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Silicon in Plants: Molecular and Genetic Approaches Under Abiotic Stresses

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Abstract

Sustainable production of agriculture encounters significant challenges due to unpredictable and unfavorable environmental conditions. The incorporation of mineral components has become a fascinating and remarkable phenomenon distinct from the utilization of conventional and applied methods to alleviate abiotic stress condition. Use of silicon (Si) is the second most abundant element in the earth's lithosphere and plays a crucial role in the cellular and developmental processes of plants. Silicon (Si) is linked with improved germination, development, photosynthesis, gas exchange, photosystem efficiency, and yield characteristics in stressed and unstressed plant conditions. The beneficial effects of silicon are more prominent in silicon accumulating plants, particularly when exposed to various abiotic stress conditions. Silicon exhibited ameliorating effects on many abiotic stressors, including salt stress, drought stress, high temperature, and low temperature. Applying Si exogenously induces alterations in morpho-physiological and biochemical traits. Silicon occurrence and source, uptake accumulation and transportation are discussed in this chapter. Furthermore, efforts have been made to investigate the role of silicon-mediated improvements through genetic and molecular approaches including genomics and transcriptomics, proteomics, silicon nanoparticles and genome editing techniques. The objective of this chapter is to investigate the role of silicon in alleviating the adverse effects of abiotic stressors.

1. Introduction

Silicon is a versatile quasi-essential component and is considered the second most plentiful component in soil. Si is considered an effective stimulant for promoting plant development and growth under stress when taken at the correct dose (Malhotra and Kapoor, 2019, Ahanger *et al.*, 2020, Singh *et al.*, 2020). Silicon is not an essential element but improves plants' quantitative and qualitative characteristics, particularly when exposed to environmental stress including salt, drought, and heavy metal toxicity. Stressed plants exhibit the benefits of silicon more readily than not stressed plants (Cooke and Leishman, 2016). Furthermore, Si is a "multitalented" element that may improve soil quality and plant nutrient levels (such as nitrogen, potassium and phosphorus). Its superiority as a fertilizer makes it ideal for promoting environmentally friendly farming practices (Zhou *et al.*, 2017). Whereas,

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since the 1840s, small and marginal farmers have directly supplied Si in their fields as regular fertilizer that is non-corrosive, non-polluting, and has favorable effects on the economy and the environment. The International Plant Nutrition Institute has changed the position of Si from "useful but non-mandatory" to "Semi-essential" due to its beneficial effects. Si is an "anti-stress agent" and promotes plant growth and development. Si lessens the effects of reactive oxygen species detoxification, noxious metal ion immobilization and compartmentalization, altered water and nutrient uptake, altered expression of genes and phytohormone biosynthesis, preserved osmotic potential and formation of the double Si-cuticle layer. Additionally, Silicon enrichment has emerged as the most economical and ecofriendly method because it is non-corrosive and non-polluted (Mehta *et al.*, 2020). The world's population is around seven billion, expected to grow by 10 billion in the next fifty years. One of the significant constraints is food security. Current statistics in agricultural production show that soil fertility is decreasing due to the overuse of natural resources, inappropriate use of pesticides, and the absence of suitable soil management methods (Malhotra and Kapoor, 2019). Abiotic stress is one of the most significant barriers to global agricultural productivity (Meena *et al.*, 2017). The unpredictable climate conditions have made abiotic stress more prevalent and challenging. The incidence and intensity of several abiotic stresses have augmented due to climatic change which has significantly decreased crop productivity (Carmen and Roberto, 2011). As a result of the degradation of land, the adverse effects on agriculture, the loss of biodiversity, and the impact of non-living factors, it has been reported that crop yields have decreased by over 70% (Malhotra and Kapoor, 2019). Abiotic stresses, including drought, floods, high and low temperatures, and heavy metal toxicity, are the principal factors limiting agricultural production (Shrivastava and Kumar, 2015).

2. Silicon and Plants

Previous studies suggested that plants do not require silicon as an essential element. However, challenges in cultivating plants without silicon led to the realization that this presumption was false, and Si was identified as a necessary component for the development and growth of the plant (Malhotra and Kapoor, 2019). Silicon's impact on higher plants is often associated with different features of plant morphology, physiology, and molecular processes, making it a valuable element for plant growth and maturation (Ma, 2004, Lobato *et al.*, 2009). Silicon deficiency can result in various irregularities in a plant's growth, reproduction, and overall development, thus acting as a quasi-essential element for plants. A good source of silicon is thought to be the sand that is put into rice fields in southern India at a rate of two to three tones/acre, once every two or three years. As a result of its capacity to improve rice growth and productivity, silicon is recognized in Japan as an essential element for rice production. Plant protection against diseases, insect attacks, and poor climatic conditions is improved by silicon nutrition (Guntzer *et al.*, 2012, Dallagnol *et al.*, 2011, Liu *et al.*, 2014).

2.1. Silicon level in Plants

The amount of silicon in plants differs significantly, with concentrations ranging from 0.1% to 10% of the dry weight of the plant (Balakhnina and Borkowska, 2013, Malhotra and Kapoor, 2019). (Malhotra and Kapoor, 2019) reported that there are three categories of Si absorbers: sugarcane, rice, wheat, and millet are examples of silicon accumulator plants that also accumulate significant amounts of silicon. Snapdragon is an example of a silicon non-accumulator plant. A plant that falls under the "silicon excluder" category has a silicon concentration below 0.5% and Si to Ca ratio below 0.5. In contrast, a plant that falls under the "silicon accumulator" category has a silicon concentration above 1% and a Si to Ca ratio over 1. Plants that do not fit these requirements are classified as intermediate plants. Monocotyledonous plants, like sugarcane, maize and rice, absorb silicon more pronouncedly than dicotyledonous plants, primarily because they have silicon transporters (Ma *et al.*, 2016). More silicon is accumulated in the aerial plant parts than in the roots. Older leaves had higher concentrations of silicon than younger leaves because plants' silicon content increases with age (Henriet *et al.*, 2006).

2.2. Silicon: Occurrence and Sources

According to the number of sources, parent rocks that have experienced intense chemical and physical weathering processes are the primary source from which the soils receive their element composition. According to the data analysis, silicon, with a quantity of 27.7%, is the 2nd most prevalent component in the earth's crust after oxygen (Mitra, 2015, Malhotra and Kapoor, 2019). Si has been deposited in the earth's crust as sand, sandstone, and quartz (SiO_2) (Malhotra and Kapoor 2019). The most effective form is silicic acid (H_4SiO_4), an uncharged molecule that is easily obtainable by plants and has significant variations ranging from ten ppm to over hundred ppm (Liang *et al.*, 2015, Zargar *et al.*, 2019). The amount of Si in soil-based solutions is comparable to that of macro elements, including calcium, phosphorus, and potassium (Malhotra and Kapoor, 2019). The amount of silicon in the soil varies depending on the soil type, with sandy soil carrying more silicon than clay soil. The amount of silicon in soil ranges typically from fifty to four hundred grams per kilogram of soil (Malhotra and Kapoor, 2019). Several variables affect silicon solubility in soil, including irrigation water, silicon fertilizer particle size, temperature, pH, organic complexes, moisture, and amounts of Fe, P, and

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Al ions, besides occurring dissolving reactions (Mehta *et al.*, 2020).

Hence, Si concentration varies significantly between plant species and within species, and this directly depends on the roots' capacity to absorb Si (Malhotra and Kapoor, 2019). Compared to oxygen, silicon makes up 27.7% of the earth's surface, but it is uncommon to find Si in its uncontaminated form (Mitra, 2015). In the earth's crust, silicon is deposited as sandstone, quartz (SiO_2), and quartz (Rédei, 2008). Agricultural wastes containing considerable amounts of silicon can be applied to growing fields to boost crop yield, including furnace ash, steel slag, rice straw bagasse, silicate slag and lignite fly ash (Kalra *et al.*, 2003). One of the most popular silicon fertilizers is calcium silicate, produced as a by-product of phosphorus manufacturing. Although potassium silicate is expensive, it is highly soluble and works well in hydroponic cultures for research purposes. Silica gel, calcium silicate hydrate, and other forms of silicon have all been employed in commercial applications.

