling by triggering phyto-hormones and antioxidant enzymes. Si has indirect effect on the expression of stress-responsive transcription factors and stress-associated genes and proteins like heat shock proteins (HSPs) which is involved in modulating the tolerance of the plant under stress. Technological advancement has enabled the in-depth characterization of Si involvement in flowering, pollen tube growth, and fertilization. Transcriptomic analysis has revealed the large number of Si-responsive transcripts, highlighting its regulatory role at molecular level. In the present scenario, there is a need for developing Si-based technology to enhance plant tolerance against heat stress without compromising plant growth and quality. Therefore, this review focus on the adverse effect of heat stress on plants and highlighted recent advancements of Si induced heat tolerance in plants and how Si can effectively contribute to crop production and act as a bio-stimulant for future-oriented sustainable agriculture under raising threat of climate change.

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Introduction: Plants being sessile face several biotic and abiotic stresses which lead to a substantial reduction in their growth and yield, resulting in global food insecurity, and posing a high risk to global agricultural sector. Stress decrease the average yield of major crops by more than 50% annually¹. Rapid industrialization, urbanization, and deforestation have adversely affected the climate change. Notably, as a response of global warming and climate change, heat stress has become the major limiting factor for the productivity and quality of crop and consequently to the global food security. Global temperature is expected to increase by 0.2°C every decade and is projected to reach 1.8-4.0°C higher than the current levels² and 3-4°C rise in temperature will reduce the crop productivity by 15-35%³⁻⁵. As the rise in temperature, even by a single degree beyond the threshold level, is considered heat stress in plants. Regardless of the variations in the heat stress vulnerability of certain plant life stages, heat stress impacts almost all stages from germination, growth, maturity, fertilization, to productivity and yield⁶. Particularly field crops, are highly sensitive to heat stress, and the reproductive stages are more sensitive than the vegetative stage⁷. Predominantly it causes photosynthetic inhibition, cell water status, cell elongation, stomatal characteristics, water movement, membrane fluidity and nutrient uptake which results in inhibition of growth and development. Thus, heat stress affects overall survival of plant, foremost effects of heat stress are illustrated in Fig. 1. Different strategies like breeding, transgenesis, and genome editing have been applied to cope up with heat stress. Plants cope up with the adverse temperature conditions by evolving different tolerance expressions, proteins and enzymes like - expression and activities of heat shock proteins (HSPs), antioxidant enzymes, accumulation of osmolyte, phytohormones, etc. Polyamines, advantageous microbiota, beneficial nutrients, and elements have also been extensively studied to mitigate the adverse impacts of stresses on plants⁸⁻¹¹. However, deployment of stress mitigators to enhance crop resiliency, yield and productivity under heat stress can be an excellent sustainable alternative to counteract the adverse effects of ever-changing climate. Among various nutrients, Si (Si) the second most abundant (27.7%) element on the earth which is not necessary for plant metabolism, and development but has rather got the status of a quasi-essential element due to its strong association and affinity with other ions and its involvement in improving plant vigor in normal as well as various abiotic and biotic stress conditions¹². Like other biostimulants, Si also acts as a booster for the pre-existing defense system of plants. Its supplementation is an effective strategy to mitigate heat stress. Si has got significant research attention in the scientific community owing to its effectiveness against a variety of stresses including heat stress. Si and Si nanoparticles (SiNPs) can be applied using different

methods like seed priming, foliar spray, and soil fertigation¹³.

Various studies report that Si supplementation increase the polysaccharide accumulation in leaves, stabilize the cell membrane, increase the water use efficiency (WUE) of plants, and tolerance level by enhancing plant antioxidant activity^{14,15}. It increases the nutrient and organic acid uptake, restrict the production of ROS (reactive oxygen species), secretes various phenolic compounds, and regulate the phytohormones. Several studies have reported the beneficial role of Si in mitigating heat stress for different crops¹⁶⁻²⁰. Despite potential applications of Si in alleviating several abiotic stresses have been extensively reported, only a few researchers have examined the molecular physiological and morphological mechanisms of heat tolerance brought on by Si applications and there have been just a few reviews regarding the role of Si in alleviating negative effects of heat stress. This review particularly provides a comprehensive and mechanistic mechanisms of Si-induced thermo-tolerance in plants, with a novel emphasis on integrating molecular, physiological, and morphological perspectives that have been underexplored in existing literature. While previous reviews have primarily focused on the general role of Si under salinity or drought conditions, the current article uniquely dissects Si-mediated signaling cascades, transcriptional regulation, and genetic transport mechanisms (Lsi1–Lsi6) that specifically contribute to heat stress mitigation. Structurally, the review progresses from effects of heat stress and morpho-physiological responses of plants, toward Si in environmental compartment (soil-plant) its role in mitigating the heat stress, culminating the molecular, genetic, and morphophysiological adaptations of plants toward heat stress. Collectively, this work establishes a transdisciplinary foundation to guide integrative research aimed at enhancing crop resilience under intensifying global warming scenarios.

