



Review

Silicon: A Powerful Aid for Medicinal and Aromatic Plants against Abiotic and Biotic Stresses for Sustainable Agriculture

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Abstract: Silicon plays a crucial role in enhancing plant tolerance to various abiotic and biotic stresses, including drought, salinity, heavy metals, and pathogen/pest attacks. Its application has shown promising results in improving stress tolerance and productivity in medicinal plants. This review synthesizes findings from numerous studies investigating the mechanisms by which silicon confers stress tolerance, including the regulation of antioxidant systems, water relations, nutrient homeostasis, phytohormone signaling, and stress-responsive gene expression. Additionally, it examines the effects of silicon supplementation on the production of valuable secondary metabolites and essential oils in medicinal plants. Silicon application can significantly mitigate stress-induced damage in plants, including medicinally important species such as borage, honeysuckle, licorice, Damask rose, savory, basil, and eucalyptus. The deposition of silicon in cell walls provides physical reinforcement and acts as a barrier against pathogen invasion and insect herbivory. Furthermore, silicon fertilization can enhance the production of valuable secondary metabolites in medicinal crops under stress conditions. The findings underscore the potential of silicon fertilization as a sustainable strategy for improving the productivity and quality of medicinal crops under changing environmental conditions, highlighting the need for further research to elucidate the molecular mechanisms underlying silicon-mediated stress tolerance and practical applications in medicinal plant cultivation.

Keywords: silicon; biotic stress; abiotic stress; medicinal plants; phytohormones



Citation: Hassan, K.M.; Ajaj, R.; Abdelhamid, A.N.; Ebrahim, M.; Hassan, I.F.; Hassan, F.A.S.; Alam-Eldein, S.M.; Ali, M.A.A. Silicon: A Powerful Aid for Medicinal and Aromatic Plants against Abiotic and Biotic Stresses for Sustainable Agriculture. *Horticulturae* **2024**, *10*, 806. <https://doi.org/10.3390/horticulturae10080806>

Academic Editor: Rossano Massai

Received: 4 July 2024

Revised: 16 July 2024

Accepted: 27 July 2024

Published: 30 July 2024



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1. Introduction

Apart from being a source of food, medicinal and aromatic plants (M&APs) and their active ingredients are also used as non-food industrial products, pharmaceuticals, herbal health products, cosmetics, and pesticides [1,2]. China, India, and some other countries have supported the official use of traditional (folk) medicine systems in their healthcare systems [3,4]. China and India are at the top of the exporting countries, and Japan and Korea are at the top of the importing countries. Countries such as Germany and the United States stand out as important commercial centers for M&AP trade [5]. More than 2500 species of M&APs are spread around the world and belong to many important plant families such as Lamiaceae, Asteraceae, Apocyanaceae, Oleaceae, Fabaceae, and more. Indeed, M&APs have been used for thousands of years to prevent and treat diseases and have a

long history in this context [6]. According to the World Health Organization, about 80% of the world's population still depends on medicinal herbs; however, the production of secondary metabolic products from medical plants depends on environmental conditions [7]. M&APs produce many beneficial secondary metabolic products, as these substances have antimicrobial properties, contain a large number of antioxidants, and have other properties for medical use [8–10]. As a result of climate change in recent decades, several adverse impacts have been observed in plants due to abiotic stresses such as salinity, drought, cold, high temperature, heavy metals, waterlogging, and nutrient imbalance, which have decreased crop productivity by 51–82% [11,12]. Contemporary climate change leads to drought and thermal stresses, which are among the most prominent types of stress that lead to a significant reduction in the productivity of several crops including medicinal plants [13,14]. Therefore, abiotic stresses are considered one of the most important obstacles globally facing plant productivity in the era of unexpected climate change [15,16].

Silicon (Si) is considered a micronutrient that has diverse benefit roles in plants, particularly under several stressful conditions [17,18]. It enhances plant growth and productivity, photosynthesis, and nitrogen fixation, and increases plants' tolerance to various abiotic and biotic stresses such as high temperature, heavy metals, drought, salinity, and pathogens [19–23]. In the past, it was believed that Si was an unnecessary element for plant growth [24], but after many studies, it was proven beyond doubt that Si has several physiological and biochemical roles that participate in enhancing plant stress tolerance and therefore it is considered as a semi-essential element [25]. Si is a plant nutrient that provides strength to the plant, as it supports the plant cell and makes the tissues more solid and strong [26]. Soluble silicon can enhance plant resistance to pathogens by interacting with the basic compounds of the stress signaling system within the plant [27,28]. Moreover, Si accumulation within the plant leads to the production of phenols and phytoalexins that make the plant more resistant to various pathogens [29,30]. Due to the positive impact of Si on achieving sustainable crop productivity, an organic liquid fertilizer containing Si has been developed as an alternative to chemical fertilizers [31].

2. Silicon's Role in Plant Growth and Development

Actually, Si is the second most prevalent element on Earth's surface and has been proven to enhance plant growth and development [32]. Although silicon is not a necessary element for plants, multiple studies have shown that it improves growth, production, and crop quality while also offering tolerance to abiotic and biotic challenges [33–36]. Si is absorbed by plant roots as uncharged silicic acid and transferred to the shoot via the transpiration stream. Aquaporins, especially the NIP subfamily, known as silicic acid channels, enhance the uptake of silicic acid [37]. In this part, we will highlight our current understanding of Si's involvement in plant biology.

