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ADVANCES IN UNDERSTANDING SILICON-MEDIATED MOLECULAR AND GENETIC RESPONSES TO ABIOTIC STRESS IN PLANTS

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Abstract

Sustainable agricultural production is increasingly threatened by unpredictable and adverse environmental conditions. The application of mineral elements has emerged as a promising strategy to mitigate the effects of abiotic stress, offering an alternative to conventional management practices. Among these elements, silicon (Si)—the second most abundant element in the Earth's lithosphere—plays a vital role in a wide range of cellular, physiological, and developmental processes in plants. Numerous studies have demonstrated that Si application enhances seed germination, plant growth, photosynthetic performance, gas exchange, and yield under both stress and non-stress conditions.

The beneficial effects of silicon are particularly evident in silicon-accumulating plant species, especially when exposed to abiotic stresses such as salinity, drought, and extreme temperature fluctuations. Exogenous application of Si induces substantial modifications in morpho-physiological and biochemical traits, thereby strengthening plant tolerance to environmental stressors.

This chapter reviews the occurrence, sources, uptake, accumulation, and transport of silicon in plants. It further highlights recent advances in silicon-mediated stress alleviation through molecular and genetic approaches, including genomics, transcriptomics, proteomics, silicon nanoparticles, and genome-editing technologies. Overall, the chapter aims to provide a comprehensive understanding of the multifaceted role of silicon in alleviating abiotic stress and to emphasize its potential as a sustainable strategy for enhancing crop resilience and productivity.

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, 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 stresses 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 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).
yields have decreased by over 70% (Malhotra and Kapoor,

2.2. Silicon: Occurrence and Sources

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).

1. 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 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 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 OsLSi2 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. 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 SiO2.nH2O, 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 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 H2O2 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. An 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 $^{+}$) 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 pectins 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 biomembranes 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., 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 is depicted and elaborated in Figure 1 and Table 1.

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).

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

Figure1. Impact of silicon fertilizer on various aspect of plant growth under abiotic stresses

3. Molecular mechanism of silicon-mediated 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 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 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 directly prompted by drought stress (Agarwal *et*

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)

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 particular transcription factors (TFs).

