



# Impact of Silicon on Plant Nutrition and Significance of Silicon Mobilizing Bacteria in Agronomic Practices

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## Abstract

Globally, rejuvenation of soil health is a major concern due to the continuous loss of soil fertility and productivity. Soil degradation decreases crop yields and threatens global food security. Improper use of chemical fertilizers coupled with intensive cultivation further reduces both soil health and crop yields. Plants require several nutrients in varying ratios that are essential for the plant to complete a healthy growth and development cycle. Soil, water, and air are the sources of these essential macro- and micro-nutrients needed to complete plant vegetative and reproductive cycles. Among the essential macro-nutrients, nitrogen (N) plays a significant in non-legume species and without sufficient plant access to N lower yields result. While silicon (Si) is the 2nd most abundant element in the Earth's crust and is the backbone of soil silicate minerals, it is an essential micro-nutrient for some plants. Silicon is just beginning to be recognized as an important micronutrient to some plant species and, while it is quite abundant, Si is often not readily available for plant uptake. The manufacturing cost of synthetic silica-based fertilizers is high, while absorption of silica is quite slow in soil for many plants. Rhizosphere biological weathering processes includes microbial solubilization processes that increase the dissolution of minerals and increases Si availability for plant uptake. Therefore, an important strategy to improve plant silicon uptake could be field application of Si-solubilizing bacteria. In this review, we evaluate the role of Si in seed germination, growth, and morphological development and crop yield under various biotic and abiotic stresses, different pools and fluxes of silicon (Si) in soil, and the bacterial genera of the silicon solubilizing microorganisms. We also elaborate on the detailed mechanisms of Si-solubilizing/mobilizing bacteria involved in silicate dissolution and uptake by a plant in soil. Last, we discuss the potential of silicon and silicon solubilizing/mobilizing to achieve environmentally friendly and sustainable crop production.

**Keywords** Silicon (Si) · Silicon mobilizing bacteria · Biotic and abiotic stress · Crop production

## 1 Introduction

Among the plant macro- and micro- nutrients, silicon (Si) is the 2<sup>nd</sup> most abundant element in the earth's crust. In most soils, the Si concentration varies from 25 to 35% [1]. It is a basic rock-forming mineral and an important component of most soils. Silicic acid ( $H_4SiO_4$ ) is most common available form of silicon in the soil. It becomes available through the pedogenic dissolution of the primary and secondary minerals. Si is also available via adsorption or desorption of hydrous oxides of Fe and Al with silicate on the cation exchange sites [2].

Even though silicon is important in plant biochemical and physiological processes but also play important role in plant survival and performance under plant stress. However, It is not a beneficial micronutrient to all plants [3]. In 2013–14,

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the Association of American Plant Food Control Officials (AAPFCO) classified and acknowledged Si as a beneficial plant micro-nutrient [4, 5] which increased the understanding of the application and use of Si for plant protection and production [6–8].

However, detailed information is still missing about its numerous beneficial roles in plant life under normal and stress conditions [9, 10]. For example, Si addition can enhance seed germination, seedling vigor and growth, and later impacts on nitrogen-fixation, photosynthesis, root-shoot morphogenesis [9, 11, 12], nutrients absorption and yield potential [13–15]. Soluble or readily available Si in soil improve the growth and crop yield. In addition, Si also helps to build resistance in various plant species against biotic and abiotic stresses [16]. Si fertilization has many positive effects on rice and wheat crops which are important staple food crops across the world [11, 17–19]. Some reports show that the application of Si alleviates heavy metal stress, extreme temperatures and water stress [20]. Si may also lower the effects of diseases such as brown spot, sheath brown [21], powdery mildew [22] and rice blast [23] while also assisting in the uptake of many important nutrients (Mg, K, P, Zn, Cu and Fe) in rice plants [24]. Multi-beneficial characteristics of Si against different stresses and various other positive effects suggests it as a beneficial element for sustainable crop production [25–28]. Soils developed from the weathering of rocks contain a significant amount of silicates, aluminosilicates and silica [29, 30] that may be unavailable to crops due to the lack of silica solubilizing microorganisms [31]. While silica is needed by some plants, rock weathering by silica solubilizing bacteria also speed up soil pedogenic processes and the release of various nutrients [32].

Though the presence of a large amount of insoluble polymeric silica has been observed in soils, these compounds are not readily available to plants except for a negligible amount of soluble Si [33]. During weathering, silicate solubilizing bacteria release acids that convert the polymeric silicate into bioavailable forms which plants preferred to absorb [34]. The formation of monosilicic acid occurs due to the weathering of silicate containing minerals, desorption from the irrigation water and soil solution [35]. Plants, soil and microorganisms also generate pools of Si by silicate mineral weathering via modifying soil physicochemical properties, altering the soil pH and developing chelates and ligands [36]. It is stated that the maximum solubility of  $\text{Si}(\text{OH})_4$  is 2 mM in solution while in soil its amount varies between 0.1 and 0.6 mM [20]. Recently, studies reviewed the role of microbial communities in biologically induced/biologically controlled mineralization, chalcedony crystals, carbonate speleothems and silicate speleothems in the caves [37]. During the silica cycle, bacteria regulate the biogeochemical cycles that transform polymerized silica into monomeric forms [38, 39]. As soil pH increases, monomeric

acids breakdown in the presence of bases and hydrogen ion is removed. This reaction continues in the presence of a base and less stabilized polymorphs formed by the removal of hydrogen ion [40].

Bacteria perform significant role in the silicon cycle that releases important crop nutrients including K, Ca, and Mg [41–43]. Unlike other synthetic fertilizers, limited quantities and brands of Silicon based fertilizers are available in the market and are often unaffordable to many farmers due to their high prices [44]. Therefore, at the global level, the use of Si fertilizer is quite rare [4, 45, 46]. This study assesses the mechanistic approach behind the Si solubilizing bacterial to solubilize and release Si from insoluble sources such as primary and secondary minerals etc.

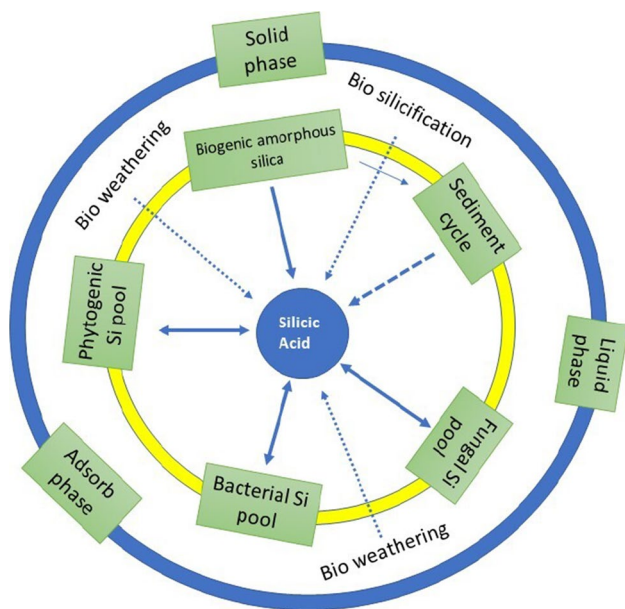
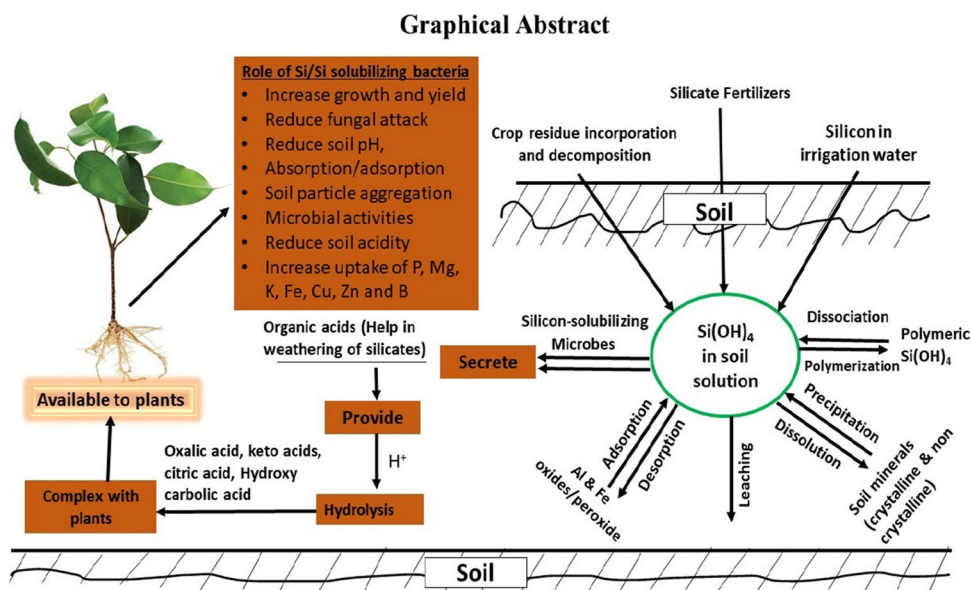
Silicate solubilizing bacteria have been characterized as bio-fertilizers that increase silicate solubilization but research studies are limited [39, 47]. Various bacterial species have been isolated and cultured that enhance the silicates dissolution in soil [19] through pedogenic processes that are considered the primary source of active Si in soil and plant systems [11]. Another novel strategy to accelerate the bio-availability of Si in the soil is to increase the growth of naturally occurring bacteria involved in soil silicate weathering in conjunction with low-cost and abundant soil silicates.