2.3. Silicon: Uptake, Transportation, and Accumulation

According to the literature, lateral roots actively take silicon as neutral, monomeric mono silicic acid, Si with amounts between 0.1 and 0.6 mM (Rao and Susmitha, 2017). The physiological pH and water content significantly impact mono-silicic acid's ability to pass the cell membrane of the lateral root (Raven, 2001). Water is the carrier for its uptake and dissemination; nevertheless, both molecules differ in size (Exley *et al.*, 2020). As a result, the rate of Si adsorption and water uptake has been divided into three categories in higher plants; (1) active, where Si uptake exceeds water uptake; (2) passive, where Si uptake is equal to one-fourth of water uptake; and (3) rejective, where Si uptake is less than water uptake (Cornelis *et al.*, 2011, Zargar *et al.*, 2019). For instance, silicon-rich rice plants, OsLSi1, OsLSi2, and OsLSi6, are the three low-silicon rice genes most influencing silicon transportation (Dhakate *et al.*, 2019). The migration of silicon from root cells to the apoplast has been demonstrated to be significantly aided by two particular genes, LSi1 and LSi2 (Rao and Susmitha, 2017) . The OsLSi1 gene is primarily expressed in the basal sections of roots and is a member of the aquaporin NIP-III (nodulin26-like intrinsic proteins) subfamily.

According to expression patterns and cellular localization studies, the $OsLSi_2$ gene, which controls efflux Si-transport, is located on the proximal side of the same cells as the OsLSi1 gene (Yamaji and Ma, 2009, Yamaji and Ma, 2011, Dhakate *et al.*, 2019). The reloading and diffusion of Si into the vascular bundles is shown to be regulated by the rice OsLsi2 gene (Yamaji and Ma, 2011, Ma and Yamaji, 2015). Once mono-silicic acid enters the apoplast, it must be unloaded from the xylem sap to prevent silicon accumulation within the xylem. In this respect, the OsLSi6 gene contributes to the movement of Si from the primary vascular bundles to the panicles (Fang *et al.*, 2011, Rao and Susmitha, 2017) . Hence, It is vital to remember that silicic acid can be produced by both apoplastic and symplastic processes (Exley *et al.*, 2020, Ma and Yamaji, 2015). After effective transportation, silicon is deposited in the vascular bundles, under the cuticle, and in the spaces between cells. A cuticle-silicon double layer is formed by the silicon deposition beneath the cuticle (silicic acid) (Rao and Susmitha, 2017).

2.4. Silicon and abiotic stresses

The only element that can boost a plant's tolerance to environmental challenges is silicon (Malhotra and Kapoor, 2019). According to the literature, Si is vital for photosynthesis, nitrogen (N2) fixation, crop yield and quality, growth enhancement, and protection from abiotic and biotic challenges in plants (Zargar *et al.*, 2019, Ahanger *et al.*, 2020) . Abiotic stresses include salt, high temperatures, UV-B rays, toxic metals and metalloids, mechanical damage, nutrient deficiency, toxicity, and drought (Sharma *et al.*, 2020). Numerous stressors cause oxidative, osmotic, and ionic disturbances in plants, which change their physiological and metabolic processes and produce reactive oxygen species (Sharma *et al.*, 2020, Mehta *et al.*, 2020). As a result, plant development and net productivity are hindered, impacting the economy as well as the farmer's fields, revenue, and profits (Sharma *et al.*, 2020).

The development and productivity of crops are adversely impacted by drought, a major abiotic factor (Bodner *et al.*, 2015). Drought poses a severe hazard to the planet's plant populations. Since it affects both a plant's morphology and physiological processes (Mehta *et al.*, 2020). Drought stress impacts physiological and metabolic activities such as photosynthesis, transpiration, stomatal conductance, growth rate, root/shoot ratio, and grass quality (Saud *et al.*, 2014). Drought or a lack of water results in stomatal closure, decreased transpiration, reduced water potential in plant cells, reduced photosynthesis, and eventually limited plant growth (Yordanov, 2003). Silicon application reduces the adverse effects of drought by increasing photosynthesis, the total water content of leaves, chlorophyll content and turf's growth rate by forty-four per cent, thirty-three per cent and forty-two per cent, respectively (Saud *et al.*, 2014). (Malhotra and Kapoor, 2019) reported that, during drought stress, silicon incorporation in the cell wall decreased transpiration and increased internal water storage. The hydrophilic property of $SiO_2.nH_2O$, which maintains the water in plant tissues and protects plant tissues from dehydration, might be responsible for silicon's ability to reduce the effects of drought stress (Gong *et al.*, 2005). Many plants have shown that Si is useful in reducing the effects of drought stress. For

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instance, exogenous Si supply regulates xylem channel structure, leaf structure, and water potential (Gong *et al.*, 2005). The transcriptome analysis has also demonstrated reduced abiotic stress by silicon augmentation to involve plant antioxidant metabolism. (Ma *et al.*, 2016) reported that Si decreased H_2O_2 and enhanced the activation of antioxidant enzyme genes (such as TaSOD, TaCAT) in wheat under water shortage.

According to (Wang *et al.*, 2015), silicon-treated plants had much higher root-to-shoot ratios than untreated plants. This was because silicon-mediated root morphology changes boosted silicon-treated plants' capacity to absorb water. According to (Ma and Yamaji, 2015) , the association of silicon with cell wall hemicellulose can enhance the structural stability of plants and provide benefits during water scarcity conditions. Exciting research was conducted to investigate how tomato varieties are drought resistant and drought susceptible responses to the addition of extrinsic silicon. An increase in amino acid biosynthesis was observed in drought-resilient tomato genotypes due to the Si-induced elevation of sulfur (S) and ammonia (NH_4^+) levels. Massive oxidative stress is a problem for Brassica napus. The application of silicon offers protection from antioxidant enzymes, including proline ascorbate-glutathione, glyoxalase and others (Hasanuzzaman *et al.*, 2018).

One of the most critical abiotic stressors on crop plants is salinity. The salinity has degraded almost twenty per cent of the overall arable area (Shrivastava and Kumar, 2015). Plant growth is hindered by salt through ion cytotoxicity, nutrient imbalance, and oxidative damage (Malhotra and Kapoor, 2019). Salinity stress is the only abiotic stress that can potentially reduce worldwide agricultural food crop yield by as much as twenty per cent (Kumar *et al.*, 2022, Hussain *et al.*, 2018). According to the investigation, silicon increases a crop's ability to withstand salt (Malhotra and Kapoor, 2019). Silicon has been linked to the development of salt tolerance in several crucial crops for agriculture including soybean, rice, maize, sorghum, tomato, barley and wheat (Rizwan *et al.*, 2015). Water, soil-bound Si, and mono-silicic acid are all forms of silica that plants can access. Plant cell walls include amorphous silica (SiO_2- H_2O), which interacts with pectin's and polyphenols to increase the stiffness of the cell wall structure. Si is frequently referred to as a "semi-essential" component for plants because monocotyledons have been shown to contain more Si^{4+} than dicotyledons (Kaur *et al.*, 2016).

Under salt stress, silicon (Si) deposition in the cuticle of leaves and epidermal cell walls helps reduce transpiration and avoid plant desiccation. Tomato germination was improved by approximately one mM of nano-Si at 50 mM NaCl, but Momordica charantia germination was improved by 1–5 mM of Si at 50–100 mM salinity (Wang *et al.*, 2010). Several genes, including leDREB-1, leDREB-2, leDREB-3, leLsi-1, as well as leAPX, leSOD, and leCAT, are stimulated to increase expression in tomatoes when they are subjected to salt stress (Ngwepe *et al.*, 2019). In contrast, a brief expression of DREB2A and DREB2B was produced when Arabidopsis was exposed to salt and dehydration (Manna *et al.*, 2021, Singh and Chandra, 2021).

Crop yields are dramatically reduced under heat stress, which has significant economic repercussions and increases the world's food insecurity (Zhou *et al.*, 2017, Raza, 2020). Furthermore, heat stress significantly impacted the development and production of tomato plants (Kumar and Kaushik, 2021, Hasan *et al.*, 2021). Heat stress alters the rate of osmotic potential, which produces an imbalance in water potential, which has a detrimental impact on metabolic pathways and damages tissue. The production of heat shock proteins (HSPs), the activation of ROS-scavenging mechanisms, and the synthesis of certain phytohormones are only a few of the strategies that plants have evolved to survive temperature fluctuations (Khan *et al.*, 2020, Haider *et al.*, 2021, Raza *et al.*, 2021). According to (Khan *et al.*, 2020), Si increases the production of phytohormones, HSPs and the antioxidant system in tomatoes, contributing to the development of thermotolerance. Moreover, it has been found that peanuts' resistance to heat stress is enhanced by small HSPs (Fragkostefanakis *et al.*, 2016). In cucumber, rice and sword fern, exogenous Si administration increased the tolerance to heat stress, improving SL and biomass productivity (Iyyakkannu *et al.*, 2014). Tomato plants treated with Si showed increased expression of the SlLsi1 and SlLsi2 genes, which code for Si transporters, increasing their tolerance to heat stress (Khan *et al.*, 2020).