2. Effects of heat stress- Plants morphological, physiological and molecular response under heat stress: Constant high temperature led to an array of morpho-physiological, biochemical and anatomical changes in plants, which affect the growth and development of plant leading to drastic reduction in economic yield. Heat stress may cause either direct or indirect injury to the plant. Direct effect involves the rapid and increased membrane fluidity as well as aggregation and denaturation of proteins. While indirect effect involves the enzymes deactivation in mitochondria and chloroplast, protein synthesis inhibition and degradation. Both, direct and indirect result in cell injury or even death. Photosynthesis is the most-thermo-sensitive part of plant function, high temperature reduced the photosynthesis, induced the production of reactive oxygen species (ROS), adversely affect the reproductive processes, including pollen germination and pollen tube growth, ovule viability, stigmatic and style positions, number of

pollen grains retained by the stigma, fertilization and post-fertilization processes, and growth of the endosperm, proembryo, and fertilized embryo. Furthermore, heat stress also effects microtubule organization. It breaks and/or lengthens spindles, promotes the development of microtubule asters in mitotic cells, and lengthens phragmoplast microtubules. Additionally, excessive heat impairs the production of osmoprotectants such as soluble sugars, proline, and heat-shock proteins (HSPs), which are known to protect cellular organelles from heat-induced dehydration. Ineffective plant growth and production could result from the combined effects of all these changes^{2,21,22}.

2.1. Morphological response: High temperature and extensive radiative affect the growth and yield of plant;

2.1.1. Growth: The first attribute of growth is germination which is highly sensitive to heat stress. Heat stress apparently causes the leaves and twigs scorching, inhibit the growth, change the color of leaves and fruits, sunburn, and leave senescence etc. High temperature affects the seed and pollen grains germination, formation of anther, and pollens, and affect the pollen tubes elongation. Some of the major impacts of heat stress documented in various cultivated plant species are reduced germination, poor seedling vigor, abnormal seedlings, reduced growth of plumule and radicle of germinated seedlings, and poor plant emergence etc. Loss in cell water content, reduced cell size and growth are the ultimate response of high temperature. Decrease of net assimilation rate (NAR) is another reason for reduced relative growth rate (RGR) under high temperature that has been confirmed in maize, sugarcane, and millet by various researchers. In sugarcane, under heat stress, morphologically, drying and rolling of leaves, destruction of leaf tips, margins, and symptoms of necrosis has been observed. Heat stress seriously affects the phenology, plant water relation, shoot extensions, portioning and growth in common bean. Due to heat stress (28/29°C), decrease in total biomass, extended leaves, and elongated stems are some sudden reported impacts, in some plant species^{23,24}. In rice plant high temperature decrease the number of florets and spikes per plants, in sorghum affect negatively on seed set, anther and pollens are more susceptible to heat stress than ovule. Moreover, high temperature significantly affects the net assimilation rate, internodal length, accumulation of biomass, and growth in sugarcane and maize^{25,26}. In wheat, extreme high temperature i.e., 45°C, strictly prohibit the wheat germination rate, decrease the number of tillers, reduce the green leaf area, and productive tiller plants, consequently, leads toward cell death^{27,28}.

2.1.2. Yield: Minimum increase in temperature 1-1.5°C, pose an adverse impact to crop yield. High temperature reduces the yield via affecting the phenological development process Table. 1. In various crop plants, like pulse (e.g., chickpea,

cowpea), cereals (e.g., rice, wheat, barley, sorghum, maize), and oil yielding crops (mustard, canola) etc. due to high temperature yield reduction has been reported²⁹⁻³¹. Elevation of seasonal average temperature by 1°C reduce the yield of grains in cereals crops by 4.1% to 10.0%³². In rice plants, at the temperature of 35–40°C, the weight of grain decreased by 7.0%–7.9%. The highest observed yield reduction was 35.3% to 39.5%³³. In *O. sativa* temperature of 32°C reduces the length and width of grain by 2% and increased the sterility of spikelet by 61%, and concentration of nitrogen in grain by 44%. All these factors reduce the yield by up to 90%³³. In wheat, high temperature affects the maturity stage, decreases the single kernel weight, and ultimately decrease the grain yield. Heat stress decreases the size and weight of filled seed by 51% and 53% respectively and consequently decrease the yield³⁴. Heat stress of 30°C decreases the stem yield by 89%, and overall, by 52% in canola³⁵. Heat shocks or stress impacts the quality and performance of crops. Under heat stress, characteristics of barley grain change significantly. Heat stress also reduces the content of carbohydrates, fructose, starch, and lipids etc. in barley³⁵. In reproductive phase, quality and yield of cereal crops reduced substantially due to heat stress. Heat stress decreases the starch, protein, and oil content. Literature reports a substantial reduction in the total number of grains, and grain weight of wheat and rice plants, studies also reveal that tillering is extremely sensitive to high temperature. High temperature also affects negatively on the yield of peanuts and common beans. In tomato heat stress affects the fertilization, meiosis, and the growth of embryo. The extent of damage cause by heat stress depends on the severity of stress, and growth stage of crop. Generally, reproductive phase is highly sensitive to heat stress and results in the extreme or significant yield reduction³⁶.

2.1.3. Reproductive development: Heat stress poses adverse threat to reproductive tissues; reproductive tissues are more susceptible and sensitive to heat stress. During flowering stage, a few degrees increase in temperature decrease the yield of entire crop or result in total loss of crop³⁷. Short term heat stress can result in a substantial decrease in floral buds. Plants may not produce flowers, fruit, or seed upon the elevation of temperature at reproductive development stage. High temperature negatively affects the meiosis, impaired the growth of pollen tube, effect the germination of pollens, decrease the ovule viability, disrupt the fertilization process, restrict the growth of endosperm³⁸. Furthermore, heat stress at heading stage substantially decreases the rate of pollen fertility, decrease the pollen number on stigma, reduce sterile seed and spikelet fertility in rice. In rice plant high temperature often leads toward extensive production of ethylene and consequently to male sterility of rice pollens. This ethylene inhibits the crucial enzyme involved in sugar starch metabolism. In wheat plants, high temperature significantly decreases the nod of

spikelet and fertile floret, and ear length, which ultimately decreases the grain yield³⁹. In soybean heat stress reduced the pollen viability, result in flower abortion, lower seed numbers, abscission, and negatively affect the young pods and developing seeds⁴⁰.