The objective of this study is to highlight the importance of Si, role of Si under biotic and abiotic stresses, application of silicon for agriculture production, role of silicon solubilizing bacteria to solubilize silicon from silicon minerals (Primary, secondary minerals and silicate), highlight the important silicone solubilizing genera of microorganisms. Furthermore, this review also briefly highlights the role of Si in the availability of P, K, Fe, Mg and Zn in soil. A detail how silicon solubilizing bacteria work shown in Fig. 1.

## 2 Silicon Pools and Fluxes in Soils

The earth's crust contains about 28.8% of silicon. Si is involved in many biogeochemical cycles through weathering processes and subsequent Si flux into oceans. In soils, various processes cause the formation of Si pools including primary minerals, secondary minerals derived from primary ones, and secondary microcrystalline as soil strata in soil formation [48]. Cristobalite is also a major source of silicon and is derived from weathering of volcanic rocks. Many environmental factors like temperature, pH, acidity, organic anions and cations assist in the formation of secondary Si-minerals. Acidification acts as a secondary source triggered by the degradation of clay minerals [49]. Years of field research is required to interpret the results of tests and other analysis of soil. When acetic acid soil extraction method was used, soils showed Si from

**Fig. 1** Graphical abstract; how silicon mobilizing/solubilizing bacteria work and improve crop production



**Fig. 2** Schematic overview of different silicon pools in the soil and role of biota in silicic acid formation

4–35 mg /L with the average range of 14 mg/L [50]. In terrestrial lands and soil ecosystems, Si fluxes are mostly mediated by water. Silicic acid is the major component of soil solution in the form of monomeric silicic acid [51, 52]. This monomeric form is converted into polymeric silicic acid under different prevailing conditions [53, 54]. This polymeric form contains two or more Si atoms arranged in different patterns inside the formulated structure [55, 56]. In soil, Si pools are present in the form of solid, liquid and adsorbed phase shown in Fig. 2. While

**Table 1** Major sources of availability silicon in soil for plant uptake

Source of silicon	Reference
Primary Silicates	Feldsars, mica, olivine, pyroxene [63]
Secondary silicates	Clay minerals [63]
Silicate materials	Quartz, disordered silica [63]
Biogenic forms	Microorganism remains, Si-rich plant and Phytoliths [63, 64]

major sources of silicon in soil which are available for plant to uptake given in the Table 1. Biogenic Si sources can be divided into three main categories as protozoic, microbial and phytogenic [57].

Microbes perform the degradation of plant leaf litter and then release the Si from the respective source. Microbial cell membranes of microbes are also responsible for the bio mineralization of Si. The precipitated Si is taken up through plant roots and assimilated into the plant biomass. In the terrestrial system, this phytogenic Si pool is also a source of Si [58].

During soil pedogenesis, Si can leach or accumulate in the soil. Most of the time, Si loss was reported as a result of desilication that mainly depends on the level of stratification, weathering contents of the Si-containing parent material, and profile saturation [59–61]. By increasing CO<sub>2</sub> partial pressure of soil solution followed by the exudation of organic components, plants increase the weathering of silicates which abruptly increases the Si influx in the bio-geosystem. This explains the obvious mechanism of Si influx by the plant in soil and this also occurs through the litter decomposition in the soil [62].

### 3 Silica Solubilizing Bacteria

Minerals are altered by microorganisms as they compete with other organisms to increase their ability to survive in a given environment [65, 66]. Mineral decomposition provides mineral nutrients, a terminal electron acceptor in cellular respiration [67], and enhances the competition among the microbial species [65]. Some minerals are absorbed to increase the uptake of specific compounds which are involved in oxidation or reduction that lead to the breakdown of inorganic species during the energy utilization process [68, 69]. Many species of bacteria are involved in the release and control of Si through various steps like the arrangement, integration or disintegration of minerals [70, 71]. Various bacterial strains are recognized for their ability to increase the release of Si from silicate and improve plant growth and development. The most obvious strains are belonging to *Bacillus*, *Pseudomonas*, *Proteus*, *Rhizobia*, *Burkholderia*, and *Enterobacter* (Table 2). However, Systematic analysis of Si solubilizing bacterial strains by using 16S rDNA based sequencing technique highlighted *Pseudomonas* and *Bacillus* as two dominant Si solubilizing microbial genera. This investigation also revealed the role of *Sphingobacterium* sp. [72]. The mechanism of silicon mobilizing bacteria and how works is shown in Fig. 5.

#### 3.1 Bacillus

*Bacillus* species are rod-shaped, facultative anaerobes. *Bacillus* are mainly Gram-positive organisms but many

species may transform into Gram-negative bacteria over time. Various species belonging to this genus have a broad spectrum of functional capacities which helps to survive in negative environmental conditions [73].

Production of  $\text{SiO}_2$  and  $\text{K}^+$  from silicate minerals by *Bacillus mucilaginosus*, *Bacillus globisporus*, and *Bacillus circulans* in fluid cultures was also examined in laboratory-based incubation tests [74]. It was found in these tests that *B. mucilaginosus* break up the micaceous minerals and increased the release and availability of  $\text{SiO}_2$  and  $\text{K}^+$  from silicate crystal lattices. It was noted that the same bacteria did not produce any change in feldspar minerals [75]. *B. mucilaginosus* also released organic acids and polysaccharides [76]. The polysaccharides adsorbed these natural acids and linked with the surface of the minerals. The polysaccharides additionally adsorbed  $\text{SiO}_2$  and this influences the exchange between the mineral and liquid stages and drives the response of  $\text{SiO}_2$  and  $\text{K}^+$  solubilization. These two mechanisms decay the silicate minerals by using the bacterial species [75].

#### 3.2 Pseudomonas

*Pseudomonas* bacteria are Gram-negative, oxygen-consuming species (aerobic bacilli) with an average size of about 0.5 to 0.8  $\mu\text{m}$  by 1.5 to 3.0  $\mu\text{m}$  [77]. This species is mostly motile with a single and polar flagellum [78]. DNA hybridization, genetic and biochemical tests are used to identify bacterial species [79].