The effects of cold stress, which includes chilling temperatures of less than 15 degrees Celsius and freezing temperatures below zero, substantially affect plant development and growth (Habibi, 2015). The production of ROS under cold stress harms nucleic acids, lipids and proteins (Suzuki *et al.*, 2012). In order to prevent this, plants have developed several methods to counteract the low-temperature stress and preserve development and growth (Dey *et al.*, 2022). The results of (Habibi, 2015) showed that silicon treatment of leaves successfully reduces the harmful effects of low-temperature stress on grapevine plants. This is accomplished by maintaining the integrity of their bio membranes and minimizing photoinhibition. According to (Qian *et al.*, 2019), Si stimulated the function of CAT, POD and SOD under cold stress, leading to the development of cold tolerance in Phyllostachys praecox. Similarly, Si improves cold tolerance in maize plants during early growth by altering the balance of hormones and micronutrient homeostasis (Bradáčová *et al.*, 2016, Moradtalab *et al.*,

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2018). According to earlier investigations, the Si-induced equilibrium of micronutrients is essential for maize to be protected against cold stress (Bradáčová *et al.*, 2016, Imran *et al.*, 2013). Silicon reduces the effects of cold stress on barley plants by controlling metabolite concentrations and apoplastic enzyme activity in the leaf apoplast (Joudmand and Hajiboland, 2019). Various effects of silicon on the growth and development of a plan are depicted and elaborated in (Figure 1 and Table 1).

3. Molecular mechanism of silicon-mediated abiotic stresses

Furthermore, many other transcription factors are also involved in the reactions to abiotic stress, which is essential for improving the ability of the organism to survive and endure these challenging environmental conditions (Figure 2, Table 2). It was stated that the mechanism involved in how plants interact with drought stress is quite complicated. Abiotic stress causes some genes to overexpress themselves and protect plant cells directly, while other genes are involved in different signalling cascades (Blumwald *et al.*, 2004). Additionally, specific transcription factors (TFs) that can change various stress-inducible genes contribute to



Figure 1. Impact of silicon fertilizer on various aspect of plant growth under abiotic stresses

3.1. Silicon-mediated expression of transcription factors and some associated abiotic stress responsive genes

When subjected to stress stimuli, plants detect the signals and initiate a series of signal transduction pathways, increasing gene expression and leading to metabolic changes that enable the plant to tolerate the stress (Agarwal *et al.*, 2007). Stress responses involve a complex gene regulatory network that may be dependent or independent of the phytohormone ABA. Finally, plant stress resistance is accomplished by ABA through ABA-dependent signaling mechanisms that encourage plants to survive abiotic challenges like water shortage (Cutler *et al.*, 2010, Kim *et al.*, 2010). By activating at least two distinct regulons, such as the regulons known as MYC/MYB (myelocytomatosis oncogene/myeloblastosis oncogene) and AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor), the ABA-dependent signaling schemes improved stress tolerance (Saibo *et al.*, 2009). The ABA-dependent and the ABA-independent pathways, both of which use members of the AP2/EREBP (ERF) family, have been identified as separate pathways for stress response mechanisms (Khattab, 2016).

regulating the plant's response to water scarcity conditions (Bartels and Sunkar, 2005). Some genes are expressed more frequently at the transcriptional level under water stress. It is believed that byproducts of these drought-inducible genes contribute to drought tolerance (Kavar *et al.*, 2008). Depending on the conditions, secondary stresses and damage responses may also contribute to the over-expression of genes (Agarwal et al., 2007, directly prompted by drought stress (Agarwal et al., 2007, Cattivelli et al., 2008). A wide variety of signalling pathways involved in developing stress resilience can also be controlled by the overexpression of transcription factors (TFs). Plant growth hormones have been observed to vary in response to salt stress, and silicon has shown the ability to alter these hormone responses (Lee *et al.*, 2010, Kim *et al.*, 2014). According to (Lee *et al.*, 2010), soybean plants cultivated hydroponically under salt stress showed increased abscisic acid levels, which decreased when silicon was applied. Gibberellin, a different plant hormone, operates oppositely (Lee *et al.*, 2010). According to (Kim *et al.*, 2014), silicon under salt stress led to a considerable reduction in the production of stress- and defense-related

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Table 1. Silicon mitigates major abiotic stress response in various plants

Stress	Plant	Impact of Si supplementation	References
Salinity	*Sorghum bicolor*	Regulation of catalase, peroxidase, and superoxide dismutase (SOD) enzyme limits the absorption of ions through the plants	(Soundararajan *et al.*, 2017, Liu *et al.*, 2019)
Salinity	Barley, Cucumber	Elevated levels of catalase, glutathione reductase, peroxidase, and superoxide dismutase function	(Malhotra and Kapoor, 2019)
Salinity	*Spartina densiflora*	Si substantially boosted the photosynthetic pigments, intercellular CO_2 concentration, stomatal conductance, and net photosynthetic rate.	(Kastori, 2015)
Salinity	Okra (*Abelmoschus esculentus*)	Stomatal conductance, transpiration rate, and stomata size all increased with the addition of Si, resulting in more effective photosynthetic activity.	(Zhu *et al.*, 2019)
Salinity	Lentil (*Lensculinaris Medik.*)	The use of silicon nanoparticles significantly enhanced seed germination and seedling growth.	(Saxena *et al.*, 2016)
Salinity	*Phaseolus vulgaris*	Using silicon led to improved seed weight and a rise in plant yield.	(Parande *et al.*, 2013)
Drought	*Brassica napus*, *Solanum lycopersicum*	Gathering of proline, GABA, and constituents of the ascorbate-glutathione	(Ali *et al.*, 2018, Hasanuzzaman *et al.*, 2018)
Drought	*Triticum aestivum*	Si decreased H_2O_2 and enhanced the expression of antioxidant enzyme genes	(Ma *et al.*, 2016)
Drought	Rice	Silicon use increased the expression of several stress proteins, including late embryogenic abundance proteins and membrane-stabilizing proteins	(Khattab *et al.*, 2014)
Drought	*Brassica napus*	Applying silicon is a successful strategy to lessen the adverse effects of dryness on seed germination.	(Pang *et al.*, 2019)
Drought	Tobacco (*Nicotiana Rustica* L.)	Silicon application improved the biomass, particularly the aboveground components, in drought and control scenarios.	(Hajiboland *et al.*, 2017)
Heat	*Salvia splendens*	By promoting the activity of superoxide dismutase (SOD), guaiacol peroxidase (GPX), and ascorbate peroxidase (APX), the application of silicon increases the tolerance of plants to heat stress	(Kumar *et al.*, 2022)
Heat	Tomatoes	Increases the productivity of phytohormones, HSP, and the antioxidant system	(Khan *et al.*, 2020)
Heat	Sword fern, cucumber, and rice	Improved shoot length and biomass production	(Iyyakkannu *et al.*, 2014)
Cold	*Hordeum vulgare*	Buildup of soluble carbohydrates and various other osmolytes	(Joudmand and Hajiboland, 2019)
Cold	Grapevine	Preserving the integrity of other biomembranes and reducing photoinhibition	(Habibi, 2015)
Cold	Barley	Regulating the apoplastic enzyme activity and metabolite concentrations in the leaf apoplasm.	(Joudmand and Hajiboland, 2019)
Cold	Maize	Altering the balance of hormones and micronutrient homeostasis	(Bradáčová *et al.*, 2016, Moradtalab *et al.*, 2018)

