



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 2nd 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

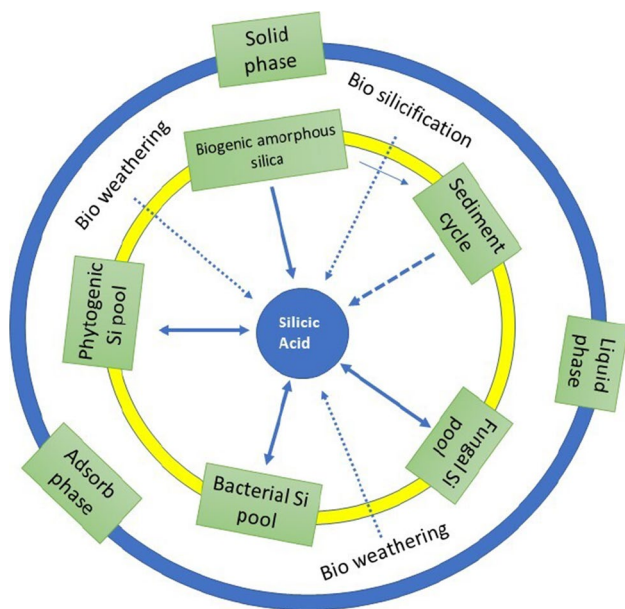
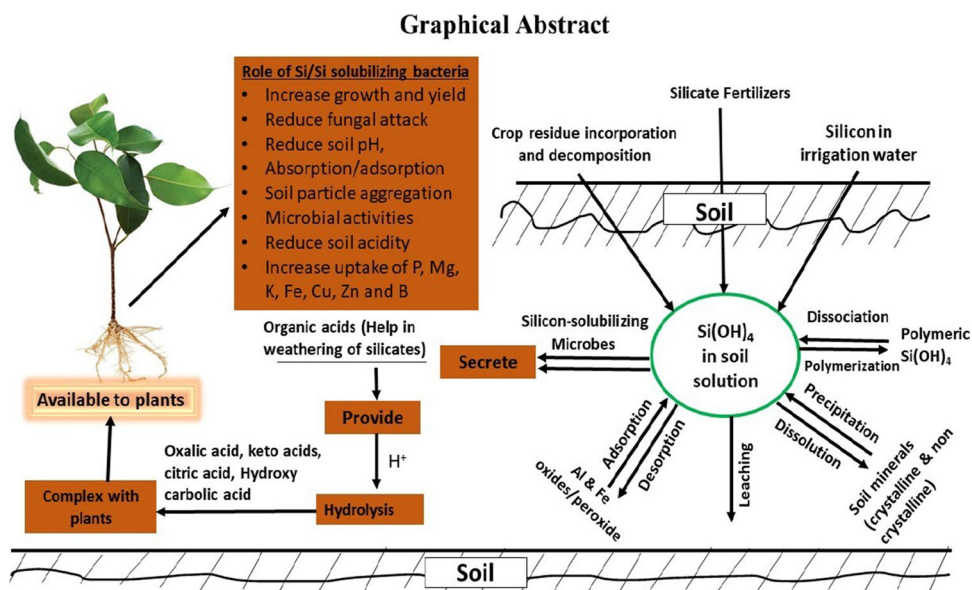


Fig. 2 Schematic overview of different silicon pools in the soil and role of biota in silicic acid formation

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_2 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 SiO_2 and 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 SiO_2 and 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 SiO_2 and this influences the exchange between the mineral and liquid stages and drives the response of SiO_2 and 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 μm by 1.5 to 3.0 μm [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 SiO_2 and 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 facultativ 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 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. yanlingense*) 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 sugarcane [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