3. Plant Structure and Function

Si is considered a non-essential nutrient for plant nutrition [38]. Nonetheless, the biostimulatory effects of Si on plant growth and development are well-documented [39,40]. Whereas elements such as silicon, selenium, cobalt, and aluminum might influence physiological processes to enhance plant growth and productivity under changing environmental conditions, silicon is often classified as a 'quasi-essential' element for higher plants [41]. Increased availability of Si could hasten plant development, while Si deficiency might result in morphological abnormalities [42,43]. One of the critical functions of Si in plants is promoting leaf erectness, which boosts light interception and canopy photosynthesis [44]. This is achieved through the deposition of polymerized amorphous silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) in the plant cell wall, which increases the rigidity of stems and leaves and minimizes lodging [45]. Moreover, Si contributes to seed germination, cell membrane integrity, carbon absorption, and plant–water interactions and stimulates the action of antioxidants, phytohormone production, and nutrient acquisition [46,47]. Silicon is required to construct the cuticle–silica double layer beneath the leaf epidermis, resulting in decreased transpi-

ration rates in Si-treated plants compared to controls. This reduction in transpiration is an important element in silicon-mediated stress tolerance. Furthermore, silica deposition in tissues reduces transpiration and improves light absorption, hence mitigating drought stress [46]. Moreover, the application of Si increased plant height, stem diameter, biomass accumulation, protected photosynthetic pigments, improved gas exchange, promoted ATP production, and enhanced enzyme activity and gene expression related to photosynthesis under low-calcium conditions [47]. The formation of phytoliths, solid particles of polymerized SiO_2 , in cell walls provides mechanical strength and structural stability [48]. Since Si is not transportable through the phloem, Si distribution was adjusted by transpiration, resulting in higher accumulation in older tissues [49].

Si interacts with cell wall components such as hemicellulose, pectin, lignin, cellulose, callose, and mixed-linked glucans, aiding in crosslinking and thus enhancing cell wall rigidity and mechanical strength [45,50]. Better growth was linked to higher foliar C:N or C:P ratios, suggesting improved nutrient-use efficiency with increased plant-available and/or foliar Si [45]. Silicon application enhances the number of chloroplasts in mesophyll cells, as well as the lamellar structure, promoting the progression of photosynthetic phosphorylation, lowering the concentration of intercellular CO_2 , delaying the decline in rice chlorophyll content, and increasing photosynthetic rate and stomatal conductance [51]. Silicon-enhanced plant tolerance is due to the elevated activity of defense-related enzymes; however, the exact mechanisms of Si action are unknown. Silicon-mediated plant stress tolerance can be attributed to (i) indirect influence by stimulating the plant signaling system, resulting in the formation or activation of defense-related enzymes; or (ii) the direct influence on the additional synthesis of enzymes and proteins involved in ROS scavenging [52]. In general, Si positively alters plant growth, development, and stress responses via modifying cell wall architecture, increasing leaf erectness, and improving structural integrity. Plants with higher Si absorption efficiency benefit more from Si availability than Si excluders, resulting in significant changes in morphology, anatomy, physiology, and metabolic activities [53–58]. Significant implications of Si include enhanced enzyme activity, antioxidant capacity, plant water relations, photosynthesis, ion absorption, hormone balance, and gene expression [21,51].

4. Oxidative Damage

Oxidative damage, a result of stress, impairs plant metabolism by overproducing reactive oxygen species (ROS), damaging proteins, lipids, carbohydrates, and DNA, and affecting metabolic functions depending on the causal stress factor [54]. To alleviate the deleterious effects of such stresses, plants adapt various mechanisms such as the compatible solutes accumulation that maintain cell turgidity and induce the antioxidant enzymes required for ROS. Actually, Si has been shown to boost the activity of various antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), and dehydroascorbate reductase (DHAR) [16,59–61]. Silicon application boosts the AOX system during drought stress in tomato plants, where a Si-mediated substantial decrease in reactive oxygen species (ROS) was reported [62]. Si treatment is also related to lower levels of reactive molecules that cause oxidative damage, such as hydrogen peroxide (H_2O_2) and thiobarbituric acid reactive substances (TBARS), as well as metabolites originating from lipid peroxidation, such as malondialdehyde (MDA) [63].

5. Water Relations

Silicon has been demonstrated to alter water relations in plants, especially under abiotic stress situations. It enhances plant growth traits like plant height, leaf area, and leaf dry weight, as well as gas exchange characteristics like photosynthetic rate and stomatal conductance, and therefore increases dry mass output by minimizing water losses through transpiration [64]. It has been reported that Si treatment minimized transpiration in plants, possibly due to the creation of a silica cuticle double layer under the leaf

epidermis, which reduces water losses through cuticular transpiration [65,66]. It might also enhance water uptake and transportation, improve leaf water potential, and modify root hydraulic conductance, leading to higher stomatal conductance and transpiration rates. Si-induced alterations in stomatal response may help plants solve the challenge of maintaining stomatal openness for CO₂ absorption while avoiding water stress. Under salinity conditions, Si treatment was also discovered to improve water relations, allowing for better growth rates and mitigating salt toxicity effects [67–69]. Si promotes root water uptake by activating osmotic adjustment and increasing aquaporin activity [67]. Under salinity stress, Si application has also been shown to improve water relations, enabling faster growth rates and mitigating salt toxicity effects by blocking the passage of Na⁺ ions into plants [68]. Silicon may improve or increase the rate of stomatal conductance by protecting the stomatal aperture from degradation [69].