The results from numerous experiments demonstrated that the most noteworthy effect of silica is the phosphorus

**Table 2** Important silicon solubilizing bacterial genera

Bacterial genera	Specifications	Mechanisms	Example	Reference
Bacillus	Rod-shaped, facultative anaerobic, Gram-positive organisms	Withdrawal of $\text{SiO}_2$ and $\text{K}^+$ from silicate minerals. Production of natural acids of organic nature and polysaccharides	<i>Bacillus mucilaginosus</i> , <i>Bacillus globisporus</i> <i>Bacillus circulans</i>	[73]
Pseudomonas	Gram-negative, aerobic bacilli	Noteworthy effect of Si on P uptake and other supplements. Helpful alternate of chemical phosphate fertilizer	<i>Pseudomonas syringae</i>	[79]
Proteus	Motile, Gram-negative rods, aerobic and facultative anaerobic bacteria	Tentatively polymerized silica	<i>Proteus mirabilis</i>	[84]
Rhizobia	Gram-negative, aerobic, nitrogen fixer	Along with silicon solubilization provide organic nitrogenous compounds like glutamine to the plant Strides $\text{N}_2$ fixation and resistance towards saltiness push	<i>Rhizobium leguminosarum</i>	[89]
Burkholderia	Gram-negative, obligative high-impact, rod-shaped microbes, motile	Along with plant growth promotion solubilization of insoluble Si	<i>Burkholderia eburnean</i>	[110]
Enterobacter	Gram-negative, facultative anaerobes	As a silicon and phosphate biofertilizer, production of plant growth hormones, alkali, and an acid generation that compel plant development advancement and supplement disintegration	<i>Enterobacter ludwigii</i>	[114]



uptake and many other nutrients in the sorghum plants is stimulated by the *Pseudomonas syringae* [80]. After utilizing 600 mg/kg Si for culturing sorghum plants, it was observed the optimum concentration for the expansion of Si component measurement, under solvent P and beneath rock phosphate (RP) fertilization [81]. Treatment of plants at this concentration of Si had a substantial effect on plant development while overall parameters under an unstressed environment demonstrated that the impact of silica was not plant specific (utilized by recombinant plants). Results also recommend that silica along with RP fertilization had a synergistic impact which could be a helpful substitute for chemical phosphate fertilizer [82, 83].

### 3.3 Proteus

*Proteus* belongs to the *Enterobacteriaceae* family. This class is comprised of motile, Gram-negative rods, aerobic, and facultatively anaerobic bacteria. *Proteus* may be part of the family *Proteaceae*, which too incorporates *Providencia* as well as *Morganella* [84].

Mesophilic *Proteus mirabilis* is known to construct monomers of silica particles [65, 85]. *Bacillus caldolyticus* is a thermophilic bacterium that benefits silica-utilizing plants in high silica environments. *Equisetum arvense*, was found to create silicate monomers from its respective polymer [86, 87]. The monomer silica, converted from minerals of either tentatively polymerized silica, is take-up by *Proteus mirabilis* and conjointly by *Equisetum*, that stores the silica as a polymer in its stem and takes off with *B. caldolyticus*, which cannot use depolymerized items under normal conditions [88].

### 3.4 Rhizobia

Rhizobium belongs to the genus of Gram-negative diazotrophic bacteria that fix atmospheric dinitrogen gas. The bacterial strains colonize plant root nodules and convert gaseous soil nitrogen into ammonia with the help of the enzyme nitrogenase and release organic nitrogenous compounds like glutamine [89, 273].

Advantageous mutualistic rhizobia-legumes associated bacteria like *Rhizobium leguminosarum* are necessary to maintain productivity in drier agroecosystems affected by salinity which is a global issue for agricultural production [90]. Growth and crop yield are negatively influenced by the salinity [91]. Several findings have reported the positive role of silicon and silicon mobilizing bacteria especially rhizobacteria under stressful conditions including salinity stress. Silicon availability affects plant physiology and can improve plant growth and production under different stresses [92–94]. However, variations in beneficial the results has been reported in plant species because Si

concentration varies from plant to plant and tissue to tissue [13]. It is also reported that the application of silicon lowers the salts uptake importantly sodium and chloride and improves germination, growth and yield. Silicon is polymerized to mono-silicic acid or amorphous silica and the inverse of monomeric silica into polymeric forms is responsible for the Si element in agricultural soils [95]. Rhizobacteria were directly involved in this conversion through weathering and improved the silicon availability in soil–plant system. A study by at Indian Institute of Rice Research (IIRR) isolated Rhizobium (IIRR-1) from rice soil-rhizosphere and reported it as Si-solubilizing bacteria (SSB). They reported that IIRR-1 has the potential to mobilize as well as release soluble silica elements from biogenic-materials and mineral-silicates. They also reported IIRR-1 also produced IAA and showed ACC-deaminase activities. They reported this specie of Rhizobium as a beneficial strain which has the potential to increase the silicone concentration in the rhizosphere by boosting the weathering of silica-minerals in the rhizosphere. Several other studies have also reported the bacteria-associated weathering of silicate-mineral and release of silica. Soil rhizosphere is considered a rich source of silica formation where bacterial activities are high due to a large number of organic acids, polysaccharides, hydroxyl ions, organic ligands, and enzyme production [96, 97]. Rice soil rhizosphere is considered an ideal condition for isolation of SSB [98, 99]. Strains CCNWC119 (*Rhizobium sp.*), H66T (*R. yantingense*) and Q34 (*Rhizobium tropici*) were isolated from the legumes rhizospheric soil has abilities to release/solubilize silica by weathering of silica-minerals [100–102]. It is also reported that the release of Si from the silicate-mineral also dependent on mineral bonds, pressure, temperature and water content because, for a strong bond, high energy is needed to break minerals into a simpler form [103, 104]. This is the reason for variation in the concentration of silica in different soil.

Major sources of Si in soil are aluminum silicates that are usually unavailable for plant uptake by roots from soil regardless of its abundant availability [105]. Silicic acid is another plant Si source in soil when soil pH is less than 9 and as pH crossed 9, dissociation of silicic acid start into silicate ions [106]. Some studies stated that foliar application of Si with PGPR (plant growth promoting rhizobacteria) inoculation improved the plants growth and yield under different stresses [92, 94]. Recently, rhizobacteria inoculants have been prepared and applied with silicon to reduce the harmful effects caused by different stress [107]. Silicon and PGPRs have different beneficial effects on the plant from germination to maturity till crop harvest [108]. It has been reported that Si and PGPRs have a synergistic relationship with each other and alleviate multiple stresses in crop plants [93]. It has also suggested that the combined application of PGPR and Si is a sustainable and powerful practice to improve plant

germination, physiology, growth and yield under harsh conditions [108, 109].

### 3.5 Burkholderia

The *Burkholderia* class title alludes to Gram-negative, obligatory high-impact, rod-shaped microbes that are motile due to the presence of single or different polar flagella, with the exemption of *Burkholderia mallei*, which is immotile [110].

Utilization of silicate-solubilizing microorganisms increases the Si take-up and has a critical impact on rice development and yield [111, 112]. In some cases, the silicate solubilization capacity of *Burkholderia eburnean* CS4-2 must be encouraged and compared with other known Si-solubilizing bacteria by utilizing varied Si sources under field conditions with diverse soils with changing pH conditions [93]. Moreover, the yield parameters of few specific rice cultivars and other high Si consuming crops like sugarcane should be considered. Most importantly, the chemical structure of CS4-2 for Si solubilization or mobilization must be understood [113].

### 3.6 Enterobacter

Enterobacter (class Enterobacter) rod-shaped microbes belong to the family *Enterobacteriaceae*. These bacteria are Gram-negative and are classified as facultative anaerobes suggesting that they can survive in both aerobic and anaerobic environments [114]. The uptake of silicon and phosphorus during plant growth and development is significantly influenced by *Enterobacter ludwigii* GAK2 [115]. The strain *E. ludwigii* GAK2 has a natural capacity to solubilize both phosphate and silicate that also delivers natural acids e.g. indole acetic acid and Gibberellic acid [116]. In this manner, *E. ludwigii* GAK2 can be utilized as the best inoculant for phosphate and silicon fertilizer to soil high in insoluble P and Si [115].

While silicate is concentrated in the earth's crust, long-term P fertilization has resulted in Cd contamination due to repeated fertilizer applications of P fertilizers containing Cd. *Enterobacter ludwigii* GAK2 helps solubilize phosphate and silicate minerals and improves the development of plants in Cd sullied soil [117]. This bacterium could be a reasonable or economical addition to phosphate and silicate fertilizer [116, 117]. Several isolated strains of *E. ludwigii* GAK2 increase the availability of silicate and phosphate through different mechanisms [118].