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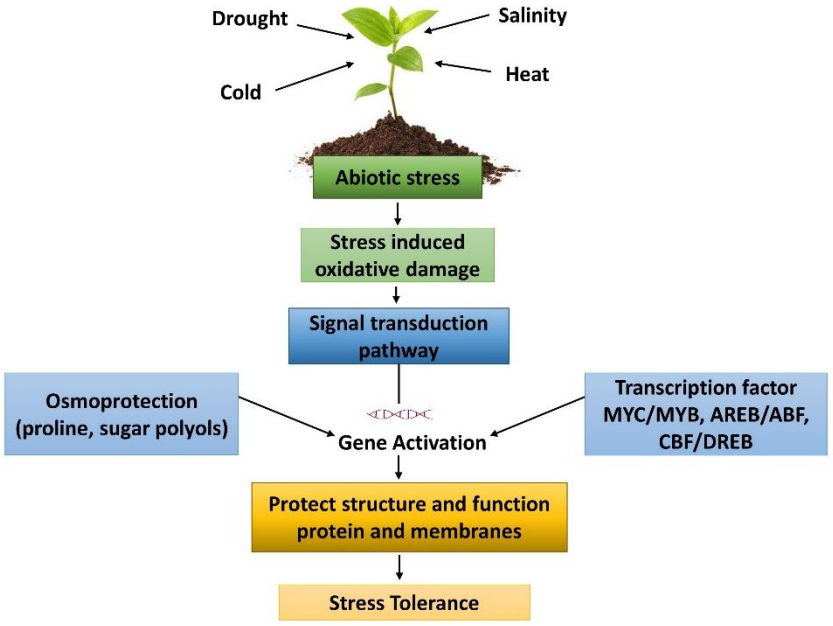


Figure 2. Stress tolerance mechanism of plants against abiotic stress

phytohormones such as jasmonic acid. In contrast, Si-treated plants' ABA levels were significantly greater under salinity stress after six and twelve hours. The genes associated with ABA biosynthesis were up regulated by Si treatment under salt stress after six and twelve hours. In contrast, their expression was significantly downregulated twenty-four hours after Si treatment. At six and twenty-four hours after the Silicon application, OsNCED3 expression significantly increased. According to these findings, prolonging the Si concentrations can control phytohormonal responses and salinity-induced stress. The findings suggest that silicon is critical in improving salt tolerance in these plants by controlling the expression of genes involved in plant hormone production under salt stress.

According to (Liang *et al.*, 2015), the expression of genes responsible for producing ethylene was enhanced in salt-exposed tobacco seedlings treated with Si, resulting in more significant ethylene emission. The tomato seedlings exposed to high salinity showed an increase in the regulation of specific genes such as DREB1, DREB2, DREB3, APX, SOD, and CAT, which are associated with salinity response and dehydration. Genes related to Si transport, such as leLsi-1, -2, and -3, were also upregulated (Muneer and Jeong, 2015). Several heat-resilient genes, including HSFA3, HSFA5, and HSF30 in date palms and DREB2, MAPK1, HSFA1a, HSFA2 and HSFA3, etc. in tomatoes were shown to be highly overexpressed as a result of Si (Khan *et al.*, 2020, Saha *et al.*, 2021) . For instance, (Janni *et al.*, 2020) studied plants' precise molecular response to heat stress to comprehend how they cope with this challenging situation. Their research showed that plants engage conserved pathways, including activating Ca^{2+}-sensing proteins, overexpressing ABA-sensitive genes, stimulating HSP-mediated protein folding, and producing genes involved in ROS scavenging. According to these studies, silicon triggers the synthesis of heat shock proteins (HSPs), which are essential for ensuring proper protein folding, preventing protein denaturation and clumping, and encouraging plants to retain their green characteristics when exposed to high temperatures (Abdelrahman *et al.*, 2017). Additionally, it is stated that these signalling cascades activate HSP genes like folding and stop the formation of non-specific proteins in tall fescue during heat stress. Most significantly, crop plants are protected from the harmful effects of heat stress by activating HSFs and HSPs; Ca^{2+} triggers several signalling pathways, phospholipids, SA, ET, ABA, H_2O_2, and NO (Liu *et al.*, 2015, Sharma *et al.*, 2020). Wheat has evolved several defence mechanisms to protect itself from the damaging impacts of high-temperature stress. This involves the activation of several components, including stress-responsive genes (HSPs, SOD, CAT, APX, GPX, etc.), heat-shock transcription factors (HSF, HSFA6e, etc.), and genes linked to signaling molecules (MAPK, CDPK, etc.). These processes work together to protect vital organelles, tissues, and enzymes from the damaging effects of high-temperature stress. These mechanisms work together to protect essential

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Table 2. Gene expression induced by silicon in plants under different abiotic stress conditions

Stress	Plant	Genes	Gene function/Protein encoded	References
Drought	*Arabidopsis thaliana*	At5g22460	Gene encoding a protein from the Esterase lipase thioesterase family with transporter function	(Mir *et al.*, 2022)
Drought	*Arabidopsis thaliana*	At5g59030	Gene responsible for encoding a protein involved in the transportation of copper	(Carneiro *et al.*, 2017)
Drought	*Oryza sativa*	NM-001074375	Gene that regulate the expression or activity of dehydrin protein	(Khattab *et al.*, 2014)
Drought	*Oryza sativa*	AK070732	Protein that is a member of the RING domain family	(Khattab *et al.*, 2014)
Drought	*Oryza sativa*	AJ578494	Enzyme for choline monooxygenase	(Khattab *et al.*, 2014)
Drought	*Sorghum bicolor*	SbPIP2;6	Aquaporins of the type 2;6 PIP (plasma membrane intrinsic protein) protein.	(Mir *et al.*, 2022)
Salinity	*Lycopersicum esculentum*	leDREB-1	Protein known as dehydration responsive element binding -1 (DREB1) in Lycopersicum esculentum is responsible for responding to dehydration condition	(Ngwepe *et al.*, 2019, Dhiman *et al.*, 2021)
Salinity	*Sorghum bicolor*	Sb10g002070	The arginine decarboxylase enzyme aids in the synthesis of polyamines.	(Yin *et al.*, 2016)
Salinity	*Sorghum bicolor*	SbPIP1, SbPIP2, and SbPIP6	Plants accumulated less sodium (Na+) because silicon altered the expression of aquaporins and improved root hydraulic conductivity	(Lesharadevi *et al.*, 2021)
Salinity	*Arabidopsis thaliana*	DREB2A	Element that is responsive to dehydration condition	(Singh and Chandra, 2021, Manna *et al.*, 2021)
Salinity	*Lycopersicum esculentum*	leDREB-2	Protein responsible for binding to the dehydration responsive element-2	(Ngwepe *et al.*, 2019)
Cold	*Arabidopsis thaliana*	DREB1A	Control growth	(Gujjar *et al.*, 2014)
Cold	*Arabidopsis thaliana*	DREB1B	Control growth	(Gujjar *et al.*, 2014)
Heat	*Triticum aestivum*	HSPs, CAT, SOD	Protect important enzyme, cellular organelles, and other tissues from the harmful effects of heat stress	(Kumar *et al.*, 2022)
Heat	*Lycopersicum esculentum*	HSFA1b, HSFA2, HSFA3	to maintain folding and stop the formation of non-specific proteins	(Khan *et al.*, 2020, Saha *et al.*, 2021)
Heat	*Lycopersicum esculentum*	SlLsi1 and SlLsi2	Silicon transporter gene	(Khan *et al.*, 2020)
Heat	*Lycopersicum esculentum*	SlHsfA7	transcription factor that responds to heat stress	(Khan *et al.*, 2020)

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enzymes, cellular organelles, and other tissues from the harmful effects of heat stress (Kumar *et al.*, 2022). Additionally, these protective mechanisms aid in stabilizing and regulating crucial metabolic processes within the plant (Kumar *et al.*, 2022). Additionally, Si influences the activation of numerous genes, notably transcription factors, to improve resistance to cold stress. Three cold resilient genes, DREB1A, DREB1B, and DREB1C, were temporarily expressed in Arabidopsis due to cold stress, an example of growth regulation in response to cold stress (Gujjar *et al.*, 2014)). Later, it was discovered that OsDREB1 overexpression increased resistance to drought and cold stress (Ito et al., 2006).