6. Nutrient Uptake and Balance

Exogenous Si supply has the function of balancing mineral uptake and mobility in stressed plants, especially when caused by uneven nutrient supply or root exposure to relatively high concentrations of harmful substances [16,48]. For example, under a high phosphorus (P) supply, zinc (Zn) deficiency can occur. However, the application of Si may successfully prevent this imbalance [18]. Furthermore, Si has been observed to mitigate the symptoms of Cu, B, and Mn toxicity and Fe-deficient stress in plants [70–72]. Si lowered Mn concentrations, enhanced SOD, APX, and ascorbate-glutathione cycle activity, and decreased H₂O₂ levels in the leaves, reducing Mn toxicity to cucumber plants [70]. Si's ability to reduce the transit of B, Cl, and Na may be attributed to its irreversible precipitation as amorphous silica (SiO₂·nH₂O) in cell walls and lumens. This has been considered to limit the transportation of salts into shoots [71]. Si and nSi (nano silicon) have significant effects on plant biomass by improving photosynthetic performance and regulating nutrient uptake–accumulation and mineral element distribution from root to shoot, as well as reducing oxidative stress [72]. The application of Si has been shown to minimize the plants' uptake of unfavorable non-nutrient ions like Na⁺ and Cl[−], as well as hazardous metals like Al, Cd, and hexavalent chromium [16,73,74]. Numerous physiological mechanisms contribute to Si's beneficial impacts on mineral uptake and transport into plant tissues. One key mechanism is Si's ability to maintain membrane selectivity to ion influx and efflux, thus avoiding or reducing increases in plasma membrane permeability produced under stresses. Reports have shown that Si protects plasma membrane integrity in plants cultivated under stress conditions [75–77]. Si can play an important role in lowering shoot sodium content in rice by blocking bypass flow, most likely through the development of silica gels or polysilicic acids, as well as improving suberization and lignification [75]. Silicon accumulation in the root is related to a reduction in apoplastic bypass flow. Casparian bands normally prevent ions and water from moving through the apoplast's endodermis [76]. Si increased the stability of lipids in plant cell membranes under drought and heat stress, implying that Si avoided the structural and functional degeneration of cell membranes when plants were stressed by the environment [77]. These findings emphasize silicon's various roles in plant stress tolerance, as well as its potential to help design sustainable cropping systems.

7. Phytohormone Regulation

Exogenous Si supply has been investigated for its impact on endogenous phytohormone levels, as well as its relationship to stimulatory Si actions on plants. Silicon has been shown to affect the levels of endogenous phytohormones, particularly in response to stress, and this interaction is critical for improving plant resilience and growth. For example, in plants exposed to heavy metals, Si has been found to decrease the endogenous levels of jasmonic acid (JA) and salicylic acid (SA) [50]. It has also been observed to boost cytokinin production [78]. Moreover, a considerable reduction in endogenous gibberellin levels was observed in plants subjected to salt stress; however, Si application prevented this reduction [79]. Rice plants that were treated with Si and exposed to wounding stress had

considerably lower JA levels than control plants. As a result, the relative expression levels of mRNA for JA biosynthesis gene regulation during Si and wounding stress treatments were investigated, and it was demonstrated that the JA synthesis-related genes respond to wounding stress during Si application [80]. However, further research is needed to acquire a better understanding of the specific processes by which Si impacts phytohormone levels, as well as their effects on plant physiology and stress responses.

8. Gene Expression

The effects of exogenous Si supplementation on gene expression in stressed plants have been investigated. Si was discovered to promote the expression of transcription factors involved in drought-responsive gene expression in rice, such as NAC5 and DREB2A, and to downregulate the mRNA expression of enzymes encoding heavy metal transporters in rice plants exposed to high-Cd and high-Cu stress [81]. Furthermore, Si was also shown to activate and regulate several photosynthesis-related genes in response to high-Zn stress, thus enhancing photosynthesis in Zn-stressed plants. Also, Si may trigger accelerated expression of the PsbY gene in rice, which encodes a new manganese-binding, low-molecular-mass protein involved with PSII (Photosystem II). The activation of PsbY mRNA transcripts may boost PSII activity and electron transfer rate in rice, as evidenced by an increase in chlorophyll content [82]. Moreover, Si also triggered the upregulation of genes involved in defense and stress response: disease resistance response protein, ferritin, late embryogenesis abundant protein, trehalose phosphatase, and acetoacetyl-CoA thiolase [83]. Si's bioactivity as a regulator of plant defense mechanisms can be explained by its biochemical characteristics. Si can bind to hydroxyl groups on proteins that are strategically implicated in signal transduction. Si may also interact with the cationic cofactors of enzymes, altering pathogenesis-related activities. As a result, Si may interact with a number of important components of plant stress signaling systems, causing induced resistance. In a previous study, different quantities of both polymer and monomer sodium silicate were investigated for their capacity to diminish the severity of miniature rose powdery mildew disease [84]. The results presented indicate that Si may regulate gene expression in plants, particularly under stress conditions, and that this interaction is critical for improving plant resilience and growth.

9. Role of Silicon in Biotic and Abiotic Stress Tolerance

The vital roles of Si that participated in biotic and abiotic stress tolerance are summarized in Figure 1.