2.2. Physiological response: High temperatures adversely affect crucial physiological processes, particularly photosynthetic efficiency, which is a key indicator of photosystem functionality. Essential physiological parameters affected by the heat stress include the maximum quantum efficiency of photosystem II (PSII), stomatal conductance, and transpiration rate.

2.2.1. Photosynthesis: Inhibition of rubisco enzyme is the foremost consequence of heat stress, combine with the reduction of chlorophyll content and PSII efficiency leading to substantial reduction in photosynthetic activity⁴¹. High temperature decreases the biosynthesis of chlorophyll in plants, ultimately inhibition of biosynthesis deactivates the various essential enzymes and decreases the accumulation of chlorophyll⁴². In cucumber chlorophyll biosynthesis at 42°C was decreased by 60%⁴³. Maintenance of CO₂ assimilation, and gas exchange parameters, directly correlates with the heat tolerance under heat stress⁴⁴. Heat stress significantly reduces the essential enzyme involved in the biosynthesis of pyrrole in wheat. In highly developed leaves, high temperature rapidly degrades the chlorophyll “a” and “b”. Deterioration of photosynthetic pigments ultimately leads toward oxidative damage. Heat stress extensively damages the thylakoid, and stroma. PSII activity also gets partially terminated because of heat stress. Oxygen evolving matter also get affected. In barley and wheat, heat stress damages the different components or constituents of PSII. Disruption of electron under heat stress inhibits the photosynthesis process in cotton plants. High temperature also inhibits the photosynthetic activity in rice plants as well. Photosynthetic activity reduces as the decline in leaf nitrogen occurs, and chlorophyll pigments get damage. Under heat stress, enzymes get denature or activity of important enzymes get affected, ultimately, starch and sucrose synthesis also get highly affected. Decrease in the activity of carbon dioxide binding enzyme reduces the net photosynthesis in numerous plants i.e., wheat, barley, maize, spinach³⁶. Studies demonstrate consistent reductions in both photosynthesis rate and PSII maximum quantum yield (Fv/ Fm) across species: photosynthesis decreases by 16.6% in maize, 20% in tomato, and 16% in Arabidopsis⁴⁵⁻⁴⁷.

2.2.2. Stomatal and transpiration responses to heat stress: Stomatal conductance is crucial physiological response in regulating gas exchange and transpiration. Literature show it exhibits the most pronounced increase under high temperature, with barley cultivars demonstrating a 50–80% rise after 5–15 days of exposure to 28°C and 38°C⁴⁵. Similarly, other species also demonstrate an increase to varying

degrees, short-term heat exposure typically enhances stomatal conductance, however, prolonged stress often leads to their decline⁴¹. To cope up with the stress some plants temporarily increase the stomatal opening for evaporative cooling while other rapidly close to conserve water⁴⁸. However, stomatal closure prevents dehydration, it simultaneously limits CO₂ uptake, decrease photosynthetic efficiency and carbon assimilation⁴⁹

2.2.3. Nutrient and water uptake efficiency: Under temperature changing situations, nutrient and water status of plant is primarily essential. As an adaptive reaction, plants try to stabilize the water content of their tissues under heat stress. In limited water availability, the increase in temperature is proves as fatal for plant. Sugarcane, when exposed to heat stress, rapid decrease in water content of tissues was observed⁵⁰. Root conductance also gets adversely affected under high temperature. In tomatoes, under high temperature studies have reported the decrease in root conductance and water content. Water loss is greater during daytime, due to high transpiration rate, and ultimately affects the physiological process of plants. High temperature also affects the root growth and consequently the availability of nutrients and water. Furthermore, heat stress significantly reduces the enzymes involve in metabolism of nutrient i.e., nitrate reductase⁵¹.

2.3. Molecular response: Plants undergo an intricate molecular response to maintain cellular homeostasis and ensure survival. The first line of defense involves the rapid induction of heat shock proteins (HSPs), which function as molecular chaperones to prevent protein denaturation and assist in refolding misfolded proteins. Heat shock transcription factors (HSFs) play a central role by sensing temperature elevation and activating the expression of HSP genes. In addition, reactive oxygen species (ROS) levels rise under heat stress, triggering antioxidant defense systems involving enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) to minimize oxidative damage. Calcium signaling and mitogen-activated protein kinase (MAPK) cascades are also activated, transmitting stress signals to the nucleus and modulating stress-responsive gene expression. Furthermore, changes in hormone balance, particularly involving abscisic acid (ABA) and ethylene, regulate stomatal behavior and stress adaptation. Collectively, these molecular adjustments enable plants to stabilize proteins and membranes, modulate metabolic pathways, and re-establish physiological balance under elevated temperatures. Water loss, due to rise in temperature causes oxidative stress comprises of single oxygen (O₂), superoxide radical (O₂⁻), hydrogen peroxide (H₂O₂), and hydroxyl radical (OH⁻). Active oxygen species perform the role of catalyst for oxidation of membrane lipids and destruction of pigments, hydroxyl radicle product of Haber–Weiss reaction may destroy chlorophyll, protein, DNA, lipids by

reducing the efficiency of plant metabolism, decreasing growth and final yield. However, many signaling molecules such as melatonin and ABA interplay can enhance the antioxidant capacity of cells under stress environment⁵².