3.2. Role of Si on aquaporins

The function of aquaporins, which are quickly and irreversibly impacted by the environment, play a substantial regulatory function in water transportation between cells (Vandeleur *et al.*, 2009)). Aquaporins are a highly conserved family among the primary intrinsic membrane proteins (Tyerman *et al.*, 2002). Plant cells include aquaporins in the plasma and the vacuolar membranes, which play a crucial role in allowing water to pass through these membranes. Hydraulic conductivity and water permeability are regulated by aquaporins in the membrane (Khattab, 2016). The more significant increases in aquaporin activity enhance plant-water relationships and increase stress tolerance. Therefore, under osmotic stress conditions, silicon treatment increased the transcription of numerous root aquaporin genes (Liu *et al.*, 2014). When silicon was applied to sorghum plants under osmotic stress, it enhanced the rate of transpiration and the manifestation of many SbPIP genes (Liang *et al.*, 2015). Si increased the drought resistance of rice, maize, and cucumbers by reducing transpiration. The results of (Malhotra and Kapoor, 2019) show that the expression of aquaporin genes in the roots supports the proper regulation of plant water intake, even in conditions of limited water availability. Silicon can improve the water status of plants under salinity or drought stress by enhancing the expression of genes related to aquaporins. Plants can recover from abiotic stress with the help of improved water status and ion balance. It is commonly acknowledged that silicon can boost nutrient intake by enhancing root activity, raising water uptake, and strengthening the hydraulic conductivity of roots (Malhotra and Kapoor, 2019). Like other stimuli, ABA, ethylene, Ca^{2+}, and reactive oxygen species all impact aquaporin activity (Khattab, 2016, Hu *et al.*, 2012).

According to studies, H_2O_2 and salt stress can decrease aquaporin activity by directly oxidant gating, controlling phosphorylation, promoting aquaporin relocalization, and thus lowering water uptake(Boursiac *et al.*, 2008). The increase in aquaporin activity may be related to the transcriptional activation of aquaporin genes and a reduction in H_2O_2 (Liu *et al.*, 2015). Additionally, it examined whether ABA could work as a catalyst for the transcription factors that help control the expression of aquaporins, a protein found exclusively in the plasma membrane(Khattab, 2016). In addition, ABA treatment affects more PIP isoforms than drought stress, which may indicate that the ABA and drought signal transduction cascades are independent (Khattab, 2016). However, the upregulation of PIP mRNA is frequently transient, ABA concentration-dependent, and not always linked with an increase in PIP protein level (Zhu *et al.*, 2005, Beaudette *et al.*, 2007).

Aquaporins are essential for maintaining water uptake and transportation across cell membranes, especially when plants are subjected to environmental stressors. In addition, they cause alteration in the amount of reactive oxygen species (Zhou *et al.*, 2017). However, under salt stress conditions, aquaporins can become impaired due to an increase in ROS levels, which triggers oxidant gating and phosphorylation. Aquaporins in plant roots play a vital role in facilitating the transportation of water and minerals for nutrient uptake (Liu *et al.*, 2019). The NIP family of aquaporins has been discovered to have an essential function in the absorption and transportation of silicon and other metalloids (Mehta *et al.*, 2020). The research focused on rice plants has demonstrated that the NIP family of aquaporins is responsible for the intake and outflow of silicon (Mehta *et al.*, 2020). In addition to NIPs, PIPs (plasma membrane intrinsic proteins) also control cellular silicon concentration in the roots of Sorghum plants in response to abiotic stress (Liu *et al.*, 2014, Liu *et al.*, 2015). Under saline conditions, the hydraulic conductivity of roots is frequently disturbed. New research on sorghum has indicated that applying silicon externally can restore hydraulic conductivity (Liu *et al.*, 2014, Liu *et al.*, 2015) . By adding Si to Sorghum bicolor, the expression of SbPIP genes increased. These genes encode PIPs that help regulate the activity of aquaporins, ultimately leading to improved water uptake (Liu *et al.*, 2015). In terms of morphology, the application of silicon stimulated the growth of suppressed lateral roots and improved the primary root's mechanical resilience (Liu *et al.*, 2019). Additionally, it has been shown that Si boosts the expression of these genes and reduces the buildup of excessive sodium ions (Na^+) in the water, boosting the resistance of plants to salt stress. (Manivannan and Ahn, 2017). (Zhu *et al.*, 2015) demonstrated that cucumber seedlings' salt tolerance could be improved by treating 0.3 mM Si, which enhanced water uptake through the roots. This effect was attributed to the upregulation of genes that encode aquaporins, facilitating the water influx. (Liu *et al.*, 2015) reported that silica-treated sorghum plants showed increased expression of PIP genes responsible for encoding aquaporin channels.

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Multiple research studies have demonstrated that monocots and dicots have various Si transporters, such as AQPs, that regulate the amount of Si in the cells. Specialized silicon transporters facilitate silicon transport within plants, such as the Lsi1 transporter for the influx and Lsi2 transporter for efflux. According to (Deshmukh *et al.*, 2015), silicon transporters Lsi1 and Lsi2 are essential for regulating Si distribution in different cellular compartments, tissues, and organs throughout plants. The first identification of silicon transporter genes in rice included Lsi1 for influx transport, Lsi2 for efflux transport, and a homolog of NIP2. These genes act as a protective mechanism in various plant species. Moreover, a silicon transporter known as NIP2 (or Lsi6) has been identified in rice, which facilitates the entry of silicic acid into roots and its transportation through the xylem to the leaves. Through a combination of symplastic and apoplastic pathways, silicon is transferred between root cells in silicic acid, which requires the passage of water (Lesharadevi *et al.*, 2021) .Under conditions of heat stress, wheat plants that were primed with Si (i.e., through seed-priming) exhibited significant upregulation of two genes that encode AQPs: Triticum aestivum's nodulin 26-like intrinsic protein 2 (TaNIP2) and plasma membrane intrinsic protein 1 (TaPIP1) are both membrane-associated proteins, as compared to plants that were exposed to high-temperature stress only (Younis *et al.*, 2020).

3.3. Effect of silicon on stress protein

Stress protein production is another defense mechanism associated with drought stress resistance (Taiz and Zeiger, 2006). Most stress proteins are water soluble and help cells stay hydrated, increasing their capability to endure water stress (Wahid *et al.*, 2007). The ability of plants to withstand stress is regulated by many gene products (proteins), including LEAs and HSPs. According to the study, drought stress significantly affects the amounts of molecular chaperone and abundant/Dehydrins gene expression during the later stages of embryogenesis. These genes and chaperones are essential for preventing the denaturation of cellular proteins (Mahajan and Tuteja, 2005). According to (Wahid *et al.*, 2007), HSPs, among the molecular chaperones often only developed under stress conditions, are crucial for a plant's ability to withstand stress by stabilizing the structures of other proteins. According to studies, HSPs play a role in ATP-dependent protein building and dissolution events and protect against protein denaturalization under stressful situations (Gorantla *et al.*, 2007). On the other hand, silicon treatment improved cellular and genetic resistance to drought stress. Si confers drought resistance by forming mechanical barriers and influencing the activation of specific genes and the resulting proteins. The study showed that silicon use increased the expression of many stress proteins, including late embryogenic abundance proteins and membrane-stabilizing proteins. These proteins are essential for giving rice plants the ability to withstand drought (Khattab *et al.*, 2014). These proteins increase water binding capacity by establishing a protective habitat for the protein or structure known as Dehydrins. Stressed plants produce dehydrins, also known as prolific late embryogenesis proteins. Dehydrins participate in hydrophobic interactions that lead to the stabilization of macromolecules. Surprisingly, Si treatment induced the up-regulation of a class III peroxidase and a protein resembling thaumatin in Cd-stressed rice plants (Nwugo and Huerta, 2011). Silicon enhances the expression of up-regulated proteins in numerous metabolic processes in *C. annum* (Manivannan *et al.*, 2016). The purine metabolism enzyme adenyl succinate synthase improves plant development and growth. The process of photomorphogenesis, floral development, and cardiac rhythm is significantly improved by the protein E3 ligase, which is involved in the ubiquitination process. The photosynthesis-related proteins RuBisCO also promote carbon fixation in Capsicum annum, a kind of pepper. The proteins as mentioned above, were upregulated in plants when si was supplemented (Lesharadevi *et al.*, 2021). Nuceoporins, which are essential in hormone signaling and plant disease resistance, were shown to be more abundant after si treatment. In addition, Si treatment increased the amounts of the calcium-binding protein CML17 and the MCUb-like isoform of the mitochondrial calcium uniporter regulatory component, both of which are important for stress resistance. Moreover, potential proteins linked to plant resistance, as well as the levels of RNA polymerase II, transcription II and ribosomal protein L16 were all increased by the Si treatment. Salinity promoted the expression of specific proteins in Capsicum annum (*C. annum*). Molybdopterin synthase, an uncharacterized protein isoform encoded by LOC104086136, -keto acyl reductase, reverse transcriptase, RAS-related protein, and F-box/kelch-repeat protein etc., are among these proteins (Lesharadevi *et al.*, 2021). Several proteins were elevated in plants when Si and NaCl were combined as a treatment. These proteins are essential for numerous metabolic processes, including growth control, disease resistance, stress resilience, photosynthesis, antioxidant systems, and nutritional balance, especially in situations of salinity stress (Manivannan *et al.*, 2016).