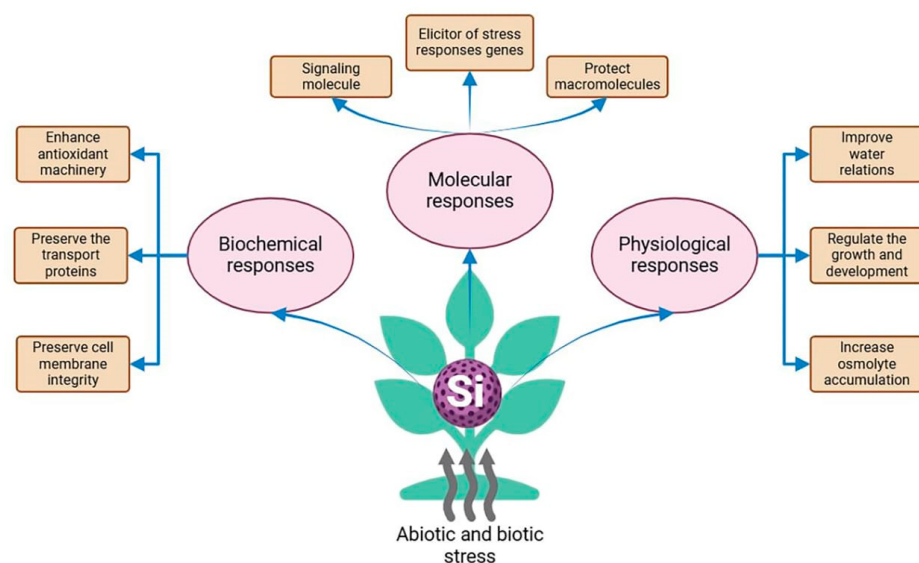


Figure 1. The vital roles of silicon in biotic and abiotic stress tolerance.

9.1. Abiotic Stress

Abiotic stresses have decreased the productivity of several crops by more than 50% [85–87]. Vital processes within the plant such as respiration, the transport of photosynthesis products, photosynthesis, the absorption of elements, the opening and closing of stomata, and seed germination are affected by several stresses such as drought [88–90], salinity [91,92], heavy metals [93], and low temperature [94]. Silicon has been demonstrated to alleviate abiotic stresses in plants by promoting photosynthesis at different levels, such as maintaining or improving limits in net assimilation rates compared to stressed plants not provided with Si [16,52,95]. The utilization of Si has been demonstrated to enhance photosynthetic rate, leaf and root water potential, and water use efficiency, while decreasing transpiration rate and membrane permeability under drought stress conditions in varied species [64,65,69]. Reports indicate that Si can affect the activities of enzymes directly engaged in photosynthesis, such as ribulose-bisphosphate (RuBP) carboxylase-oxygenase, which is considerably enhanced by Si supply [96–99]. Furthermore, Si was connected to boosting leaf rigidity and erectness, resulting in enhanced photosynthesis [16]. These findings highlight silicon's ability to boost photosynthetic efficacy while mitigating the negative impacts of stress on plant growth and development.

9.1.1. Drought

Drought is considered one of the most dangerous types of stress affecting the environmental balance and agricultural systems, as drought reduces the rates of photosynthesis, which ultimately affects the growth and productivity of M&APs [100,101]. Silicon protects plants against drought stress through various mechanisms such as regulating the action of the aquaporin gene; enhancing the accumulation of soluble sugars and/or amino acids in the wood sap, which increases the osmotic driving force; or activating the transfer of potassium to the wood sap via the SKOR (Stelar K⁺ Outward Rectifier) gene. Additionally, it is also possible for silicon to improve the hydraulic conductivity of the roots by modifying root growth and increasing the root/shoot ratio along with raising the activity of aquaporin and the osmotic driving force, which improves water absorption under water deficiency or drought conditions [67,102]. Exogenous application with Si improved seed germination under drought stress and protected young seedlings from oxidative stress by improving antioxidant defense. The application of calcium silicate also improves maize seed germination under drought stress [103,104]. The application of silicon increases the rate of photosynthesis and water use efficiency and improves osmotic potential while reducing the rate of transpiration and membrane permeability under drought stress conditions in several plants such as fennel [105], Kentucky bluegrass [88], oil palm [106], and white lupine [107]. One of the main effects of drought stress is to reduce the absorption of essential elements [108]. In this regard, it was found that the application of silicon increases the rate of absorption of macro-elements (P, K, Ca, and Mg) and micro-elements (Fe, Cu, and Mn) under drought stress [108]. Otherwise, the phosphorus and potassium contents in rice straw were markedly increased due to Si treatment under water deficit conditions compared to untreated plants [109]. It was also noted that applying Si under drought stress helps regulate gaseous exchange attributes [106,110]. It has also been reported that Si reduces oxidative stress by activating antioxidant enzymes (SOD, APX, CAT, and POD) under conditions of water deficiency stress in many plants like sunflower [108], tomato [56], and chickpea [71]. Moreover, Si treatment activates the expression of drought-tolerance genes in rice plants [111].

9.1.2. Salinity

Recently, soil salinity has limited the production of agricultural crops, leading to a severe shortage in food production at the industrial and commercial levels [92,112]. Globally, 6% of agricultural lands are classified as saline, and this percentage is expected to increase by 2050 due to accelerating climate change, which will increase the challenges facing global food production [16,113]. Actually, Si reduces the adverse impacts of salt stress