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

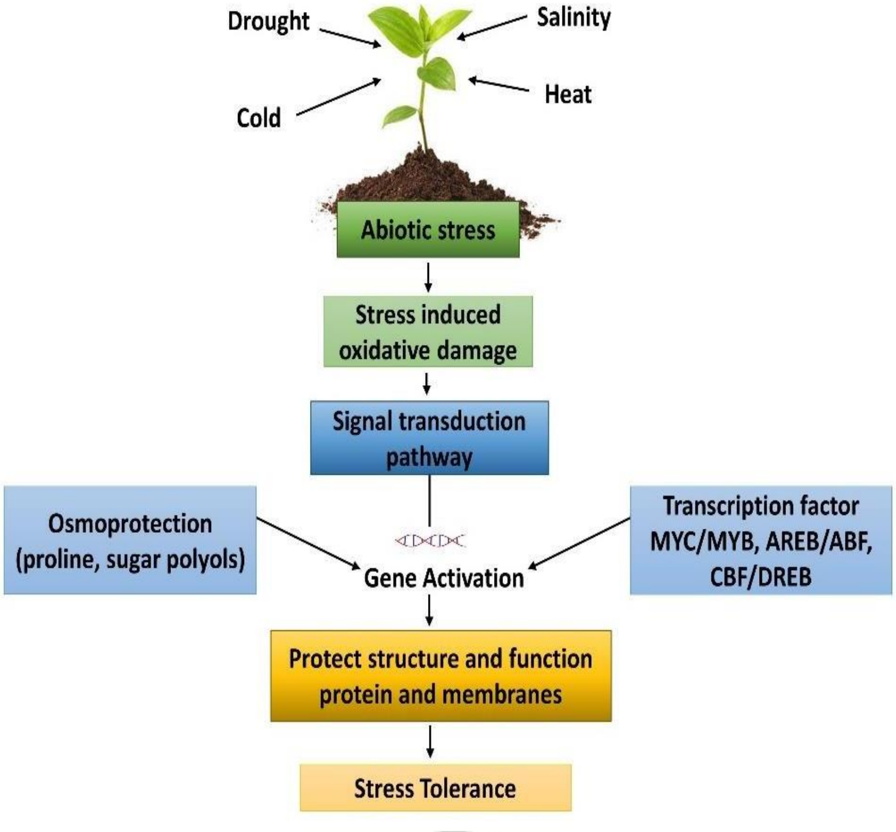


Figure 2. Stress tolerance mechanism of plants against abiotic stress

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). In salt-stressed soybean, the gibberellin level fell but significantly rose when Si was present. According to (Kim et al., 2014), silicon under salt stress led to a considerable reduction in the production of stress- and defense-related 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 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 HSP18, HSP70, and HSP90 by activating HSFA2c

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)

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, H2O2, 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 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, H2O2 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 H2O2 (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 was 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.

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 defence 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). Nucleoporins, 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 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 application 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 amount 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 was 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 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 itsfunctionin 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 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 SiO2 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. SiO2 nanoparticles are added to lentil genotypes under salinity stress to improve seed germination, early seedling growth, and other associated features. Hence, SiO2 nanoparticles improve many plant defence systems against salt toxicity (Sabaghnia and Janmohammadi, 2014). The effects of nanosilicon 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 nanoSiO2 have been proposed to reduce ionic toxicity and improve crop growth and yield, which could be beneficial for crop resilience under unfavourable 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) (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 Si4 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).

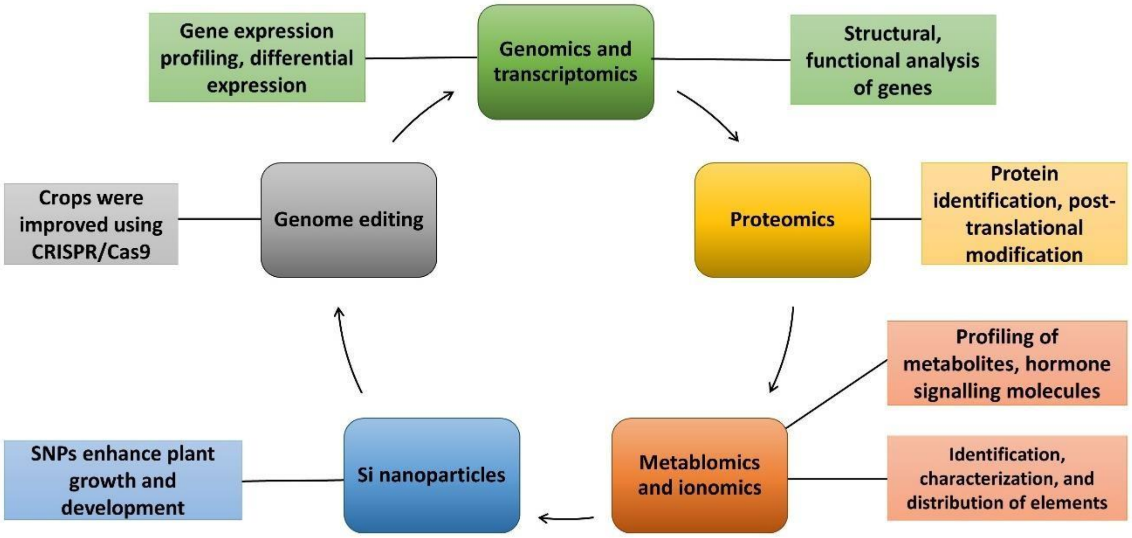
4.5. Genome editing technique

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. 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 (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, 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 simultaneous editing of 25 different genomic sites (Campa et al., 2019).The approaches 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 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 enhancing growth, optimizing the process of photosynthesis, regulating metabolic activities, and eventually enhancing crop yield. Applying silicon enhances chlorophyll's



concentration, enhances photosynthesis's efficiency, elevates antioxidant levels, and promotes the occurrence of reactive oxygen species. Si improve 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 no conflict of interest.

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