## 4 Application of Silicon Solubilizing Bacteria for Agricultural Production

Si plays a versatile role in agricultural soils and taken up by plant via mass flow and a plays vital role in germination, growth and yield of many crops e.g. maize [119], cotton

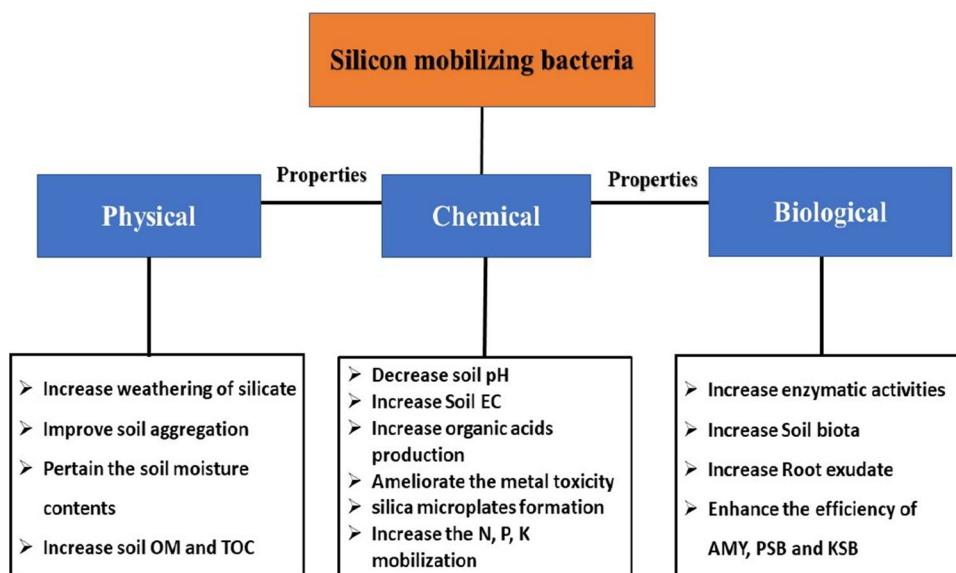
[120, 121], rice [122], barley [123], oat [124] and sugar-cane [125] shown in Table 2. In 2012, wheat and rice had increased contents of Si and were assigned to be Si accumulators due to these observations [126, 127]. In agricultural lands, Si compounds are available in the form of liquid, solid as well as adsorbed fractions. The conversion of monomeric silica into polymeric forms is responsible for Si nutrients in agricultural soils [95]. Si accumulation in the plant pose positive impacts on the performance like as pest control, enhance nutrition and protection against biotic and abiotic stresses.

Silica solubilizing bacteria are widely used in agriculture due to their location within the rhizosphere. These bacteria constitute a strong possibly symbiotic relationship with the crop to increase their yield and fruit development [128]. This equilibrium establishes a strong holistic relationship to resist pests and increase plant growth [47, 129]. Due to this fact, silica solubilizing bacteria are being evaluated as Yield Increasing Bacteria (YIB) [130]. Many species of the *Pseudomonas* and *Bacillus* are reported to increase the fruit development in maize, oil content in canola, pest resistance in wheat, drought resistance in pulses, and insect resistance in many legumes. The Chenopodiaceous plants, e.g., sugar beet, will increase its energy reserves when these bacteria are applied for plant uptake [131].

These bacteria produce enzymes, growth hormones and several other metabolites that help to compete for the ecological niche [11, 132, 133]. They are also involved in the breakdown of organic amendments that increase humus content in the soil for better adaptability and better crop growth [134, 135]. Further, these bacteria help the plants to resist the infection by certain aphids and other pests [136, 137] thereby enabling the plant to cope with several other adverse environmental and climatic disturbances including water deficiency or elevated metal concentrations in soil [138–140]. Silicon mobilizing bacteria effectively improve the soil chemical, physical and biological properties through different mechanisms as shown in Fig. 3. Recent studies suggest that *Oryza sativa* can enhance the plant growth promoters including auxins while accumulating solutes like prolines [68, 141, 142].

Silicon-based formulated chemicals are sprayed on the crops to improve the growth and crop yield under stressed conditions [116, 143]. Significance of silicon fertilization in soil health and crop production are given in Table 3. Formulations available in the market include a variety of agrochemicals.  $R_2SiO$  ( $R$  = any organic component) is used as a wetting agent in rice fields [144] and it is also considered an agricultural adjuvant due to its qualities as a good transporter of organic molecules [29, 95]. Silicic acid is transported in major parts of the plant biomass and is transported in the xylem which is mediated by *Lsi6* in the shoot while in roots by the *Lsi1* and *Lsi2* [145, 146].

**Fig. 3** Effect of silicon mobilizing bacteria on soil physical, chemical and biological properties



**Table 3** Significance of silicon fertilization in soil health and crop production

Type of silicon-based fertilizer	State of fertilizer	Crop	Function	Yield(tons/hectares)		Reference
				Control	Silicon fertilizers	
Monosilicic Potassium silicate	solid	Wheat	Reduced fungal attack, increased yield	3.20 ± 1.0	4.96 ± 3.0	[147, 148]
Calcium silicate	solid	Sugarcane	Reduced soil acidity, increased biomass	57.0 ± 4.0	74.0 ± 2.0	[148, 149]
Magnesium silicate, Monosilicic acid	solid	Rice	Reduced soil acidity, Increased soil phosphorus availability	1.48 ± 1.1	2.87 ± 2.7	[148, 149]
Diatomites	Solid & liquid	Maize	Increased soil aggregation, microbial activities	3.86 ± 3.6	4.29 ± 4.3	[112, 149]
Calcium silicate	Solid & liquid	Barley	Reduce pH, increased nutrients absorption and plant biomass	3.34 ± 2.4	5.99 ± 5.6	[112, 149]

## 5 Mechanisms of Si Solubilization by Si Solubilizing Bacteria

While there are many microorganisms in the soil, not all microbes are Si solubilizers. Common silicon solubilizing bacteria are belonging to *Bacillus* sp., *Rhizobia* sp., *Pseudomonas* sp., *Burkholderia* sp., *Proteus* sp. and *Enterobacter* sp. and discovered very effective in solubilizing the silicon. Most soil Si is derived from natural silicates [142] through different biological and chemical processes. Many species of bacteria are involved in the release and control of Si through various steps in the disintegration of primary minerals into secondary and tertiary minerals [70, 71]. These bacteria break down the silicates especially to primarily and secondary silicates such as calcium silicates and aluminum silicate and change into available form of mobilize Si [150] as shown in Table 3. During

solubilization process, these microorganisms secrete several types of organic compounds that can be acidic or basic in nature. In addition to these acids and bases, the soil electrical conductivity (EC), pH and soil water content are also important factors in the silicate mineral breakdown process [40, 151] shown in Fig. 1 and 2. These compounds initiate the weathering process and release  $\text{SiO}_2$  and K. Microbial breakdown and solubilization of silica minerals is regarded as the primary plant source of silicon in the natural soil environment [68]. When these bacteria solubilize the silicon, the efficiency and activity of silicon mobilizing and other beneficial rhizobacteria increased. These rhizobacteria start to reuse the different compounds released during these solubilization and weathering processes shown in Fig. 1. During metabolism, silicon-solubilizing bacteria release a large number of organic acids, polysaccharides, hydroxyl ions, organic ligands, and

enzymes that further aid in the silicate weathering process [96, 97]. During this process, organic acids (keto acids, oxalic acid, citric acid, and carbolic acid) are produced that combine with different type of cations and become readily available to plant by stimulating the hydrolysis and supplying  $H^+$  ions to the medium [152, 153]. As soil pH increases, monomeric acids breakdown in the presence of bases and hydrogen ions are removed [74]. This reaction continues in the presence of a base and the less stabilized polymorphs formed by the removal of hydrogen ion. The release of protons, hydroxyl-anions, enzymes, organic ligands and polysaccharides provide easy access to microorganisms for silicate minerals. These microorganisms convert silicates to soluble forms of silicon that are available for plant uptake [154].