through various mechanisms. The basic mechanisms of Si that participate in salt stress alleviation are maintaining the water balance within the plant, increasing the absorption and assimilation of elements, regulating the biosynthesis of compatible plant hormones and solutes, reducing oxidative stress, modifying gas exchange, modifying gene expression, and reducing sodium absorption and accumulation. It has been widely confirmed that treatment with silicon reduces sodium absorption and increases the potassium-to-sodium ratio under conditions of salt stress [103,114,115]. Salt stress leads to severe nutritional disorders within the plant [103,116]. It has been reported that applying silicon increases the calcium and magnesium content of leaves and roots in tomato plants under salt stress [117]. It also increases potassium, calcium, phosphorus, and magnesium in Egyptian clover [118]. The Si treatment also increases the rate of photosynthesis, the water-use efficiency, the hydraulic conductivity of the roots, and the size and number of stomata in wheat [114], faba bean [119], sorghum leaves [120], wheat [121], rice [122], okra [123], sweet pepper [124], and maize [125]. The application of silicon reduces the oxidative damage that occurs to plants under conditions of salt stress by increasing the activity of antioxidant enzymes (SOD, CAT, POD, GSH, and APX), maintaining the fluidity of the plasma membranes in their optimal state, and reducing the generation of ROS [126,127]. The application of silicon can also enhance the plants' tolerance to salt stress by controlling the levels of dissolved organic acids such as proline and glycine and total free amino acids in the leaf and root tissues of okra [123]. It also regulates the level of phytohormones such as gibberellin (GA) and reduces the level of abscisic acid (ABA) in soybean plants under conditions of salt stress [79]. Silicon regulates the gene expression of AQP in addition to improving water absorption in cucumber plants exposed to salt stress [128]. Moreover, the application of Si activates genes related to salt tolerance (leDREB-1, leDREB-2, and leDREB-3) in tomato plants under salinity stress [127].

9.1.3. Heavy Metals

Heavy metals, whether in the soil or reaching agricultural crops through irrigation water, greatly affect soil dynamics [12,129]. Mechanisms for mitigating the effects of stress with heavy elements in plants were investigated under Si application. It was found that Si reduces the concentration of heavy elements inside the plant by activating antioxidant enzymes and chelating and dividing the metals into inactive parts [130]. In this context, Si application reduced the accumulation of cadmium inside the rice plant by fragmenting cadmium in the root cell walls [131] and modifying gene expression and structural modifications in various plant parts [132]. Furthermore, soil application with Si reduces the transfer of heavy metals by raising the pH of the soil or binding these metals in the form of silica complexes [133]. The role of silicon in alleviating the harmful effects of heavy metals such as silver and manganese in many species such as pumpkin, sorghum, and soybeans [134] has been reported via reducing LPO density and improving the enzymatic and non-enzymatic (ascorbate and glutathione) antioxidant system [135]. It has also been found that Si application reduces the oxidative stress caused by arsenic contamination by reducing arsenic accumulation and enhancing the antioxidant system in the rice plant [136]. The silicon treatment of bean seeds exposed to cadmium and lead stress led to significant increases in the germination rate and relative water content compared to untreated plants [137]. The application of Si reduces the absorption and transport of heavy metals in the tissues of rice exposed to cadmium stress [70,138]. Otherwise, Si application significantly increases the regulation of the expression of genes responsible for silicon transport (OsLSi1 and OsLSi2) and regulates the expression of genes encoding heavy metal transporters (OsHMA2 and OsHMA3) in rice plants [80,139]. The treatment of Si increases the thickness of the epidermis, xylem diameter mesophyll, and the transverse area of collenchymas and the middle vein, which enhances the cells' tolerance to cadmium and Zn stress [140]. The application of silicon increases the value of (Soil–Plant Analyses Development) water use efficiency, transpiration rate, chlorophyll efficiency, and net photosynthesis rate in barley plants under conditions of chromium toxicity [141]. It was also confirmed that

the application of silicon enhances the gas exchange properties in barley under chromium stress [141], in cotton under lead stress [142], in peanuts under aluminum stress [143], and in rice under zinc stress [82]. In hydroponic solutions, Si application also led to an increase in the absorption and transfer of macro- and micro-nutrients under chromium, copper, and cadmium stresses [144,145]. In addition, Si treatment inhibits the absorption of zinc and its accumulation in the leaves and roots of maize and cotton [146,147].

9.1.4. Ultraviolet

Silicon also plays an important role in protecting plants from the danger of ultraviolet radiation by enhancing growth, improving the rate of photosynthesis, and activating antioxidants in soybean seedlings [148]. Silicon also increases the tolerance of wheat seedlings to ultraviolet radiation by improving the level of antioxidant compounds [149]. Under ultraviolet radiation stress, the application of Si also markedly improved the antioxidant machinery in corn relative to the control [150].

9.2. Biotic Stress

9.2.1. Physiological Effects of Silicon on Plants

Silicon accumulates in plant tissues, primarily in the form of silicon dioxide (SiO_2), which forms a physical barrier on the plant's surface. This barrier acts as a protective shield against several pathogens, including fungi, bacteria, and viruses. It makes it difficult for pathogens to penetrate the plant's epidermal cells and gain entry and also makes it more difficult for sucking insects and nematodes to penetrate plant cell walls with their stylets and for chewing insects to feed on plant tissue [151–153]. In a study aimed at enhancing rice resistance to blast disease, Kim et al. [154] observed the increase in silicon layers in the epidermis underneath the cuticle, in the middle lamella, on stomatal guard cells, and in the intercellular spaces in silicon-treated plants. This is considered evidence that silicon induces cell wall fortification. Additionally, the increased Si in rice biomass was accompanied by an increase in lignin, cellulose, and hemicelluloses [155]. The Si deposition enhances the strength and thickness of cell walls, making them more resistant to pathogen penetration and therefore reducing the chances of infection by pathogens. Mehrabanjoubani et al. [156] proved that the application of silicon under excess Fe nutrition can increase the root tip thickness and lignification of rice plants. Silicon application to plants stimulates antioxidant defense systems including enzymatic and non-enzymatic antioxidants and activates the genes responsible for stress defense [157]. Thus, Si treatment was proven to improve plant stress tolerance through several strategies such as controlling ROS production, decreasing malondialdehyde (MDA) content and ion leakage, and preventing the absorption of Na and other toxic ions [60]. Moreover, Si application interacted with salicylic acid and reduced the adverse impact of boron toxicity in peas and improved the growth and development via alleviating the oxidative damage, therefore maintaining the cell membrane integrity [158].