4. Genetic and molecular approaches under abiotic stresses

4.1. Genomics and Transcriptomics Approach

Si enhances plant resilience to stress and promotes plant development by increasing the activity of specific genes, such as PsbY, PsaH, and PSII, responsible for photosynthesis (Arif *et al.*, 2021). The expression of the PsbY gene is linked to the

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oxygen-evolving manganese subunit of PSII, while the PsaH gene's transcription enhances PSI's activity and the photosynthetic antenna complex system (Song *et al.*, 2014). The PetH gene, which contributes to the electron transport chain complex's role in NADPH synthesis, is upregulated due to silicon (Si) exposure. Moreover, the PetH gene also stimulates the accumulation of glutathione (Arif *et al.*, 2021). Si applications can also upregulate genes like Os03g57120 and Os09g26810, which help mitigate plant stress (Manivannan and Ahn, 2017). The enzyme S-adenosyl-L-methionine decarboxylase (SAMDC), which produces polyamines (such as putrescine, spermine, and spermidine), is more active when silicon (Si) is present. These polyamines are essential for reducing the effects of abiotic stress(Arif *et al.*, 2021). Si increases the expression of defence-related genes in plants, such as pathogenesis-related proteins (PR1), peroxidase (POX), chalcone synthase (CHS), chitinase, and PAL(Manivannan and Ahn, 2017) . Si supplementation also boosts the expression of genes involved in systemic acquired resistance and the phenylpropanoid pathway, which is responsible for the biosynthesis of phenols and flavonoids (Manivannan and Ahn, 2017) . The addition of Si to tomato plants helps alleviate stress by increasing the expression of the glutathione reductase gene (LeGR) (Kaushik and Saini, 2019) . Applying Si to Solanum lycopersicum plants promotes the upregulation of genes coding for antioxidant enzymes such as SlGPX, SlSOD, SlCAT, SlGST and SlGR, thereby improving plant resilience to stress (Khan *et al.*, 2020).

Transcriptomic analyses are frequently used to discover a wide range of genes whose expression is altered in response to silicon (Si) application under stressful conditions, allowing for the investigation of the role of Si. According to reports, these genes contribute to hormone signaling and biosynthesis, solute transport, and stress response in biotic and abiotic environments. Transcription factors comprise a significant portion of the genes whose expression was altered (Zhu *et al.*, 2019, Arif *et al.*, 2021). According to (Liu *et al.*, 2015, Manivannan and Ahn, 2017) , the overexpression of the SbPIP gene, which produces the plasma membrane intrinsic protein (PIP), is essential for boosting water uptake by favorably influencing aquaporin activity. Additionally, it has been discovered that this upregulation improves sorghum's ability to tolerate salt. Similarly, it is crucial to improve S-adenosylL-methionine decarboxylase (SAMDC) activity in order to increase Si's production of polyamines, which is crucial for reducing abiotic stress factors. Stress-tolerant genes like Os03g57120 and Os09g26810 must also be upregulated (Manivannan and Ahn, 2017). The OsRDCP1 gene's increased Si expression resulted in less water loss from plant cells, thus reducing the effects of drought stress (Khattab *et al.*, 2014). According to transcriptome research, Si increases the expression of genes, including PsbY, PsaH, PsII, and LHC, to reduce stress. These genes control the function of the light-harvesting complex, the oxygen-evolving manganese component PSI, and the PSII, all essential for photosynthesis (Song *et al.*, 2014, Lesharadevi *et al.*, 2021). Si activates the ABA-independent route to increase the expression of transcription factors that reduce osmotic stress, such as dehydration-responsive element binding protein (DREB2) and NAC (Manivannan and Ahn, 2017, Almutairi, 2019). According to Zhu *et al*. (2019) comparative transcriptome research, Si can act as an elicitor and cause salt stress in cucumber plants. The research findings show that a substantial number of genes (609 and 595, respectively) affected by salt stress returned to normal expression levels after Si treatment. This shows that the transcriptome of cucumber plants under salt stress can be restored to its initial form with the help of Si application (Mir *et al.*, 2022). In a different investigation, DEGs in wheat seedlings treated with Si were discovered using RNA-seq technology by (Hao *et al.*, 2021). According to their findings, the expression of 3,057 genes involved in protein processing, phenylpropanoid biosynthesis, chaperons, transcription factors, and chaperons were altered after exposure to silica. About 28 transcription factors from the MYB transcription factor family showed downregulation in their expression levels after being treated with Si.

4.2. Proteomics

Proteomics provides a novel method for identifying proteins and comprehending the pathways involved in stress tolerance by revealing a variety of stress-responsive proteins that react to abiotic factors at the gene expression and protein synthesis (Kosová *et al.*, 2018). Understanding the metabolic proteins and pathways involved in stress tolerance is crucial for biotechnological interventions to enhance strains' capacity to withstand stress. Abiotic stressors prevent the synthesis of new proteins and result in protein loss. According to research, Si effectively reduces stress by promoting the production of a protein involved in signal transduction mechanisms and the antioxidant defense system. According to proteomics research, plants exposed to silicon (Si) exhibit a noticeable increase in stress-tolerant proteins of about 17%. Additionally, there is an increase of around 11% in the proteins necessary for hormone production, RNA synthesis, numerous cellular processes, and the production of secondary metabolites intended to reduce abiotic stressors (Al Murad *et al.*, 2020). The identification of the proteins that are elevated by silicon (Si) exposure and give plants increased tolerance to abiotic stress has been made possible by proteomic research. These proteins include MADS-box transcription factors (TFs), transcription elongation homologs (like SPT4), tRNA-lysidine synthase, RNA polymerase mediator, ribosomal protein L16 and reverse transcriptase (Al Murad *et*

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al., 2020, Muneer and Jeong, 2015). Additionally, proteomic research has demonstrated that silicon (Si) contributes to the reduction of environmental stressors like salt and temperature challenges through the activation of specific proteins such as Carotene desaturase which participates in the synthesis of -carotene, chaperone proteins such as ClpC3, glutelin, -keto acyl reductase, plasma membrane intrinsic protein (PIP1), and nodulin 26-like proteins are a few of these. These proteins help the plant counteract salt and heat stress (Younis *et al.*, 2020, Cao *et al.*, 2020). Rice, like other grasses, accumulates Si and is primarily stored in its leaves. Silicon (Si) has been discovered to significantly impact the production of numerous proteins based on studies focusing on modifying the leaf proteome in rice plants. These proteins are crucial in disulfide isomerase, protein synthesis control, defence against pathogens, class III peroxidase, chaperone activity, photosynthesis, NADH-ubiquinone oxidoreductase, and redox homeostasis. Additionally, Si has shown that it may be used alone or in conjunction with Cd to promote tolerance, highlighting its function in reducing the negative consequences of heavy metal stress. This indicates that silicon (Si) significantly promotes plant-induced tolerance (Mir *et al.*, 2022).