A few studies report that silica particle size influences the microbial population and subsequent soluble silica content [155]. Similarly, silica particle size also influences crop growth which is proved by a comprehensive analysis study by Kalia and Kaur. Still more investigation is needed to understand the potential use of silica using microbial mechanisms [156]. Plant are unable to uptake or absorb Si directly [157]. The manufacturing cost of synthetic silica-based fertilizers is high, while plant absorption of synthetic silica is quite low. Therefore, applications of silicon solubilization bacteria could be a very important strategy to improve the silicon plant uptake. Silicon fertilization is absorbed by plants through the xylem with water by the active and passive process through the transpiration stream and transfer into plant via mass flow [158]. Silicon is mostly polymerized into mono-silicic acid or amorphous silica ( $SiO_2 \cdot nH_2O$ ) in the plant factory's oldest tissues, notably in the interior of epidermal cells which thickens cell walls and promotes tissue strength and rigidity [158]. Comparable to glandular trichomes, silica deposition can occur in the cellular structures during cellulose biosynthesis. Silicon transport over long distances is limited by the xylem; however, significant Si quantities are collected in the xylem vessels by deposition in cell walls [159]. When the transport rate is high in situations with high vapor pressures, the deposition of Si is reduced in the xylem vessels [160]. This is a reason that the Si concentration in supporting tissues, grains, stems and leaves can still be detected at certain levels [161]. Usually, Si contents in the root system are one-tenth of the total available in leaves and stems; however, soybean roots contain a higher concentration of Si than leaves [162, 163]. Silica is mostly deposited in the sheath cells, epidermis and vascular bundles but also in cell lumens, cell walls, intercellular matrix, and beneath the cuticle [164, 165]. Sometimes during the degradation of protoplast silica is deposited in greater concentration in infected tissues [166, 167]. Silicon contents increase in plant parts of high permeability, such as stomatal-guard cells, leaf epidermis around trichomes, thorns, and reduce the negative effects of biotic and abiotic stresses [168].

## 6 Role of Bacteria in the Dissolution of Si from Insoluble Resources

Silica rocks (mica, feldspar, pyroxene, and quartz) include a wide variety of important minerals and are a potential source of micro and macronutrients. These silicates can be an important source to fulfil a plants nutritional requirements [169, 170]. Despite of that, several silicate rocks seem unsuitable for plant fertilization. Therefore, mineralogical and chemical properties of such rocks should be appropriate to meet soil properties and crop requirement. Most important determinant factor of nutrient mobility and availability in soil is the dissolution rate of mineral from rocks [170]. In this aspect, the soil microorganisms play a vital role to increase weathering of silica rocks Fig. 4. Silicate rocks could remineralize the soil via the formation of smectite minerals. The application of silica sources and SSB together could improve the soil physicochemical properties decrease the toxicity by excess elements [171].

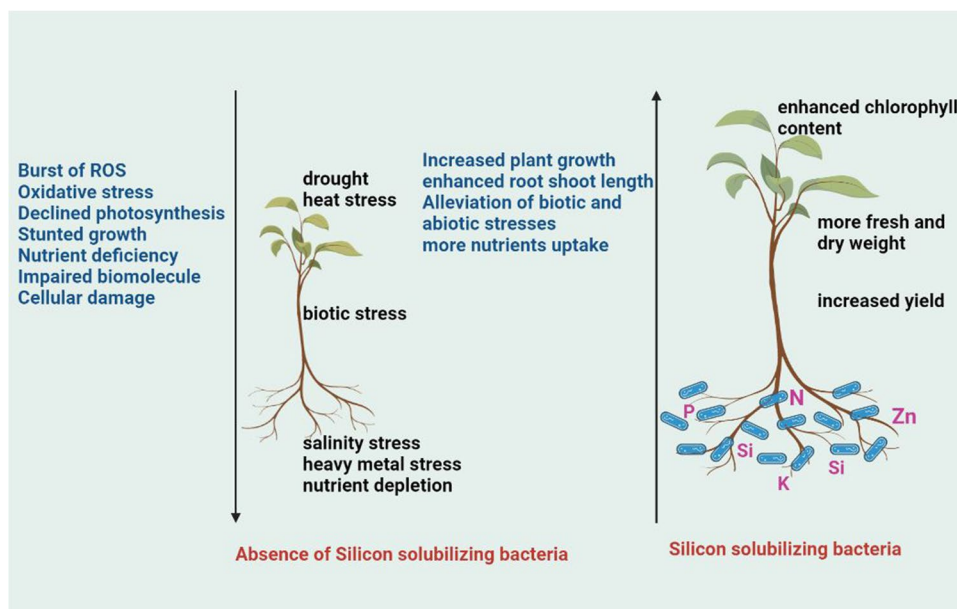
All the essential nutrients required to plant except nitrogen are derived and available through the weathering rocks (mineral rocks). Plant releases different exudates through roots that are mixture of chemical-ligands and organic acids that increase the mineral solubilization/mobilization [172]. Root exudation increases with increasing demand of nutrition and upsurges with increase of primary-root surface area [173]. Root exudates coupled with sugars, amino-acids, certain enzymes, fatty-acids, sterols, and secondary-metabolites and create a nutritional environment around rhizosphere that help plant to sustain under diverse microorganisms population [174]. In rhizosphere, the combined activity of bacteria and root exudates stimulates the weathering and solubilization minerals at higher rates [175].

Silicate dissolution from insoluble resources by microbial activities can either be a collateral or an active process. This is high energy-consuming process which releases certain metabolites that influence the silica solubilization [176]. However, most frequently occurring weathering occurs in response of microbial growth under cellular control and satisfying their nutritional requirements. Consequently, microbial community and mineral composition are both directly influence the minerals solubilization/mobilization from insoluble [176]. The key mechanism behind microbial solubilization involves chelation, pH changes and redox reactions that lead to the dissolution of minerals in the matrix of insoluble particles/mineral resources that promote the proton-dependent dissolution of silicates, furthermore the chelation of elements via various acids and enzymes, and redox reactions [177].

Some bacteria release inorganic acids e.g. sulfuric acid by sulfur-oxidizing bacteria (*Thiobacillus* genus) and



**Fig. 4** Direct/indirect role of Si solubilizing bacteria in plant growth enhancement under stress conditions



nitric acid by nitrifying bacteria [178]. These acids also promote the weathering of silica-minerals. Furthermore, organic acids like pyruvic-acids, formic-acids, citric-acids, gluconic-acids, acetic-acids, lactic-acids, oxalic-acids and succinic-acids also produced by bacteria that enhance the weathering. The pH alteration by microbial activities also promotes the solubilization of silica ions. These acids are released as byproducts of the carbon metabolic processes [177, 179]. Presence of carbonic anhydrase involved in aerobic respiration release  $\text{CO}_2$  that led to carbonic acid formation, an important mechanism related to acidification. Enzyme production activities of several bacterial strains [180], also promote Si weathering [181]. Organic acids create acidic condition in the surrounding environment of minerals, and their deprotonated form develop a specific type of chelate ions that enhance dissolution rates of insoluble silica. Similarly, carboxylic groups associated with this organic acid are mostly negatively charged after dissociation from  $\text{H}^+$  ion and act as ligand sites for cations. Therefore, their number affects the chelating capacity of microbes. It is noted that di and tricarboxylic acids are comparatively more efficient mineral solubilizers in comparison to monocarboxylic acids [182]. Siderophores are foremost chelating-agents released by bacteria promote the mineral weathering [183].

Dissolution of a mineral can also be done through changing the crystalline structure of minerals via oxidation–reduction reactions by specific compounds present in it [184]. During anaerobic respiration, microbial strains use metals as terminal electron acceptors and accelerate the S- solubilization. Bacterial strains belonging to *Desulfuromonas* and *Shewanella* have oxidize  $\text{Fe}^{2+}$  and carbonate and use as electron acceptor under anaerobic condition.

This reaction accelerates the weathering of phyllosilicates mineral such as glauconite and biotite. This property also detected in *Geobacter ferrihydriticus* Z-0531 T [185].

Rhizobacteria strain CS4-2 (*Burkholderia eburnean*) have the ability to solubilize and mobilize the silica and enhance Si-uptake in rice that improved plant-growth relevant to control or uninoculated [129]. Significantly improvement in the growth and yield of plant has recorded by combined application of silica solubilizing bacteria and insoluble silica fertilization.