The accumulation of Si in plants depends on the plant's ability to continue absorbing silicon once the silicification process begins in older tissues. Additionally, Si-accumulator plants such as barley, wheat, and rice continue absorbing Si after the initial stages of silicification; hence, plant shoots contain more silicon than roots [159]. Contrarily, roots contained higher Si levels than shoots in non-silicon-accumulator plants [160].

9.2.2. Effects of Silicon on Plant–Pathogen Interactions and Field Applications

Plant resistance to diseases caused by fungi, bacteria, viruses, and other disease causal agents has been enhanced in different species by Si application. There are several methods for Si application to control diseases caused by pathogens, such as spraying, soaking seeds, or soil application. The choice of the best application method depends on the plant species, the type of disease, and the optimal plant growth stage. In this context, the lesions caused by *Colletotrichum* spp. were reduced by 80–87% and disease was decreased by 87–89% in tomatoes due to soil application with silicon compared to the untreated plants [161]. Interestingly, it was reported that Si acts as a physical barrier on the plant surface that blocks

the fungus from invading plant cells; therefore, Si-treated plants showed a higher number of fungal appressoria as infection signs of plant obstruction. The foliar application of Si effectively controlled leaf blast disease in rice compared to soil application. Additionally, Si treatment was more effective on the race-specific resistance against *Pyricularia grisea* when it was applied at the vegetative growth stage. Moreover, it caused a 100% suppression in all tested races of blast disease and was more effective than edifenphos (a fungicide used to control Anthracnose disease), and this effect was attributed to the increase in both silica deposits and the activities of defensive enzymes (Kim et al., 2002) [154]. Furthermore, soil or foliar application of Si increased its concentration in rice plants and significantly reduced the area under the disease progress curve (AUDPC) and disease index caused by blast disease [162]. Treatment with Si markedly reduced Fusarium wilt disease (*Fusarium oxysporum* f. sp. cubense) in banana by approximately 30–40%; foliar application was more effective than soil application. Such an effect was attributed to the inhibition of mycelial growth and spore production [162]. Silicon also helps plants tolerate attacks from sucking insects such as aphids, whiteflies, planthoppers, leafhoppers, thrips, and mites and chewing insects such as caterpillars, beetles, locusts, and grasshoppers. This effect is attributed to the physical barrier formed by silica deposition that prevents insects from penetrating the plant's epidermal tissue. The other reasons for such effects are inducing morphological changes in trichomes and leaf tissues that inhibit the feeding process and movement of insects on the surface of plant tissues, as well as inducing toxicity in the insect body once ingested [163].

Silicon has also been proven to induce systemic resistance in plants against various pathogens. Systemic resistance can be defined as an increase in a plant's ability to defend itself against pathogens (biotrophic or necrotrophic) after infection by a pathogen or treatment with chemical agents [164]. Gene resistance in plants is caused by the induction of the expression of pathogenesis-related proteins or the expression of genes related to the synthesis of phytoalexins [28]. Reports revealed that Si application increased the resistance of plants to diseases caused by bacteria, fungi, and viruses in several species such as rice [164,165] and cucumber [166]. The resistance to powdery mildew disease caused by *Erysiphe cichoracearum* in *Arabidopsis* has been increased due to Si application [167]. Foliar spray with a 2% solution of potassium silicate (K_2SiO_3) once every 2–3 weeks effectively controls blast disease in rice [154]. The most effective application method of Si to control leaf diseases caused by *Colletotrichum* spp. in tomatoes is foliar spray at the growth and flowering stages [159]. Actually, the mechanism of resistance induction by silicon in plants is not yet fully understood, but it is assumed that silicon stimulates the expression of pathogenesis-related PR proteins, increases the synthesis of phytoalexins, and induces a defense response mediated by jasmonic acid and ethylene.

10. Vital Roles of Silicon on Alleviating Abiotic and Biotic Stresses in M&APs

Silicon has been shown to effectively increase the tolerance of plants to various abiotic and biotic stresses, a role that has also been confirmed in several M&APs. For instance, the application of silicon has been found to improve the growth and productivity of borage (*Borago officinalis*) under salt-stress conditions. Such an effect was attributed to the role of Si in stabilizing the cell plasma membrane, preventing its deterioration, and therefore reducing the absorption of sodium ions. It also activates enzymatic and non-enzymatic antioxidants, thus enhancing the tolerance to salt stress [168]. Similarly, the performance of *Lonicera japonica* L. plants under salt stress has been improved due to Si application via enhancing photosynthesis, antioxidant systems, and reducing sodium ion absorption [169]. The treatment of Si successfully alleviated the negative impacts of salt stress in Licorice (*Glycyrrhiza glabra*) via improving the gas exchange, photosynthesis rate, chlorophyll content, and antioxidant defense systems. Further, it reduced the accumulation of sodium ions and increased total sugars, glutamine synthetase, and nitrate reductase enzymes' activity, as well as the total nitrogen in plant tissues [170]. Silicon application also enhanced the morphological characteristics of licorice leaves, increasing water content, vascular bun-

dle conductivity, palisade tissue size, chlorophyll content, and photosynthesis efficiency, thereby enhancing plant growth and development under salt-stress conditions [171,172]. Additionally, Si treatment in *Satureja hortensis* plants exposed to salt stress markedly increased the relative water content, chlorophyll content, essential oil yield, and K/Na ratio and enhanced the antioxidant machinery. It also reduced the levels of reactive oxygen species such as hydrogen peroxide and malondialdehyde compared to untreated plants [173]. The application of silicon nanoparticles considerably improved the growth of basil under salt-stress conditions accompanied by increasing the leaf chlorophyll content and proline level, indicating enhanced tolerance to salt stress [174].