3. Adaptations of plants toward heat stress

3.1. Morphological and phenological adaptations of plants toward heat stress:

Plants vary greatly in terms of response and tolerance to heat stress. Plant mechanisms involve in heat stress mitigation are illustrated in Fig. 2. Plants survive heat stress by various tolerance and adaptive mechanisms. In various plant species, under high temperature smaller loss of yield directly relate with early maturation. Protective waxy covering, cuticles, and small hair present on plant forming a thick coat on the surface of leaf helps the plants to reduce the absorption of solar radiation. Leaf blades rolling reduce the solar radiation absorption. Short leaves plants can easily avoid or restrict the effect of heat stress, due to smaller resistance produce by surrounding air boundary. Intensive transpiration in well hydrated plants also protect the plants from heat stress⁵³. Some plant species fulfill their reproductive cycle in cooling time and prevent the effect of high temperature on reproductive development. Leaf rolling of wheat maintain the water efficiency under high temperature. Heat resistance in plants depends upon the seasonal variation some species reflect heat resistance in summer and some in winter. Crop management practice can also help to protect the plants from high temperature i.e., selection of proper sowing method and date of sowing, proper irrigation method, having some knowledge about cultivars and their requirements. Seed priming also protect the plant from heat stress. High temperature effect on fruits can easily be avoided by giving the shade to fruits via foliage⁵⁴. Various species of plants have capability to tolerate the heat stress, heat tolerance is basically, plant's ability to sustain their growth and development under high temperature and produce yield. Plants have developed various mechanisms to sustain their growth and development under high temperature, includes long term adaptation via the process of evolution or short-term avoidance mechanisms. Some essential approaches or mechanisms are embryogenesis proteins, ion transporter, osmo-protectants, and antioxidant defense mechanism etc. Leaf orientation, change in the composition of membrane lipid, and transpirational cooling etc. are some short-term responses, to sudden rise in temperature. Initial stress signal helps the plant to establish stress responsive mechanism, that initial signal can be in the form of osmotic or ionic stress or in the form of change in membrane fluidity⁵⁵.

3.2. Molecular adaptation in plant toward heat stress:

Molecular adaptations of plants toward heat stress involve long-term regulatory adjustments that enhance their thermotolerance and survival under elevated temperatures. Plants reprogram their gene

expression networks to favor the synthesis of protective proteins, such as heat shock proteins (HSPs), late embryogenesis abundant (LEA) proteins, and chaperonins, which safeguard cellular structures and maintain protein stability. Epigenetic modifications, including DNA methylation and histone acetylation, alter chromatin structure and enable stress memory, allowing faster responses upon recurrent heat exposure. Transcription factors such as HSFs, DREB, WRKY, and bZIP families coordinate the expression of stress-responsive genes, while non-coding RNAs fine-tune mRNA stability and translation efficiency under heat conditions. Additionally, lipid remodeling of cellular membranes enhances membrane fluidity and integrity, and metabolic adjustments shift energy flow toward the production of osmoprotectants and antioxidants. These integrated molecular adaptations collectively improve photosynthetic efficiency, stabilize cellular homeostasis, and enable plants to sustain growth and productivity under prolonged heat stress conditions.

4. Si in environmental compartments

4.1. Si in soil environment: During the weathering process of silicious rocks, reserves of silicates and aluminosilicates are formed from the parent material as described in Fig. 3. Solid phase of Si in the soil consists of quartz, silicate crystalline form, secondary clay minerals, and amorphous silica. All these forms are inert and can undergo various chemical and biological process while the agronomically crucial phase of Si is liquid phase. Liquid phase of Si is more complex. In liquid phase Si usually exist as a mixture of monomer or polymer. In monomer form as mono-silicic or monomeric acid, plant can easily uptake mono-silicic form, while in polymer form Si occur as poly-silicic acid. This form poses a significant effect on water holding capacity, soil texture, soil erosion, and adsorption capacity⁵⁶.

4.2. Si in plant environment: Si is absorbed by plants via transpiration, diffusion, metabolic pathway or via aquaporin type channel⁵⁶ as illustrated in Fig. 4. Based on Si uptake and accumulation ability, plants vary greatly. Si is absorbed by the roots and Lsi1 transporter and Lsi2 transporter import the Si in root symplast and then further released it into the apoplast, from root translocate toward the shoots via xylem and to leaves through transpiration stream. Lsi6 transport Si from leaves to silica cells, in rice Lsi3 distributes Si to panicles. NIP2 transporter also helps in the transport of Si and some of them have been cloned^{57,58}. Molecular pathways include activation of antioxidant defense mechanism, uptake of mineral, and development of stress-responsive hormones like abscisic acid (ABA) and salicylic acid as shown in Fig. 5. Roots, stem, and leaves concentration of Si greatly influenced by the pH. Plant species based on Si accumulation has been categorized into three classes i.e., Si excluders (accumulate < 0.5% Si), Intermediate (accumulate 0.5 to 1% Si), and Si accumulators (accumulate Si > 1.0%). *Cyperaceous* and *Poaceous*

species are Si accumulator⁵⁹⁻⁶¹. Rice, maize, wheat are major, most important agricultural crops that can translocate more than 90% of Si from root to shoot. Soluble mono-silicic acid may penetrate through cell membrane and in shoot convert into colloidal silicic acid and finally into silica gel via the process of polymerization. Depending upon the plant species, the concentration of mono-silicic acid in plants vary from 6% to 38%. Si present in cell wall and epidermal tissues range from 15% to 79% as a fine layer of Si. Sugarcane absorbed the highest concentration of Si followed by rice and wheat i.e., 300-700 kg Si ha⁻¹, 150-300 kg of Si ha⁻¹, 150-150 kg of Si ha⁻¹ respectively^{25,62}.