Bacteria strains IIRR-1 (*Rhizobium* sp) has the ability increase the release of Si from the silica minerals [186]. Besides Si solubilization bacteria also showed ACC deaminase activity and IAA production that promote associated plant growth and capacity to fight against different stresses. Si-solubilizing bacterial strains 3C1 (*Flavobacterium* spp.) 4A2 (*Bacillus* spp.) and 3C5 (*Pseudomonas* spp.) isolated from the gut of the earthworm has potential to solubilize and release of Si from mineral (quartz and feldspar). It is reported that strain 3C1 enhanced the Si contents in the soil along with uptake in maize plants [187].

## 7 Soil Silicon Chemistry

Silicon significances as a beneficial element has been increased since last few decades due to its role in the plant functionality and agricultural production. It is reported that the Si concentration in the uncultivated soil is more than the agricultural soils. This is because of crop harvest practices which are generally associated with the Si loss. How this is not true in all case, few agricultural activities such

as crop residue burning, Si fertilization and liming [59, 274, 275]. Generally in agricultural as well as non-agricultural soil Si-pools are present in liquid/solution form, solid phase and as an organic complexes [188]. Si fraction in the soil solution present in the form of monomers and oligomers which lately changed into Si-polymers and precipitate and become available to plant in different fraction. The solubility of silicon increased with increasing pH and temperature of the medium and in pure water silicone has almost 100 ppm solubility [189]. Several other factors than pH and temperature like concentration of silicic acid, other ions (Ca, K, Na etc.), organic C, crop residue etc. also influenced the Si concentration [190]. A study conducted in UK at Rothamsted center reported that continuously removal of wheat straw from field significantly reduced the Si concentration in the soil [276]. Klotzbucher team concluded that the mobility of Si in soil sorption ability of Si with other competitive compounds [277]. Comparatively, Si element has more complexity as compared to many other elements due to its slow rate of reaction and reliant on different Si sources and species. However, the solubility of Si in the soil is influenced by different soil processes such polymerization, depolymerization, and condensation and Si releases varies in the soil system. It is recorded in a forest study that the polymerization of Si increased with increased in pH after pH of 4 [191]. Sometimes, Si become unavailable due to absorption on the soil particle especially Fe or Al oxides/hydroxide [188, 192]. While solid phase of Si consisted of different amorphous Si: (1) minerogenic form like silica-nodules such as pedogenic oxides (iron oxide); (2) biogenic form such as phytoliths and shells (radiolarian, diatom, testate amoeba, etc.) [188, 193]. Other solid Si forms included micro and poorly crystalline such as imogolite, allophane, secondary quartz, and chalcedony. Mineralogists used the term amorphous to define the non-crystalline form of Si. While in soil chemist, used this term to quantify the amount of Si in the soil by reagent extraction methods. Additionally, crystalline form of Si classified as a primary silicate (pyroxenes, olivines, micas, quartz, etc.). Si leaching is a major process through Si leached to down soil profile and this process call soil desilication and accumulates in the soil. Desilication is most common process in the soils of tropical areas [194]. Desilication has also chances to occur in young soil especially soils of boreal regions [193]. While soils of temperate humid areas enriched with Si may be due to the formation of fragipan in the subsoil [193]. In acidic soils, Si is present in the form of amorphous Si which coated on minerals [188]. This Si accumulates in soil pores as a SiO and forms distinct soil horizons and this process called duripan [194]. In semi-arid soils, frequent desiccation during the dry season developed a silicate layer (massive sedimentary fraction) and hardening caused the precipitation and redistribution of SiO<sub>2</sub> [188, 190]. Therefore, it is very important to shed the light on the

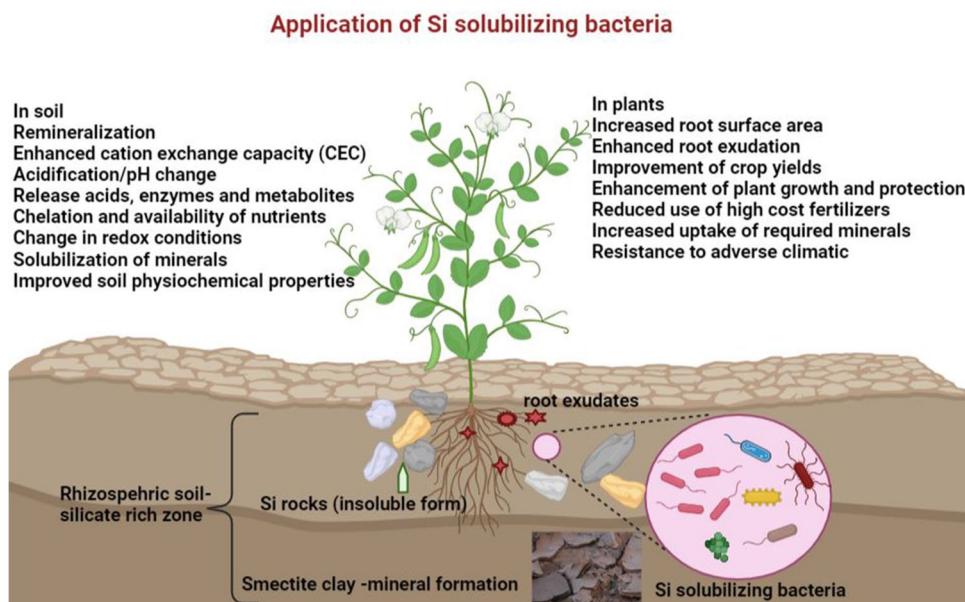
silicon soil chemistry for better understanding of Si-cycle, soil availability and functionality and factors which effects the Si-cycle.

## 8 Silicon Effects on Plants

Generally, silicon is not considered as an essential nutrient but recently its status has changed to a beneficial element [142] because of its beneficial role in plant growth and yield particularly under stress conditions (Fig. 5). These beneficial and positive impacts have been recorded in different crops including sugarcane [125], barley [123, 124] and rice [122, 195]. From the soil solution, Si is taken up mostly from silicic acid by plant roots and translocated through different paths to shoots where it is stored and precipitated in plants during plant growth and development activities [196, 197]. Most of the silicon solubilizing bacteria are involved in enhanced nutrient uptake, increased photosynthesis, plant growth attributes and crop yield along with the alleviation of various biotic and abiotic stresses [16]. Plants with Si concentrations > 1% are considered accumulators and those plants with < 0.5% as excluders and plants having concentrations between these limits are recognized as intermediates [9, 10]. Seven major crops (maize, wheat, sugarcane, rice, soybean, barley and sugar beet); are classified as accumulators [127]. Several forage grasses are also called accumulators because their leaves accumulate Si between the ranges of 1–5% [198]. Silicon among all the beneficial elements is one element that does not behave in a detrimental role in plants when accumulated in excess [199]. In a natural ecosystem, Si returned to the soil through the decomposition of plant litter into biogenic Si pools and again become the part of Si cycle in soil. In agricultural systems, a significant amount of this phytolith Si is taken up by plants and potentially lost during harvest due to crop removal. It is reported that globally on an average year 210–224 million tons of Si are removed through crop production by crop harvest [193]. This kind of continuous Si removal at harvest is considered the scenario that could promote the desilication in agricultural soils if the plant biomass is not returned to the soil surface. Therefore, to replenish lost Si, Si fertilization under 100 ppm concentration is considered the good strategy to improve the Si concentration in soil for soil health and future crop production [200].