Similarly, Si application has been beneficial in alleviating drought stress in M&APs. In this concern, Si treatment improved the growth of Damask rose (*Rosa damascena*) and enhanced the content of active ingredients in essential oils such as geraniol and citronellol. It also enhanced chlorophyll content, Rubisco enzyme activity, and photosynthesis efficiency [175]. Otherwise, the adverse effects of drought on young eucalyptus seedlings were alleviated due to Si treatment by preventing the decrease in chlorophyll, reducing oxidative stress by increasing the activity of guaiacol peroxidase and superoxide dismutase enzymes, improving the water use efficiency, reducing the transpiration rate, and enhancing osmotic regulation [66]. Additionally, Si treatment has been shown to reduce damage resulting from heavy metal toxicity. For example, Si application effectively reduced copper toxicity in *Arabidopsis thaliana* by modifying the genetic expression of the COPT1 gene responsible for copper transport, leading to improved plant growth and enhanced copper stress tolerance [176]. Furthermore, even in normal conditions, the exogenous application of silicon has been found to improve the vegetative growth, flower production, and quality of *Narcissus tazetta* L. [177].

In terms of biotic stress, silicon treatment has shown effective roles in combating insect pests and pathogens in several plant species, including M&APs. In this context, Si application reduced the sensitivity of plants to leafhoppers and both stem and leaf borers by acting as a physical barrier under the epidermis of the leaves, preventing the penetration of insects and fungi. It also enhances plant resistance to pathogens by increasing the production of lignin, phytoalexins, and phenols [178]. Additionally, the resistance of rose plants to powdery mildew has been improved due to silicon treatment [84]. The defense system against infection with the *Botrytis* fungus in *Arabidopsis* was markedly enhanced due to Si application via improving the gene expression of the PDF1 gene [179]. The vital roles of silicon on alleviating abiotic and biotic stresses in M&APs have been summarized in Tables 1 and 2.

Table 1. The vital roles of silicon on alleviating abiotic stresses in medicinal and aromatic plants.

Plant	Kind of Stress	Silicon Role	Reference
1- <i>Foeniculum vulgare</i> L.	Drought	Reducing the rate of transpiration and the permeability of membranes and improving the use of water and osmotic capacity.	Asgharipour and Mosapour 2016 [105]
2- <i>Helianthus annuus</i> L.	Drought	Increasing the activity of antioxidant enzymes (SOD, APX, CAT, and POD).	Gunes et al., 2008 [108]
3- <i>Scrophularia striata</i> L.	Drought	Increasing gas exchange indicators, increasing the rate of photosynthesis, increasing the moisture content and total protein inside the plant.	Shohani et al., 2022 [180]
4- <i>Sorghum bicolor</i> L.	Drought	Increasing leaf area, increasing the percentage of chlorophyll, and improving photosynthesis rates.	Ahmed et al., 2014 [181]

Table 1. Cont.

Plant	Kind of Stress	Silicon Role	Reference
5- <i>Ocimum basilicum</i> L.	Drought	Increasing enzymatic antioxidant activity, improving osmotic regulation, and improving essential oil productivity.	Farouk and Omar 2020 [182]
6- <i>Nicotiana Rustica</i> L.	Drought	Improving the activity of antioxidant enzymes; increasing the percentage of free amino acids, soluble proteins, and proline; and reducing H ₂ O ₂ levels within the plant.	Hajiboland et al., 2017 [183]
7- <i>Calendula officinalis</i> L.	Drought	Improving the rate of seed germination and seedling growth under drought stress.	Saeedeh et al., 2021 [184]
8- <i>Tanacetum parthenium</i> L.	Drought	Improving the absorption of some elements such as phosphorus and water use efficiency and increasing the water content within the plant.	Esmaili et al., 2021 [185]
9- <i>Ygophyllum xanthoxylum</i> L.	Drought	Increasing the chlorophyll content of the leaves as well as the water content and increasing the activity of antioxidant enzymes.	Kang et al., 2016 [186]
10- <i>Coriandrum sativum</i> L.	Drought	Increasing the efficiency of used water, total soluble sugars (TSS), phenols, and total flavonoids.	Afshari et al., 2021 [187]
11- <i>Ocimum basilicum</i> L.	Salinity	Increasing chlorophyll, carbohydrates, and the activity of antioxidant enzymes and reducing the proportion of H ₂ O ₂ in the plant.	Sharifian Jazi et al., 2023 [188]
12- <i>Stevia rebaudiana</i> L.	Salinity	Reducing sodium absorption and increasing steviol glycoside production.	Yavaş et al., 2019 [189]
13- <i>Ocimum basilicum</i> L.	Heavy metal (Cd)	Increasing the activity of antioxidant enzymes, phenols, flavonoids, caffeic and choric acids, reducing cadmium absorption and accumulation, and reducing MDA content and the rate of electrolyte leakage.	Gheshlaghpour et al., 2021 [190]
14- <i>Salvia officinalis</i> L.	Heavy metal (Cu)	Strengthening the enzymatic antioxidant system, increasing protein content, regulating the gene expression of the SOD enzyme, and reducing oxidative damage.	Pirooz et al., 2021 [191]
14- <i>Brassica napus</i> L.	Heavy metal (Cd)	Si treatment reduced the H ₂ O ₂ and MDA contents and improved the activity of antioxidant enzymes.	Hasanuzzaman et al., 2017 [192]
15- <i>Nigella sativa</i> L.	Heavy metal (Cd)	Improving relative water content (RWC) and chlorophyll content and reducing Cd absorption	Sharifi Rad et al., 2014 [193]
16- <i>Aloe barbadensis</i> L.	Low temperature	Enhancing the activity of antioxidant enzymes and increasing the percentage of total dissolved sugars.	Azarfam et al., 2020 [194]