4.3. Metabolomic and ionomic approach

Si has been shown to induce changes in plants' metabolomic and ionomic profiles, resulting in increased tolerance to stress. When Si is applied to plants during stress, it has been shown to increase the levels of various metabolites, including antioxidant and osmoregulatory compounds, which help to mitigate stress-related disturbances (Arif *et al.*, 2021). It has been noted that applying Si selectively increases the quantities of antioxidant substances like myristic acid, pyridoxine, boldine and cepharanthine. The quantities of osmoregulators like mucic acid, lactoglutathione, and glutamyl conjugates have also been shown to be increased by Si. In addition to serving as osmoregulators, these substances also scavenge reactive oxygen species (Arif *et al.*, 2021). Si has been shown to increase the accumulation of several metabolites that significantly promote plant development and growth and help plants withstand environmental stresses (Jana *et al.*, 2019) . Many different metabolites, such as tocopherol, flavonoids, ascorbate, glutathione and phenols, have been seen to have their levels controlled by the presence of Si. This modulation helps reduce the harmful effects of abiotic stress, promote plant development, and increase crop productivity (Metwally *et al.*, 2018). Si application considerably increases the content of anthocyanins and carotenoids, which can help to lessen the effects of abiotic stress on plants (HABIBI, 2016). Si has been observed to upregulate the metabolic content in plants' leaves, shoots, and roots, which helps mitigate stress and improve plant tolerance. Si increases the level of succinate in the roots, which triggers long-distance transport of iron and helps to alleviate heavy metal stress (Kaushik and Saini, 2019). Applying silicon increases proline levels, soluble sugars, starch, carbohydrates, and amino acids. Additionally, it results in a phosphorus deficiency and subjects the plant to alkaline stress (Qin *et al.*, 2016, Zhang *et al.*, 2019). To counteract the adverse effects of stress, silicon treatment alters the metabolic profile and promotes the synthesis of polyamines like putrescine, spermine, and spermidine. Furthermore, silicon encourages the production of gamma-aminobutyric acid (GABA), which is essential as an osmoprotectant and signalling molecule. However, silicon results in higher levels of glutathione, threonine, methionine, glycine, proline, and serine, improving the plant's resistance to harsh environmental conditions (Ali *et al.*, 2018). Silicon usage promotes the production of suitable metabolites such as GB, sucrose, mannitol, trehalose, GABA, sorbitol, etc. These metabolites are essential for maintaining osmotic equilibrium and helping the plant adapt to harsh environmental conditions (Khan *et al.*, 2019). Silicon is essential for boosting histidine and nicotinamide levels in cucumber leaves, which improves the plant's ability to withstand stress (Bosnić *et al.*, 2019). Using silicon improves plants' mineral nutritional composition, leading to higher concentrations of vital minerals. The treatment of silicon regulates the uptake and internal levels of ions within the plant, which helps alleviate environmental stress's impact. Ionomics is a technique employed to examine variations in the levels of micro and macronutrients in plants' mineral content. Therefore, when a plant undergoes abiotic stress, the presence of silicon causes an increase in the buildup of sulfate and ammonia (Ali *et al.*, 2018). Additionally, silicon promotes the uptake of manganese and potassium, lessening the adverse effects of stress-related ionic damage and improving cellular and plant growth. Utilizing silicon also results in the buildup of the metals zinc, iron, and copper, co-factors for many enzymes involved in stress control and detoxification systems (Banerjee *et al.*, 2021). By raising the concentrations of nitrogen, phosphorus, and silicon, silicon treatment increases plants' capacity to endure drought and improves their morpho-physiological traits (Siddiqui *et al.*, 2020). Silicon treatment increases plants' capacity to endure drought and improves their morpho-physiological traits by raising the concentrations of nitrogen, phosphorus, and silicon. In addition, supplementing with silicon boosts manganese, magnesium, sodium, calcium, potassium and iron (Zhang *et al.*, 2019). As a result of silicon's ability to control the stoichiometric ratios of carbon (C), nitrogen (N), and phosphorus (P) (C:N:P), leading to more biomass is produced, photosynthesis is improved, carboxylation activity is boosted, and many developmental processes advance (Frazao *et al.*, 2020). When silicon is used, leaves depleted by salt stress have higher nitrogen, phosphorus, and

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potassium levels (Siddiqui *et al.*, 2020) . According to (Van der Ent *et al.*, 2020), the technique of μ-XRF scanning is crucial in examining the ionomic changes and modifications after supplementing soybean and sunflower plants with silicon.

4.4. Silicon nanoparticles

Silicon nanoparticles have an excellent ability to disperse over a large area. One gram of 7.0 nm-diameter silica nanoparticles was calculated to have a large absorption surface of 400 m^2. The influence of silica nanoparticles on xylem moisture content, water movements and enhanced turgor pressure will also boost plant water utilization efficiency (Saxena *et al.*, 2016). Plant growth is hampered by drought, which also affects photosynthesis and the germination of plant seeds. Silica nanoparticles (SNPs) have been discovered to improve the drought resistance of various crops, including cherries, barley, strawberries, and wheat (Wang *et al.*, 2022). Plants respond to dehydration by expanding to maintain certain solute levels and cellular functioning, which is facilitated by the osmotic adjustment and build-up of compatible solutes (Blum, 2017). The osmotic potential in strawberries and barley decreases during drought due to silica nanoparticles (SNPs) altering the osmotic pressure of cells. This change improves the capacity of plant tissues to absorb and store water, permitting enhanced water storage capabilities (Luyckx *et al.*, 2017, Boaretto *et al.*, 2014). Silicon has been found to aid in the absorption and retention of water in lentil plants, and this ability to restore water during periods of water shortage stress may be linked to a double layer of SiO_2 stratum corneum located beneath the leaf epidermal cells (Luyckx *et al.*, 2017). Malondialdehyde (MDA) builds up excessively in plants during drought stress, resulting in oxidative damage (Luyckx *et al.*, 2017, Parveen *et al.*, 2019). Applying silicon nanoparticles (SNPs) increases the activity of enzymatic antioxidants in plants and lowers the quantity of MDA under water shortage conditions (Namjoyan *et al.*, 2020). In general, water shortage stress causes a substantial decrease in leaf expansion, disrupts photosynthesis and retards leaf senescence (Ashkavand *et al.*, 2015). Drought typically causes damage to photosynthesis, considerably slows down leaf senescence and significantly limits leaf expansion (Ashkavand *et al.*, 2015). . SNPs boost photosynthetic rate and stomatal conductance in hawthorn to lessen the effect of drought on the plant (Ashkavand *et al.*, 2015). SNPs significantly improve the SPAD value in wheat under drought stress by 12.54 per cent, thus reducing the negative effect of drought stress on plant growth (Behboudi *et al.*, 2018). According to a study by (Saxena *et al.*, 2016), using sodium silicate at the right concentration (1.0 mM) could help wheat resist drought stress's negative impacts. Despite the unknown mechanism, silicon helps stressed plants preserve their leaf water potential, boost shoot growth, and raise their chlorophyll concentrations. It also lowers wheat's membrane lipid peroxidation (Saxena *et al.*, 2016) . Salt stress slows down the development of plant tissues and organs, which lowers photosynthesis and respiration rates. As salt concentrations rise and the stress period lengthens, salt stress also inhibits leaf growth and reduces plant biomass (Parida and Das, 2005). SNPs may considerably increase a plant's ability to resist salt stress (Sabaghnia and Janmohammadi, 2014, Tantawy *et al.*, 2015). (Alsaeedi *et al.*, 2018) found that adding 200 mg kg1 SNPs (10 nm) improved cucumber seeds' vitality index and germination rate during salt stress. According to(Naguib and Abdalla, 2019), using SNPs produced equivalent results because it increased the activity of antioxidant enzymes, which counteracted the harmful effects of salt stress. When exposed to salt stress, plants first slow down the expansion of their leaf surfaces before inhibiting photosynthesis. Additionally, SNPs control the stomatal conductance of leaves, providing a constant transpiration rate even when plants are subjected to salt stress. This modification helps shield plants from an excessive buildup of sodium (Na^+) and chloride (Cl^-) ions(Haghighi and Pessarakli, 2013). When silicon nanoparticles were applied to lentil varieties under salt stress, seedling emergence rate and growth significantly increased, whereas they significantly decreased when the nanoparticles were not used. SiO_2 nanoparticles are added to lentil genotypes under salinity stress to improve seed germination, early seedling growth, and other associated features. Hence, SiO_2 nanoparticles improve many plant defense systems against salt toxicity (Sabaghnia and Janmohammadi, 2014). The effects of nano silicon particles on tomato seeds and young plants under salinity stress were also investigated. The findings showed that salt stress significantly reduced the harmful effects of salt toxicity on the emergence of seeds, root length, and the total dry weight of the plant in basil (*Ocimum basilicum*) (Haghighi *et al.*, 2012). Salt stress can decrease crop growth and yield due to the toxicity of Na^+ ions. Still, nanoparticles such as nanoSiO_2 have been proposed to reduce ionic toxicity and improve crop growth and yield, which could be beneficial for crop resilience under unfavorable environments (Savvas *et al.*, 2009). silica nanoparticles apply a method to relieve salt stress in plants by possibly lowering the concentration of sodium ions (Na^+) by inhibiting Na^+ uptake by plant tissues. The reduction in osmotic potential and the toxicity brought on by sodium ions (Na^+) are the principal effects of salinity stress on plant growth. Silica nanoparticles may aid in enhancing plant development in salt stress after Na^+ ion toxicity (Saxena *et al.*, 2016). Additionally, SNPs might greatly impact how plants react to stressful situations. SNP exposure improved tomato plants' tolerance to salt by downregulating salt stress genes (MAP K3, APX2, MAPK2, RBOH1, and DDF2)

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(Almutairi, 2016). Exposing wheat plants to Si-NPs resulted in downregulating TaPIP1 and TaNIP2 genes during high-temperature stress. Si-NPs may be unable to control the expression of TaPIP1 and TaNIP2 because they are less dense than Si_4 and can more easily diffuse through the cell wall (Younis *et al.*, 2020). Applying Si-NPs causes the downregulation of several genes, including dwarf and delayed flowering 2 (DDF2), respiratory burst oxidase (RBOH1), and mitogen-activated protein kinase 2 (MAPK2), which increases plant resiliency to stress and improves plant growth and development, including germination (Almutairi, 2016).