5. Si as a heat stress alleviator: Si is absorbed in plants as silicic acid and monosilicic acid, can easily interact with organic molecules with hydroxyl functional groups. Therefore, Si in bioavailable form can easily bind with macromolecule such as carbohydrates and proteins, especially in its hypervalent form. Si couple with cellular macromolecules like proteins, lipids, and phenols in plants. Plethora of studies have reported the beneficial role of Si in plants mainly in stressed environments⁶³. Generally, Si application to soil enhance seed germination, root and shoot development, photosynthesis, nutrient uptake, nitrogen fixation, secondary metabolism and different growth, development and yield attributes of crops⁶⁴. Khan et al. reported that under normal and heat stress conditions the shoot weights of Si-supplemented tomato plants increased by 61% and 70%, respectively, compared with those of Si-deprived plants. They also demonstrated that Si application significantly improved root morphological traits and root length in tomato plants under both heat stress and normal conditions⁶⁵. Si supplementation also significantly enhances the water potential, stomatal conductance, gas exchange capacity of leaves and formation of epicuticular wax. Si exogeneous application substantially upregulate heat shock transcription factor encoding genes (HSF), e.g., *HSFA1a*, *HSFA1b*, *HSFA2*, *HSFA3* and *HSFA7* in tomato, and *HSFA3*, *HSFA5* and *HSF30* in date palm and heat stress-responsive genes, e.g., *DREB2* and *MAPK1* in tomato through activation of HSPs, which coincided with the reduction of ROS level. Studies hypothesized that Si deposited in the epidermal cell wall (as amorphous insoluble biogenic silica, i.e., silicified cells) of leaves might play a role as low thermal conductor, which could help improve the thermal-stability of cells under heat stress. Studies hypothesize that Si deposited in the epidermal cell wall (as amorphous insoluble biogenic silica, i.e., silicified cells) of leaves might play a role as low thermal conductor, which could help improve the thermal-stability of cells under heat stress⁷. Si significantly enhances the antioxidant activity, mediate the accumulation of phenolics strengthens the cell wall and cuticle, stabilize chloroplast membrane and

photosynthetic pigments, modulate the expression of heat shock protein, maintain protein stability and ionic homeostasis at cellular and subcellular level, improve osmolyte accumulation, and ensure metabolic activity, ultimately regulate the heat stress^{66,67}.

Mainly under high temperature root absorb the Si as monosilicic acid (H₄SiO₄) and transported via aquaporin-like transporters (e.g., Lsi1 and Lsi2) to phyllosphere where it polymerizes to amorphous silica (SiO₂·nH₂O) beneath the cuticle. This way it maintains the leaf temperature and cuticular transpiration. Si at cellular level interacts with plasma membrane proteins and by stabilizing phospholipids minimize the heat induced lipid peroxidation. Where it also maintains the protein folding and prevents denaturation by enhancing heat shock proteins (HSP70 & HSP90) and HSFs. It modulates the hormonal pathway, enhance the D1 protein repair cycle, improve photosystem II (PSII) stability and ultimately sustain the photosynthetic efficiency. Through these mechanisms Si efficiently protects plant cell from thermal damage and ensure physiological function during heat stress^{68,69}. Si is mainly involved in inducing resistance potential of plants against plethora of environmental stresses. The external supplementation of Si is well known to mitigate the heat stress within various plants⁷⁰.

5.1. Role of Si in enhancing yield of different crops: Si has been reported to enhance the growth and yield of numerous cereals and other crops as represented in Table 2. Prabakaran et al., noticed Si positive impact on the yield of rice crop⁷¹. Khan et al., reported that Si increase the growth attribute i.e., leaf/shoot length, leaf/shoot dry biomass, chlorophyll content by 31%, 70%, and 38% respectively⁷². Naz et al., observed that foliar supplementation of Si increases the height of spinach plant up to 27.1 and 21.4 cm, leaf fresh weight by 11.93g, leaf dry weight by 1.15g and root fresh and dry weight by 3.72 g and 0.39 g respectively⁷³. Si seed priming increases the yield of maize plants as reported by⁷⁴. Overall Si application enhances the growth attribute, seed germination, relative water content (RWC), chlorophyll content, and yield of different crops^{67,75}.

5.2. Si influence on signaling network under heat stress: Si exist as silica inside the soil, and have high affinity with oxygen, in plants Si accumulate from roots, toward stems, leaves, and spikes, in different tissues of plants⁷⁷. Si enhance ROS scavenging capability of cells by increasing activity and accumulation of antioxidant enzymes⁷⁸. Expression of transcription factor upregulate using Si. Si upregulate the linker histone, modulates intercellular signaling by triggering phytohormones and antioxidant enzymes. In rice plant, for the transmission of intracellular signals Si induces the leucine-receptor and upregulate the zinc finger proteins homologs (Si-ZFPs) to modulate the growth of plants⁷⁹. Si also enhances the polyprotein essential for photosystem. In rice plants under high temperature,

Si enhance the expression of choline monoxygenase, dehydrin, and DREB2A, NAC5, RING domain containing protein (OsRDCP1). It also upregulates the OsNAC5 expression involved in lipid peroxidation regulation⁸⁰. Moreover, Si also enhance the activity of aquaporin and ultimately, they increase water uptake in sorghum. Si supplementations increase in the antioxidant enzyme activity of salvia splendens, and consequently, it reflects high tolerance toward heat stress. Synthesis of ions also decreased in the Si treated plants⁸¹.