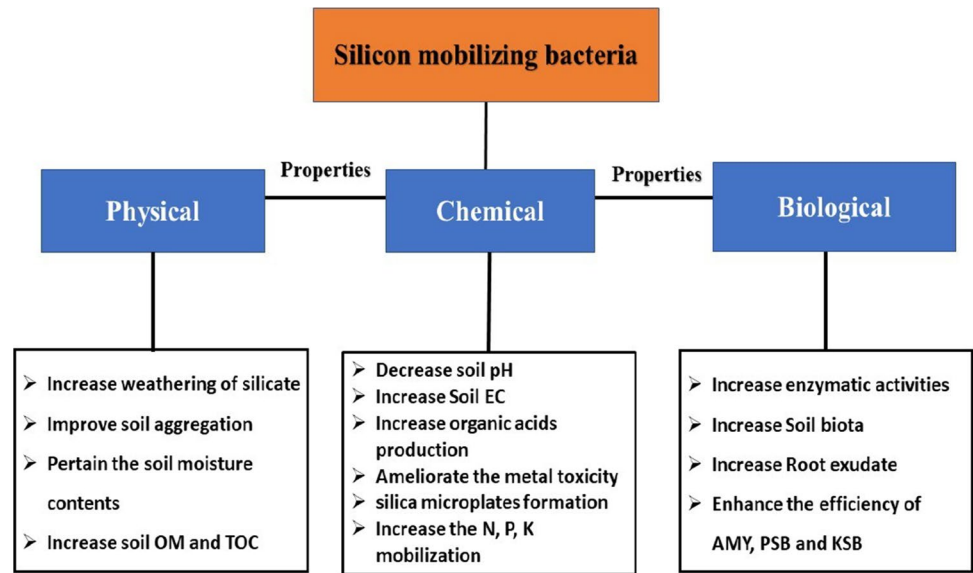


Table 3 Significance of silicon fertilization in soil health and crop production

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 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

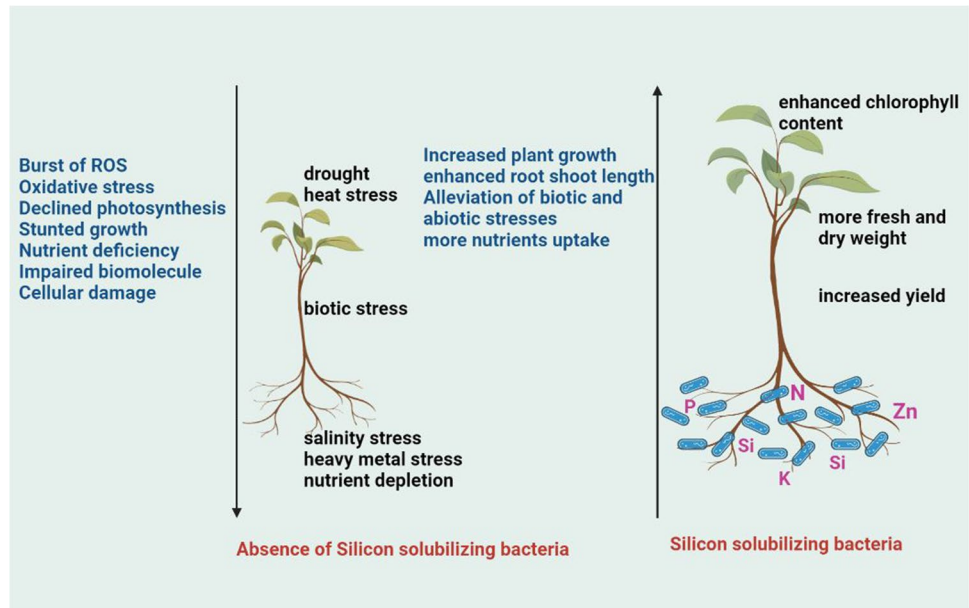
Silica rocks (mica, feldspar, pyroxene, and quartz) include a wide variety of important minerals and are a potential source of micro and macronutrients. These silicates can be an important source to fulfil a plants nutritional requirements [169, 170]. Despite of that, several silicate rocks seem unsuitable 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 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 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 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 SiO₂ [188, 190]. Therefore, it is very important to shed the light on the

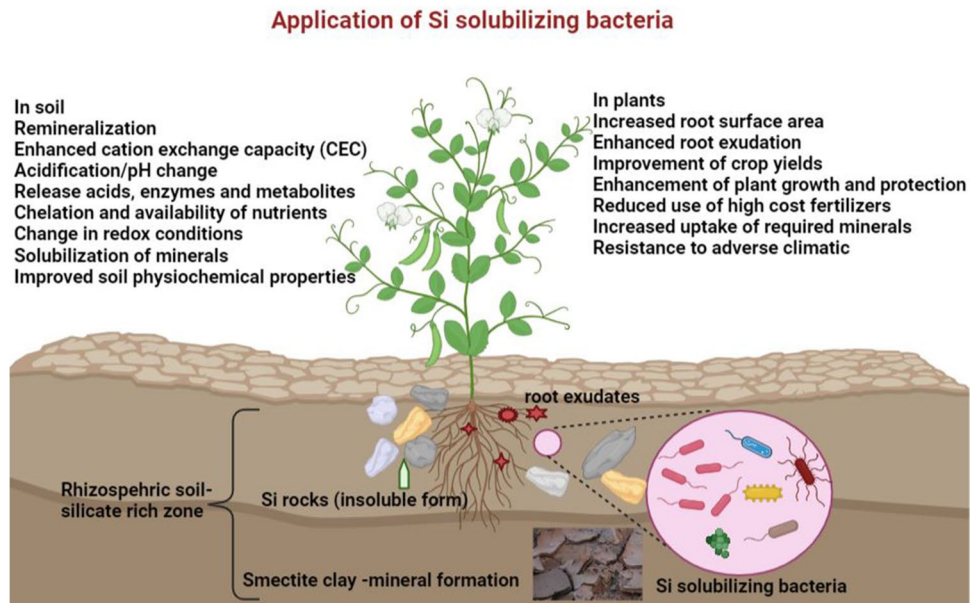
silicon soil chemistry for better understanding of Si-cycle, soil availability and functionality and factors which effects the Si-cycle.