Table 1. *Cont.*

Plant	Kind of Stress	Silicon Role	Reference
17- <i>Euphorbia pulcherrima</i> L.	High temperature	Improving photosynthesis, regulating the opening and closing of stomata, reducing oxidative damage, and reducing MDA and H ₂ O ₂ levels within the plant.	Hu et al., 2020 [195]
18- <i>Phyllostachys praecox</i>	Low temperature	Activating the plant's enzymatic antioxidant system.	Qian et al., 2019 [196]

Table 2. The vital roles of silicon in alleviating biotic stresses in medicinal and aromatic plants.

Plant	Kind of Stress	Silicon Role	Reference
1- <i>Rosa</i> sp.	Powdery mildew	Improving the gene expression of the phenylalanine ammonia-lyase PAL.	Elsharkawy et al., 2015 [84]
2- <i>Arabidopsis thaliana</i>	Botrytis	Improving the gene expression of the PDF1 gene.	Cabot et al., 2013 [179]
3- <i>Panax ginseng</i>	Ginseng root rot	Decreasing the expression of the PgSWEET gene results in controlled sugar transport into the apoplast and improving tolerance to <i>I. mors-panacis</i> .	Abbai et al., 2019 [197]
4- <i>Nicotiana tabacum</i>	Viral infection	Silicon accumulation in leaf tissue delayed infection compared to untreated plants.	Zellner et al., 2011 [164]
5- <i>Lolium perenne</i>	Fusarium patch	Increase resistance to disease by depositing a physical protective barrier on the leaf tissue.	McDonagh and Hunter, 2010 [198]
6- <i>Momordica charantia</i>	Powdery mildew	Si accumulates below the cuticle, forming a barrier against pathogens and inducing metabolic defensive responses in plants.	Ratnayake et al., 2016 [199]
7- <i>Pennisetum glaucum</i>	Downy mildew	Increasing the level of silicon in tissues led to an increase in the level of glycoproteins rich in hydroxyproline, which led to the increased resistance of plants to the pathogen.	Deepak et al., 2008 [200]
8- <i>Stenotaphrum secundatum</i>	Gray leaf spot	Increasing plant resistance to gray leaf spot by the accumulation of calcium silicate	Brecht et al., 2007 [201]

11. Conclusions and Perspectives

This review highlights the pivotal role of silicon in enhancing plant tolerance to a wide range of abiotic and biotic stresses. The findings from numerous studies demonstrate that silicon application can significantly mitigate the adverse effects of drought, salinity, heavy metal toxicity, and pathogen/pest attacks in plants, including medicinally important species. The mechanisms by which silicon confers stress tolerance are multifaceted, involving the regulation of antioxidant systems, water relations, nutrient homeostasis, phytohormone signaling, and the expression of stress-responsive genes. Moreover, the deposition of silicon in cell walls provides physical reinforcement and acts as a barrier against pathogen invasion and insect herbivory.

Notably, several studies on medicinal plants, such as borage, honeysuckle, licorice, Damask rose, savory, basil, and eucalyptus, have shown that silicon supplementation can effectively alleviate stress-induced damage and enhance the production of valuable secondary metabolites and essential oils. These findings underscore the potential of silicon

fertilization as a sustainable strategy to improve the productivity and quality of medicinal crops under changing environmental conditions. While the beneficial effects of silicon are well-documented, further research is warranted to fully elucidate the molecular mechanisms underlying silicon-mediated stress tolerance. Elucidating the intricate signaling pathways and gene regulatory networks involved in silicon-induced stress responses could pave the way for the development of more targeted and efficient approaches for enhancing plant resilience. Additionally, field trials and practical applications of silicon fertilizers in medicinal plant cultivation should be explored to validate the findings from controlled experiments and facilitate the adoption of this promising strategy in sustainable agriculture.

Author Contributions: Conceptualization, K.M.H., A.N.A., M.A.A.A. and M.E.; validation, K.M.H., R.A., A.N.A., M.A.A.A. and M.E.; investigation, K.M.H., R.A., A.N.A., I.F.H., F.A.S.H., S.M.A.-E. and M.E.; resources, K.M.H., R.A., A.N.A., M.A.A.A., I.F.H., F.A.S.H., S.M.A.-E. and M.E.; writing—original draft preparation, K.M.H., R.A., A.N.A., M.A.A.A., I.F.H., F.A.S.H., S.M.A.-E. and M.E.; writing—review and editing, K.M.H., R.A., A.N.A., M.A.A.A., I.F.H., F.A.S.H., S.M.A.-E. and M.E.; visualization, A.N.A., M.A.A.A., I.F.H., F.A.S.H., S.M.A.-E. and M.E.; supervision, K.M.H., R.A., I.F.H., F.A.S.H., S.M.A.-E. and M.E.; project administration, K.M.H., R.A., I.F.H., F.A.S.H. and S.M.A.-E. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Conflicts of Interest: The authors declare no conflicts of interest.

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