4.5. Genome editing technique

When canola is under drought conditions, pod shattering occurs; as a result, it is commonly recommended to apply Si by foliar spray. (Habibi, 2014) investigated the effects of applying Si to canola plants to increase the plant's rate of photosynthesis. Applying Si during their growth and maturation stages improved the canola plants' nutritional balance. Due to the reduction of pod breaking, increased resistance to insect infestation, and strengthened disease resistance, this development increased yield and overall quality.

(Ahmad *et al.*, 2022). The successful use of novel gene knockouts has resulted in notable advancements in critical agro-morphic features of rapeseed, including plant height and multilocular silique (Yang *et al.*, 2017). Pod shatter resistance was slightly impacted by CRISPR/Cas9 targeting of the BnALC gene (Braatz *et al.*, 2017). The CRISPR/Cas9 approach was successfully applied in canola to create knockout plants for several genes, successfully creating all the needed clones (Yang *et al.*, 2018, Li *et al.*, 2018). The BnALC gene was targeted using CRISPR/Cas9,which had a small influence on pod rupture tolerance (Braatz *et al.*, 2017). The effectiveness of the CRISPR/Cas9 technique in a polyploid species is demonstrated by the simultaneous targeting of two BnALC homologues without any prior alterations and the insertion of TDNA (Braatz *et al.*, 2017). The CRISPR/Cas9 technique was successfully used to specifically target the BnIND and BnALC genes linked to canola resistance to pod breaking.(Shi *et al.*, 2017) have developed a maize genotype that exhibits enhanced yield under drought stress using CRISPR/Cas-based genome editing. The gene ARGOS8, which plays a role in inhibiting ethylene reactions, was the subject of the investigation (Shi *et al.*, 2017). In another study, truncated gRNAs (tru-gRNAs) and Cas9 were activated by a tissue-specific AtEF1 promoter,

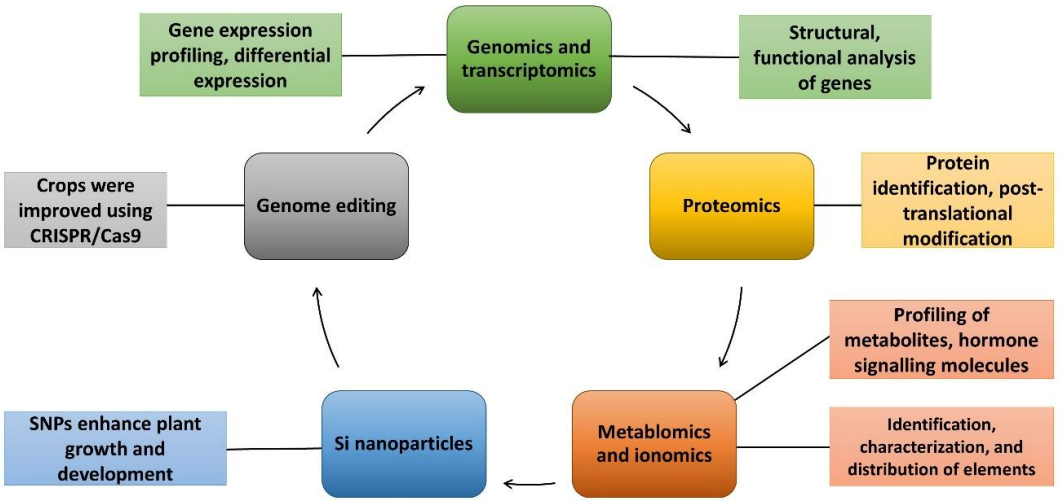


Figure 3. Role of genetic and molecular approaches to mitigate abiotic stresses

Plants lacking in silicon exhibit lower growth, inadequate pod formation, and poor regeneration, making them essentially weaker than silicon-rich plants. Sequence-specific nucleases (SSNs) have recently been shown to be an effective method for crop modification via site-specific genome editing. The most well-known and user-friendly tool among these SSNs is CRISPR/Cas9. Crops were improved using CRISPR/Cas9 as an efficient specific mutation technique causing induced mutations in genes responsive to abiotic stress, especially OST2/AHA1. The stomatal reflexes of Arabidopsis plants were improved due to this genetic alteration (Osakabe and Osakabe, 2017). Researchers have focused on the rice genes OsRR22 and OsNAC041 to improve salinity tolerance (Zhang *et al.*, 2019, Bo *et al.*, 2019). In recent work, the RNase/DNase activity of the Acidaminococcus Cas12a (Cpf1) enzyme allowed for the

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simultaneous editing of 25 different genomic sites (Campa *et al*., 2019). Theapproaches mentioned above might be helpful for simultaneously addressing several abiotic stress-related genes. Through altering aquaporins, genome editing can be used to alter the control of solute transport, including the movement of water, urea, H2O2, and silicon (Zargar *et al.*, 2017, Shivaraj *et al.*, 2019). Abiotic stress tolerance can be improved by targeting more transporter proteins with genome editing approaches (Vishwakarma *et al.*, 2019, Bhat *et al.*, 2019) . The findings suggest that the CRISPR/Cas system offers substantial promise for efficiently targeting minor genes linked with complicated quantitative features related to abiotic stressors, and it is expected to play a vital role in the future of genetic research in this field (Vats *et al.*, 2019). Summarized pictorial view of genetic and molecular approaches to hamper the effects of abiotic stress tolerance is depicted in (Figure 3).

5. Conclusion/Future Prospectus

The agricultural sector serves an essential and vital function in ensuring the provision of an adequate and nutritious food supply to sustain human well-being. The advancements made in agricultural technology research enable researchers to work towards a world devoid of food scarcity while also exploring methods to alleviate the impacts of diverse plant stresses. Abiotic stresses are the main factors responsible for the reduction in plant growth, development, and yield. To address this issue, researchers are focusing on plant genetic and molecular approaches to increase stress tolerance in plants. Silicon is recognized as a beneficial element among various approaches aimed at enhanceing growth, optimizing the process of photosynthesis, regulating metabolic activities, and eventually enhancing crop yield. Applying silicon enhances the concentration of chlorophyll, enhances the efficiency of photosynthesis, elevates antioxidant levels, and promotes the occurrence of reactive oxygen species. Si improves the functionality of proteins and genes in plants under abiotic stress conditions such as drought, salt, heat and cold stress. This chapter summarizes the role of silicon in plants, the occurrence and source of silicon, uptake, accumulation, and transportation, the mechanisms of silicon-mediated abiotic stresses, and genetic and molecular approaches. We concluded that summarizing the topics discussed above could assist researchers in directing their efforts towards boosting crop yield by implementing silicon-based techniques across various plant species.

The current knowledge of the molecular mechanisms behind the contribution of silicon to abiotic stress tolerance is limited, primarily due to a lack of clarity regarding the pivotal role played by this versatile element. Furthermore, it is important to examine the impact of silicon on the alteration of genes linked to phytohormone, and this specific area of research requires additional investigation. Further investigation is necessary to explore the omics approach and its influence on modifying the metabolic and cellular responses of plants in the presence of stressors. Moreover, the study of silicon-mediated post-translational changes is unquestionably an area that needs more research. In the future, the CRISPR/Cas system has the potential to be utilized for the purpose of targeting silicon-encoding genes to enhance tolerance in major crop species.

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8. Conflict of Interest

The authors declare that they have no conflict of interest regarding the publication of this article.

9. Authors' Contribution

Sana Khan contributed to the conceptualization and initial drafting of the manuscript. Abdul Rehman provided critical revisions, supervised the study, and ensured the overall coherence of the review. Komal Mazhar assisted in literature collection and manuscript organization. Muhammad Mubashar Zafar contributed to data interpretation and manuscript refinement. Abdul Qayyum reviewed and edited the manuscript for accuracy and clarity. All authors read and approved the final version of the manuscript.

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