5.3. Si and stress related genes: Transcriptomic and proteomic approaches can help to better understand the proficient role of Si. Several studies documented that plants respond to Si by activating reactive oxygen species or ROS related genes i.e., SOD, CAT, POX, APX etc. and significantly reducing oxidative stress. Si triggers myriads of plant genes under stressful environment Khan et al., report that tomato plant prevents oxidative stress by upregulating antioxidant enzymes and stress tolerance by decreasing superoxide radicles⁸². Si increase the transcription factor and downregulate the ABA and SA biosynthesis genes. Researchers also found that Si efficiently promotes the heat shock proteins (HSP) expression and heat stress responsive genes. TFs are facilitated by regulons and make plant able to tolerate stress. NAC regulons and TFs are well known thermotolerant. Foliar Si promote the growth and development of plant under heat stress. Si also regulate the defense and metabolic pathway associated genes and helps to mitigate the stress. Saha et al., observed increase in expression of heat stress responsive genes and antioxidant enzymatic genes⁸³.

7. Future perspective and conclusion: This study is showing an efficient and clear participation of Si in heat stress mitigation, Si plays an efficient role in promoting the plant growth and development and mediating the heat stress but surprisingly rare literature is available on morphological, physiological, and molecular dynamics of Si in plants under high temperature. Si supplementation increases the quality of grains, growth, and yield of various crops and reduce the temperature induce oxidative damage by activating the antioxidant defence system, synthesis of heat shock proteins, by exogeneous protectants and by accumulation of osmolytes at the different stages of development. Moreover, literature also reveals that Si accumulation in epidermal cell wall give the structural support to plant against heat stress. Si enhance heat stress tolerance by improving photosynthetic performance, tissue water potential, leaf gas exchange capacity, stomatal conductance, and epicuticular wax production. Furthermore, influence of Si in mediating heat resilience in plants is associated with variations in endogenous phytohormone levels as well as modifications in the expression of genes and proteins in response of high temperature. Thus, elucidating Si-mediated heat tolerance in terms of physiological, biochemical, and molecular responses of plants using

integrative OMICS techniques between Si-treated and Si-deprived plants is highly essential. Additionally, the development of heat-stress tolerant plants by manipulating Si transporter gene using overexpression and gene editing techniques, such as CRISPR-Cas9, could open the way for a long-term solution to counteract the negative impacts of heat stress on crop production during climate change problems.

Conflicts of interest: There are no conflicts of interest to declare.

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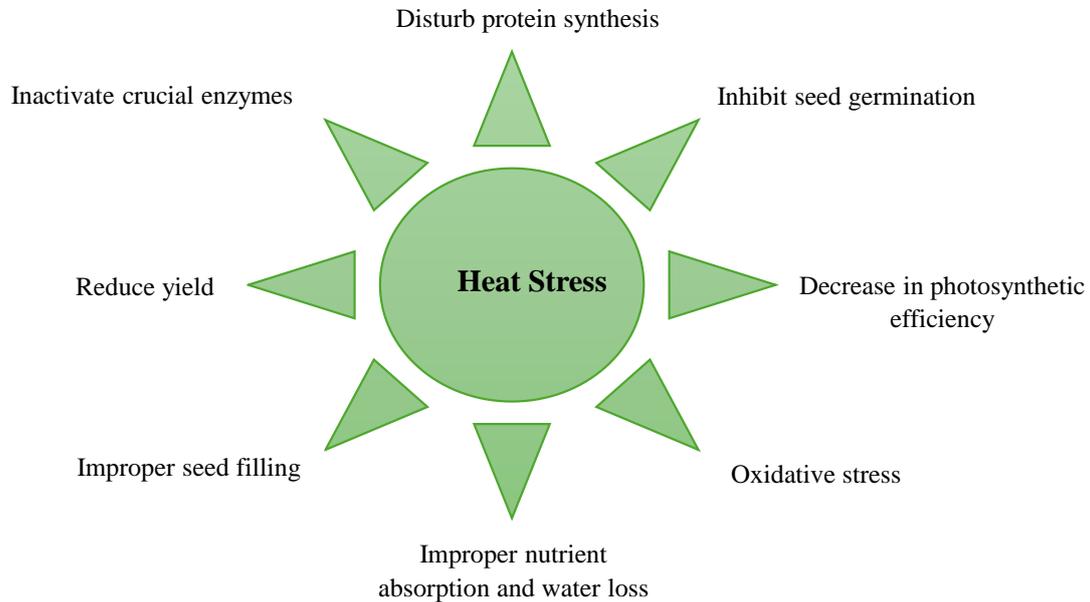
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Fig 1. Toxic effects of heat stress in plants