Enhanced soil Si bioavailability is generally associated with increased Si content in the plant [163]. Numerous grasses have shown improved productivity and growth because of silicon application. Rice, sugarcane, sorghum, millet, are common crops that benefit from silica fertilization. Overall, Si concentration in plants varies from 0.1 to 10% of the total dry matter [20]. Accumulator plants have leaves consisting of more than 1% of their dry matter, while

**Fig. 5** Application of Si-solubilizing bacteria result in dissolution of insoluble Si to improve soil properties and enhance plant growth



non-accumulator plants have leaves consisting of less than 0.5% [201]. The absorbing ability of plants for Si varies significantly, and is even different in genotypes of the same species and sometimes varies in tissues [126]. It is reported that the accumulation of Si in the rice is directly linked with the yield increment in the rice [202]. Lab study also demonstrated a decrease in the concentration of Si led to a reduction in rice yield. Silicon plays an important role to mitigate the drought stress for many crops [203]; [105] through the reduction of plant transpiration by increasing resistance in the plant against the drought [204]. A few studies also suggested that it increased the transpiration rate while decreasing during drought stress conditions [205]. Interestingly, stress mitigation in the plant by the application of Si is not totally due to improving the plant performance but can also be due to improving the plant-soil-water relationship. It is also reported in the literature that the application of Si increased the soil water holding capacity. The application of amorphous silicon increased the soil water holding capacity and increased the plant water availability [105]. Another study suggested that the accumulation of silicon in the leaves above-ground biomass of the plant reduces the heat stress caused by ultraviolet radiations. Studies reported that a silicon layer is formed near the epidermis which may work as a filter against this radiation [206]. Moreover, studies also reported that the application of decreased metal/metalloids toxicity and mitigated salts stress [207, 208]. Silicon accumulation in the plant-biomass work as a defensive tool against insects and mammals (herbivores) [209, 210]. Several studies concluded that fungal diseases reduce in the rice on the application of Si which may be due to the formation of a Si layer around the mesophyll cell [211]. The

soil management practices of Si increase and/or maintain the crop yield/production. Si application increases nutrient use efficiency (NUE), plant nutrition, crop growth, and yield/production, especially under stress conditions. Finally, improving the Si fraction in the soil stimulates the Si accumulation in the plant biomass and acts as a promising alternative to chemical fertilizers and pesticides at the farmer level [212].

Indeed, growth promoting bacteria act via several mechanisms and during various activities, expression of their genes relies on fluctuating environmental conditions and requirements. Silica and silica-based nanoparticles were reported to have an impact on the microbial biomass and colony formation and this elevation directly or indirectly enhance the fertility of soil. Sensitivity of microbes to various chemical substances, amendments or bio augmentations, furthermore application of nutrients like silica subsequently favors and design the selective enrichment of various microbial communities. In this context, rhizosphere play a very important role in the maintenance of healthy and nutrient rich soil profiling and plant's health and yield. Influential role of silicon particles was noted in context of increased soil microbiota and soil nutrient content that enhance plant growth. Application of silicon and silicon-based nanoparticles increased population of phosphate solubilizing bacteria and nitrogen fixing bacteria in the rhizosphere. Silicon application also augment the rhizospheric population of *Rhodobacteriaceae*, *Paenibacillus* and fungal genera *Chaetomium* by modulation of signaling system that regulate the expression of certain genes. Changes in metabolites, organic acids, sugars, alcohols and fatty acids revealed the effects of Si on the nitrogen and carbon pools in rhizospheric soil. However,

oversaturation of Si or Si nanoparticles result in the alteration in the gene expression (amoA), dehydrogenase and urease activity of bacteria and archaea residing in the soil. Silicon is also reported to modulate the signaling system of defense genes related to the structural modification of cell walls, hypersensitivity response, and hormone synthesis and protein production. Silicon was also reported to regulate significant genes in the plants amended with Si as compared to plants without Si that not only control abiotic stresses but also suppress various bacterial and fungal pathogens. Higher expression of *Lsi1* gene in roots of rice plant that increase plant growth from panicle initiation to heading in *Oryza sativa*. Upregulation of another gene expression osNAC proteins by Si involved in proline synthesis, biosynthesis of certain sugars, redox homeostasis, reduced oxidative stress and enhanced photosynthetic activity alleviate the salt and heavy metal stress in plants. Application of Si under saline conditions enhance the expression of AREB, TAS14, NCED3 and CRK1 gene that were noted to trigger modifications in plant cell metabolism in *Solanum lycopersicum* plants. Furthermore, Si transported genes were discovered in plants that regulate the uptake and loading/unloading of Si in plants [138–140].

## 9 Significances of Silicon in the Uptake of Nutrients

Jörg Schaller et al. [212] shed light on the role of Si in the availability and uptake of nutrients and reported that silicon plays a vital role in the OM decomposition and the availability of many micro- and macro-nutrients. Therefore, it is very important to investigate the role of Si in agricultural production under different practices. Ofir Katz et al. [213] reported that Si not only involved in the dynamic of Si-cycle but also influenced the C-, N- and P-cycle.

N is an essential macronutrient and basic component of plant cell but its deficiency in the soil considered to be most important factor for controlling plant growth and output [213, 214]. The crop quality and yield can be enhanced by using considerable amount of N fertilizers. However, in many condition desired yield not achieved due to N deficiency like abiotic stress [215, 216]. In many cases, most fraction of applied N is lost which enforced pressure on the farmers to achieve maximum crop production [217]. Plant uptake < 40% of applied N and leftover fraction is leached into groundwater or lost into environment and cause threat to ecosystem [218, 219]. Studies proved that presence of Si in the soil increase the availability of nutrients (N, P and K) but extent of increased is not known well. Studies also proved that the external application of Si play vital role in the N-metabolism and N-dynamic in soil (uptake, loss and

assimilation/remobilization) [220, 221]. It is reported that application of Si alleviates the nitrogen deficiency in different crop by improving the nitrogen acquisition through root system [222]. Under limited availability of N, application of silicic acid has increased the uptake and accumulation of plant N [223, 224] in rice, maize, cowpea, rapeseed and wheat [59, 201, 225–277]. Experimental findings revealed that foliar as well as soil application of Si reduced the mineral nitrogen-fertilizers requirement in several crops [225, 229]. Deus et al. [225] stated that Si-fertilizer increased 19% of crop production in several crops as compared to control treatment under N deficit soil [225]. Exact mechanism is still unknown but it has been partially reported that silicic acid production increased the amino acid production which remobilizes the N in soil [230].

Jörg Schaller et al. [212] also reported that presence of Si increased the P availability in soil. Soil mineral compositions and biogeochemical activities are the important factors which influence the P availability. Phosphorus and Si deficiency lead to reduced P accumulation hence retarded plant growth and physiology can be observed. Inclusion of Si solution can raise P accumulation that reduce electrolyte leakage due to stress and increase chlorophyll index of sorghum plant leaves [270]. Several studies stated that Si alleviate the P-deficiency in potato, maize, wheat and rice under limited P conditions [228, 231, 232]. Two major phenomenon are reported commonly involved in the alleviation of P deficiency by Si included: (1) increased P-uptake by roots, (2) enhancement of P acquisition and utilization in plant tissues [233]. In addition to low P situation, under high P fraction case P also become unavailable to plant due binding and complexation with iron oxide, Aluminum, calcium minerals. Likewise N, the P availability in soil also depend on the soil pH, mineral surface area and mineral composition. Furthermore, P availability also influence by soil type, amount and type of Si fertilizers, their application rate and soil biota composition [234]. At higher pH than 6.5, P become immobilized by forming mineral complexes like calcium phosphate. While under low pH, P absorbed or bounded with Fe, Al, Mn as well as their hydrous oxides [235]. This is the major reason of P distribution among Si, Ca, Al or Fe highly dependent on pH and mineral composition and parent material [236]. For this reason, bioavailability of Si is often very low in the many soils. Increased P availability in soil is usually associated with the increase of P concentration in plant tissues and thus plant growth improve under low-P concentration [237]. P stress has also been reported in a few hydroponic cultures and greenhouse studies even P sources were applied [238]. This is proved by studies that P mobilization is affected by the Si. In high silicate mineral soils, P particle less bound to the soil mineral [239]. P binds with different form of iron like Fe (II and III) while Si interact with both Fe and P [240]. It is recorded



that in permafrost soils, high concentration of Si mobilizes both P and Fe from Fe (II) P and boost the P fraction in the soil. Furthermore, P can also mobilized and bind from/to Fe (III) oxide [241]. Study by Sigg and Stumm, [242] described that the  $\text{H}_3\text{PO}_4$  and silicic acid compete for the Fe mineral site. This may be the main reason that releases P into soil under high Si. Releases of silicic acid from the Si source in the soil compete with other nutrients for surface area on the mineral sites and cause immobilization of the nutrients [241, 243]. Under such circumstances, application of Si fertilizers can be work as plus point to increase the P availability from unavailable P sources [244] and P availability also increased from soil to plant. The second major reason of higher P in the Si rich soil is the role of Si in OM decomposition. Higher Si concentration increased the OM decomposition and release the nutrients in the soil. However, Si has not significantly changed the P uptake in rice even Si source was applied [245]. This study did not show any significant changes in the P uptake due to presence or absence of Si. However inorganic P contents in shoots were found double where Si solutions were applied as compared to non-application [246]. The Si concentration in shoots reduced slightly as P concentration increased, but P concentration did not change Si uptake. It has also been reported that under low P concentration, Si decreased the uptake of Fe and Mn by almost 20% and 50%, respectively and in result in P:Mn and P:Fe ratios increased in plants [247]. Furthermore, results also showed that plant growth and development improved by Si application under P stress. Low concentration of Mn and Fe might be responsible for increase of P availability in plant under P-deficient conditions [248, 249].