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 H_3PO_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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References

1. Liang Y, Nikolic M, Bélanger R, Gong H, Song A (2015) Silicon in Agriculture. Springer, Dordrecht

2. Haynes RJ (2014) A contemporary overview of silicon availability in agricultural soils. *J Plant Nutri Soil Sci* 177:831–844
3. Heckman J (2012) Silicon and soil fertility. *The soil profile* 20:1–12
4. Heckman J (2013) Silicon: a beneficial substance. *Better Crops* 97:14–16
5. Vicedo DO, de Mello PR, Toledo RL, dos Santos LCN, Hurtado AC, Nedd LLT, Gonzalez LC (2019) Silicon supplementation alleviates ammonium toxicity in sugar beet (*Beta vulgaris* L.). *J Soil Sci Plant Nutri* 19:413–419
6. Golubkina N, Zayachkovsky V, Sheshnitsan S, Skrypnik L, Antoshkina M, Smirnova A, Fedotov M, Caruso G (2022) Prospects of the application of garlic extracts and selenium and silicon compounds for plant protection against herbivorous pests: a review. *Agriculture* 12:64
7. Mostofa MG, Rahman MM, Ansary MMU, Keya SS, Abdelrahman M, Miah MG, Phan Tran LS (2021) Silicon in mitigation of abiotic stress-induced oxidative damage in plants. *Crit Rev Biotechnol* 41:918–934
8. Vasanthi N, Saleena LM, Raj SA (2014) Silicon in crop production and crop protection-A review. *Agri Rev* 35:14–23
9. Frew A, Weston LA, Reynolds OL, Gurr GM (2018) The role of silicon in plant biology: a paradigm shift in research approach. *Ann Bot* 121:1265–1273
10. Zhang W, Xie Z, Lang D, Cui J, Zhang X (2017) Beneficial effects of silicon on abiotic stress tolerance in legumes. *J Plant Nutri* 40:2224–2236
11. Javaid T, Farooq MA, Akhtar J, Saqib ZA, Anwar-ul-Haq M (2019) Silicon nutrition improves growth of salt-stressed wheat by modulating flows and partitioning of Na⁺, Cl[−] and mineral ions. *J Plant Physiol Biochem* 141:291–299
12. Yan G-C, Nikolic M, Ye M-J, Xiao Z-X, Liang Y-C (2018) Silicon acquisition and accumulation in plant and its significance for agriculture. *J Integr Agric* 17:2138–2150
13. Abdel Latef AA, Tran L-SP (2016) Impacts of priming with silicon on the growth and tolerance of maize plants to alkaline stress. *Front Plant Sci* 7:243
14. Debona D, Rodrigues FA, Datnoff LE (2017) Silicon's role in abiotic and biotic plant stresses. *Annu Rev Phytopathol* 55:85–107
15. Hussain I, Parveen A, Rasheed R, Ashraf MA, Ibrahim M, Riaz S, Afzaal Z, Iqbal M (2019) Exogenous silicon modulates growth, physio-chemicals and antioxidants in barley (*Hordeum vulgare* L.) exposed to different temperature regimes. *SILICON* 11:2753–2762
16. Epstein E (2009) Silicon: its manifold roles in plants. *Ann Appl Biol* 155:155–160
17. Ali S, Rizwan M, Ullah N, Bharwana SA, Waseem M, Farooq MA, Abbasi GH, Farid M (2016) Physiological and biochemical mechanisms of silicon-induced copper stress tolerance in cotton (*Gossypium hirsutum* L.). *Acta Physiol Plant* 38:1–11
18. Chaiwong N, Prom-u-Thai C, Bouain N, Lacombe B, Rouached H (2018) Individual versus combinatorial effects of silicon, phosphate, and iron deficiency on the growth of lowland and upland rice varieties. *Int J Mol Sci* 19:899
19. Tuna AL, Kaya C, Higgs D, Murillo-Amador B, Aydemir S, Girgin AR (2008) Silicon improves salinity tolerance in wheat plants. *Environ Exp Bot* 62:10–16
20. Epstein E (1994) The anomaly of silicon in plant biology. *Proc Natl Acad Sci* 91:11–17
21. Datnoff L (2002) In Abstract of second silicon in agriculture conference, 2002
22. Miyake Y, Takahashi E (1983) Effect of silicon on the growth of solution-cultured cucumber plant. *Soil Sci Plant Nutr* 29:71–83
23. Onodera I (1917) Chemical studies on rice blast (1). *J Sci Agric Soc* 180:606–617
24. Chen J, Caldwell RD, Robinson CA, Steinkamp R (2000) Silicon: The estranged medium element. *Bull* 341:1–5