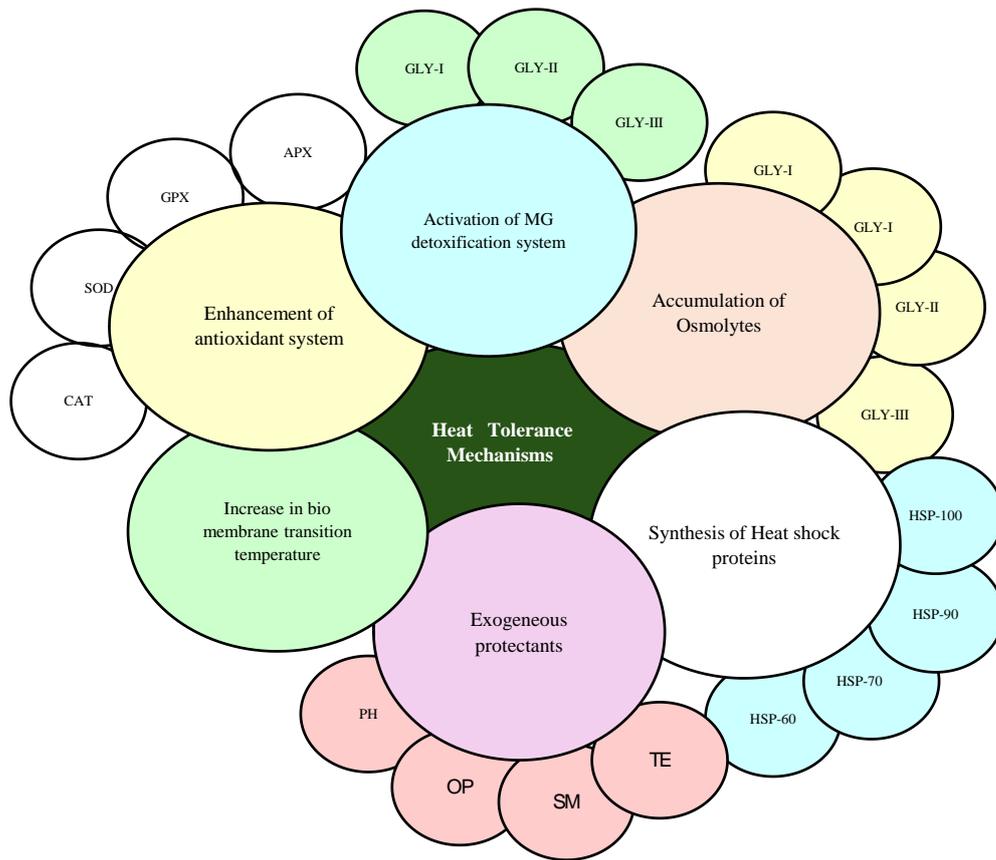


Fig 2. Heat adaptations and tolerance mechanisms in plants

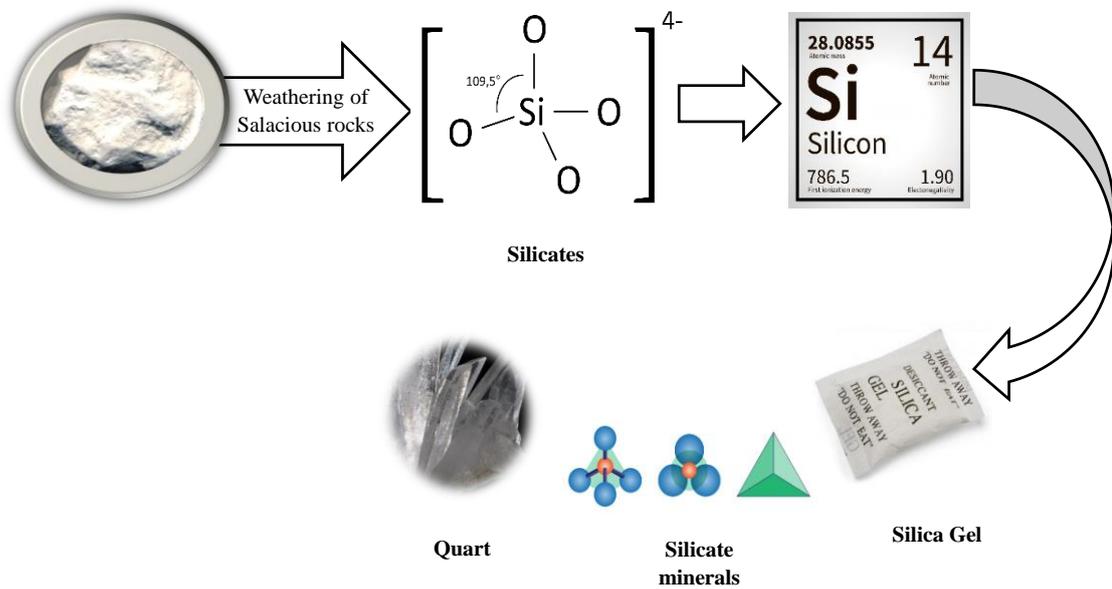


Fig 3. Formation of silicates and aluminosilicates by weathering process of silicious rocks