Additionally, application of Si has a significant impact on the Fe availability in soil rhizosphere to root along with the genes that are involved in Fe transport at the root and leaf levels [238]. It has also influence the remobilization and dispersion of Fe within various plant organs and tissues [250].

Si interact with plant Fe through two strategies; strategy-1 dicots and non-graminaceous monocots with reduction-based Fe uptake, and strategy-2 graminaceous monocots that exhibit chelation-based Fe uptake. In both strategies, plant species have demonstrated the relieving effects of Si on Fe insufficiency [251]. Additionally, researchers discovered that the Si-ameliorative impact on Fe deficiency was pH- and species- dependent. In a cucumber study, it is demonstrated that enhancing the expression of important genes that are responsible for the production of organic acids can be work as powerful Fe chelators which enhance apoplastic Fe-mobilization by extending the adsorption pool for Fe in the root apoplast and Si input to roots [252].

Numerous studies on the role of Si in Fe-toxicity in rice have shown that Si reduces Fe-toxicity by precipitating Fe in the growth media or forming Fe film at the root surface. According to one theory, the presence of Si in rice reduces

the translocation and uptake of Fe to aerial portions, lessening Fe concentrations in both leaf and root tissues of plants subjected to excessive Fe [253]. In some recent studies on rice and cucumber, Si was found to increase the forming of Fe plaques, which reduced Fe uptake and triggered root reactions to Fe deficiency [254]. These studies also suggested that Si may cause an apoplastic obstruction even at optimal Fe supply [255].

Potassium (K) is another essential macronutrient play vital role in plant physiology, biology, growth, and crop yield. Therefore, K nutrient role cannot be underestimated [256, 257]. Thus, under salt stress increasing K levels and K/Na ratio have been emphasized as essential traits of salt-tolerant plant species [258, 259]. Many studies have reported, silicon (Si) removes K deficiency symptoms during salt stress in many crops [260]. In barley under salt stress, Si additions have promoted the K absorption by roots [261, 262]. In wheat, Si application has also increased the K contents in shoots and roots cultivated under 100 mM concentration of NaCl [205]. In sugarcane under salt stress, Si application reduced the K/Na ratio and improved K concentration of sugarcane shoot [263]. It is reported that application of Si increases the survivability of plants against salt stress under limited production of K. Conversely, earlier research has focused on Si-induced variations in K concentration, leaving that gap on how Si could improve K status in plants under salt stress which is still unanswered. Salt stress has negative effect on K nutrition in plant and plant biology. Recognizing the importance of K, it is no surprise that plants have a complex K uptake and transport system with a variety of functional and regulatory features that allows them to adjust to changing K concentrations in the growing medium [264]. K assimilation and transportation system definitely play an important role in the governing effect of Si on K status in plants under salt stress [238]. K channels and K transporters in plant roots facilitate internal and external transport of K from substrates through trans-membrane. However, the relative importance of these channels and transporters to uptake K in plants for growth varies with K concentrations [265, 266].

In a hydroponic study, it was recorded that Si application mitigate the nutritional stress and reduce the visible symptoms of nutrient deficiency in plants under varying nutrients treatment. It was noted that Si did not completely manage the damage caused by nitrogen deficiency in plants however, mitigation of K and S deficiency stress [267]. Nutrient deficiency is quite common in forages fields, Ca, P and N are dominantly the depletion from such soil. Use of balanced Si nutrient solution can enhance ability of plants to uptake nutrients from soil, their growth, vigor and yield by increasing shoot dry weight, phenolic contents, and photosynthetic pigments. Further, it decreases the extravasation of cellular based electrolytes. Ability of a plant to uptake N, P and S nutrient in deficient soils enhanced the yield of *Urochloa*

*brizantha* and *Megathyrus maximum* which revealed Si can be used to amendment under nutrient deficient soil [268]. In maize, soil application or foliar spray of Si alleviate the K deficiency and enhanced growth and yield. Under K deficiency conditions plants showed low photosynthetic rate, less nutrient uptake and reduced gas exchange which led to stunted vegetative growth. However, Si application relieve the stress by enhancing water use efficiency, increased dry matter with elevated level of chlorophyll pigments [269]. In *Chenopodium quinoa* plants Si augmentation mitigates the deficiency of N, P, K, Ca and Mg by protecting photosynthetic machinery and its metabolism. Moreover, Si amendment increase the membrane integrity, reduce the electrolyte leakage and stabilizes the plant as compared to plants without any Si application [271]. K deficiency is a common problem in bean plant and foliar application of Si limits the drastic effects of deficiency and enhance plant growth and yield [269]. Finally, it is very important to understand the role of silicic acid in the Si-cycle and availability of nutrient under different environment and cropping system to obtain knowledge better nutrients management.

## 10 Conclusion

This review paper evaluates the significance of silicon (Si) and silicon mobilizing bacteria and their impact on agricultural crop production. Overuse of inorganic fertilizer increased yields but may be deleterious to beneficial microorganism and the soil–plant ecosystem. In such circumstances, the application of beneficial microbes is an alternative and eco-friendly strategy for a sustainable agricultural system. In this review, we stay focused on biochemical processes that are modified by the activities of silicon mobilizer/solubilizer bacteria to enhance the effectiveness of agronomic practices. We found that the application of silicon fertilizer or silicon mobilizer/solubilizer bacteria suppresses the pathogens, increased soil fertility, and improved plant growth and yield under stress as well as in normal conditions. The application of these bacteria as an inoculum through soil or seed increased the plant health and yield, especially under stressful conditions and also increased the availability of other plant nutrients in the rhizosphere. We also found that organic matter, EC, pH, clay contents, and Al/Fe oxides are important factors to be considered for the recommendation of Si-fertilizers or Si-inoculum. Application of cheap industrial byproducts as a source of Si and Si mobilizer/solubilizer bacteria may become potential agronomic practices for several crops, especially under stresses (biotic and abiotic) that may reduce the yield of crops. This approach is more sustainable than conventional fertilization practices and may contribute to reducing climate change that is linked to agricultural activity. This review arose due

to the need to gain a better understanding of the role of Si nutrients and Si mobilizer/solubilizer bacteria for soil health and crop production; 1) what is the size of the silicon pool in the rhizosphere; 2) how much Si is lost from the soil every year through the different processes such as leaching, etc. 3) What factors drive Si-cycling? 4) What are the major factors influencing soil Si availability; 5) What major factors control microbial silicon decomposition; 6) The impact of increased microbial weathering of to meet the Si nutritional requirement? 7) What is the effective way to apply Si mobilizer/solubilizer through seed inoculation or with mineral fertilizers? 8) Regardless of lab trials, long-term field research trials are required to validate the effectiveness of Si mobilizer/solubilizer bacteria in agronomic practices. Moreover, awareness campaigns by extensions and agriculture officers to farmers about the important potential role of Si in crop production.

**Abbreviations** Si: Silicon; AAPFCO: Association of American plant food control officials; AE: Agricultural efficiency; PE: Physiological efficiency; NUE: Nitrogen use efficiency; PGPR: Plant growth promoting rhizobacteria; RP: Rocks phosphate; YIB: Yield increasing bacteria; AMF: Arbuscular mycorrhizal fungi; SSB: Silicone solubilizing bacteria; PSB: Phosphate solubilizing bacteria; PSB: Potassium solubilizing bacteria; OM: Organic matter; TOC: Total organic carbon; RP: Rock phosphate

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