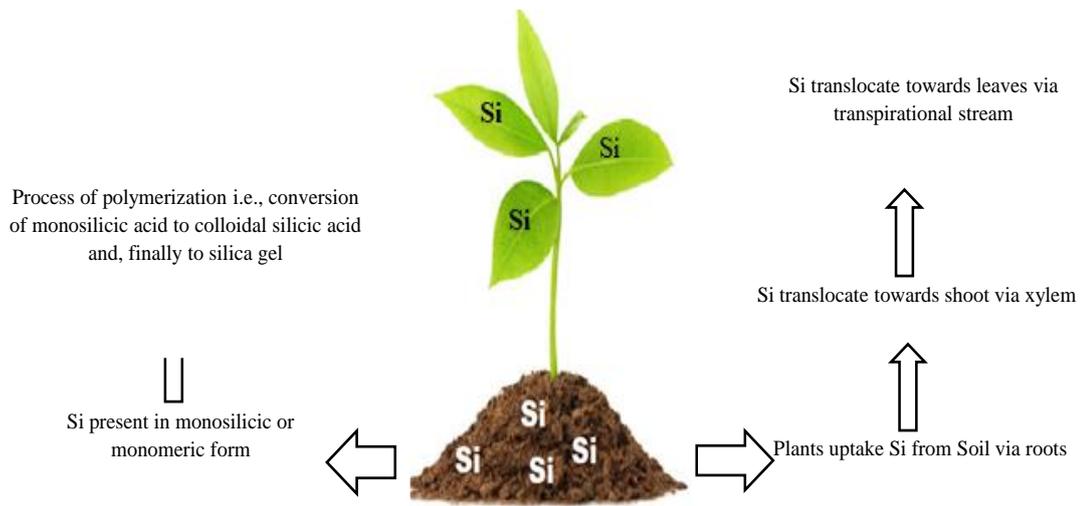


Fig 4. Silicon transpiration route in plants

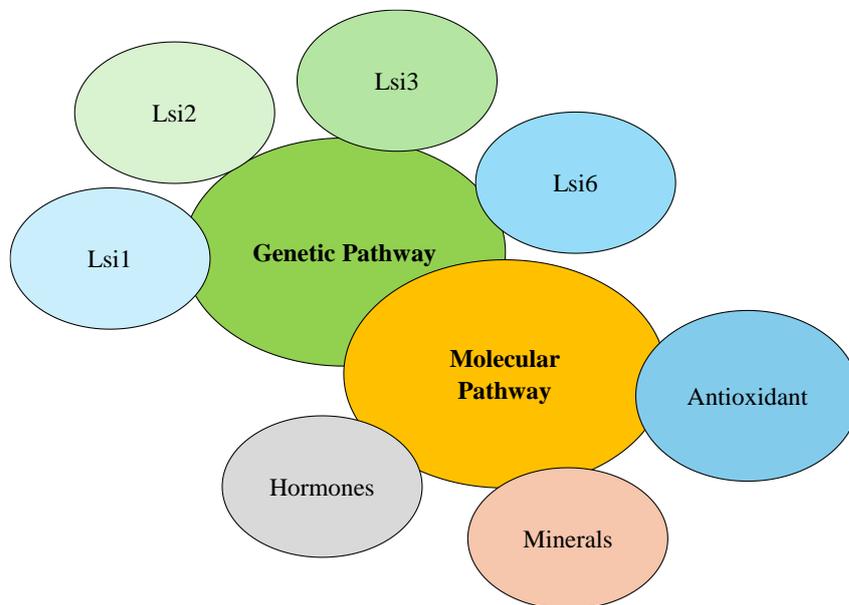


Fig 5. Genetic and molecular pathway for transport and uptake pathway of silicon in plants

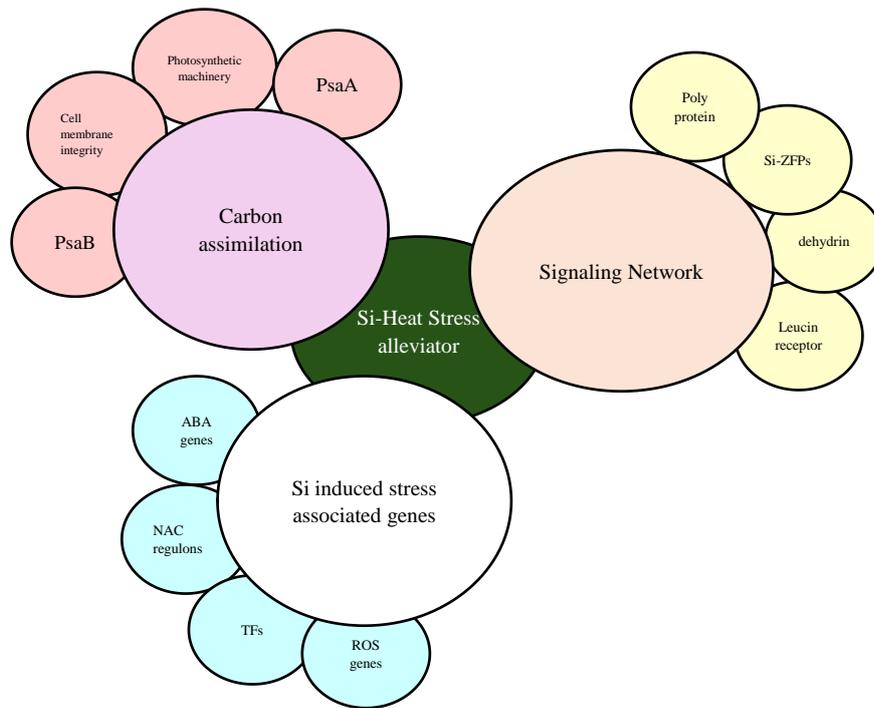


Fig 6. Role of Silicon as Heat stress mitigator

Table 1. Effect of extreme temperature the yield of crops

Crop	Temperature increases up to	Decrease in Yield
Cereal crop	1°C	4% to 10%
Rice plant	35–40°C	35.3% to 39.5%
O. sativa	32°C	90%
Canola	30°C	89%

Table 2. Beneficial effects of Si on the crops

Plant Specie	Heat stress condition	Mode of regulation	Growth attribute					Chlorophyll Content/Photosynthetic attribute	Relative Water content	Si induce protective mechanisms	Reference
			leaf /Shoot length	leaf/Shoot dry weight	Root length/root fresh weight	Root dry weight	Plant Fresh weight				
Tomato (Solanum Lycopersicum)	43°C 6h	Increase (Upregulation)	31%	70%	41%	28%	62%	38%	20%	Enhance antioxidant enzyme activity and reduce ROS	14
Soyabean	30°C 25days	Upregulation		13.62%		41.70%		43.79%		Enhance antioxidant defence system, proline and osmoprotectants	76
Date Palm	44°C 6h	Upregulation	35.10%	100mg	14.10%	42mg	2.68%	25mg/g	80%	Enhance antioxidant defence system, Prevent ROS, and alleviate heat stress induce negative impacts	18
Spinach	35°C 15days	Upregulation	13.5cm	0.96g	3.36g	0.39g	20.40%	158%	77.22%	Enhance osmolytic attributes and antioxidant enzyme activity	73