25. Elsokkary I (2018) Silicon as a beneficial element and as an essential plant nutrient: an outlook. *Alex Sci Exch* 39:534–550
26. Fox RL, Silva JA (1978) Symptoms of Plant Malnutrition-Silicon, an Agronomically Essential Nutrient for Sugarcane. University of Hawaii, Honolulu (HI)
27. Pereira HS, Korndörfer GH, Vidal AdA, Camargo MSd (2004) Silicon sources for rice crop. *Sci Agri* 61:522–528
28. Richmond KE, Sussman M (2003) Got silicon? The non-essential beneficial plant nutrient. *Curr Opin Plant Biol* 6:268–272
29. Choy J-H, Choi S-J, Oh J-M, Park T (2007) Clay minerals and layered double hydroxides for novel biological applications. *Appl Clay Sci* 36:122–132
30. White AF, Blum AE, Schulz MS, Bullen TD, Harden JW, Peterson ML (1996) Chemical weathering rates of a soil chronosequence on granitic alluvium: I. Quantification of mineralogical and surface area changes and calculation of primary silicate reaction rates. *Geochim Cosmochim Acta* 60:2533–2550
31. Gadd GM (2010) Metals, minerals and microbes: geomicrobiology and bioremediation. *Microbiol* 56:609–643
32. Webley D, Henderson ME, Taylor IF (1963) The microbiology of rocks and weathered stones. *J Soil Sci* 14:102–112
33. Minden V, Schaller J, Venterink HO (2021) Plants increase silicon content as a response to nitrogen or phosphorus limitation: a case study with *Holcus lanatus*. *Plant Soil* 462:95–108
34. Chandrakala C, Voleti S, Bandeppa S, Kumar NS, Latha P (2019) Silicate solubilization and plant growth promoting potential of *Rhizobium* sp. isolated from rice rhizosphere. *SILICON* 11:2895–2906
35. Klotzbücher T et al (2015) Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. *Basic Appl Ecol* 16:665–673
36. Cornelis J-T, Delvaux B, Georg R, Lucas Y, Ranger J, Opfergelt S (2011) Tracing the origin of dissolved silicon transferred from various soil-plant systems towards rivers: a review. *Biogeosci* 8:89–112
37. Lavoie K, Northup D (2001) Geomicrobiology of caves: a review. *Geomicrobiol J* 18:199–222
38. Sauro F et al (2018) Microbial diversity and biosignatures of amorphous silica deposits in orthoquartzite caves. *Sci Rep* 8:1–14
39. Vasanthi N, Saleena L, Raj SA (2018) Silica solubilization potential of certain bacterial species in the presence of different silicate minerals. *SILICON* 10:267–275
40. Zijlstra HJ (1987) Early diagenetic silica precipitation, in relation to redox boundaries and bacterial metabolism, in Late Cretaceous chalk of the Maastrichtian type locality. *Geol Mijnb* 66:343–355
41. Artyszak A (2018) Effect of silicon fertilization on crop yield quantity and quality—A literature review in Europe. *Plants* 7:54
42. Mo Z, Lei S, Ashraf U, Khan I, Li Y, Pan S, Duan M, Tian H, Tang X (2017) Silicon fertilization modulates 2-acetyl-1-pyrroline content, yield formation and grain quality of aromatic rice. *J Cereal Sci* 75:17–24
43. Solanki P, Bhargava A, Chhipa H, Jain N, Panwar J (2015) In: Mahendra R, Caue R, Luiz M (eds) Nano-fertilizers and their smart delivery system, Springer International Publishing Switzerland
44. Meena V, Dotaniya M, Coumar V, Rajendiran S, Kundu S, Rao AS (2014) A case for silicon fertilization to improve crop yields in tropical soils. *Proceedings of the National Academy of Sciences, India Section B: Biol Sci* 84:505–518

45. Etesami H, Jeong BR, Rizwan M (2020) In: Rupesh D, Durgesh K, Tripathi, Gea G (eds), *Metalloids in Plants: Advances and Future Prospects*, John Wiley & Sons Ltd.
46. Yeshe A, Gourkhede P, Vaidya P (2022) Chapter-5 Role and Application of Silicon in Agriculture. *Current Res Soil Fert*: 63
47. Sheng XF, Zhao F, He LY, Qiu G, Chen L (2008) Isolation and characterization of silicate mineral-solubilizing *Bacillus globisporus* Q12 from the surfaces of weathered feldspar. *Canad J Microbiol* 54:1064–1068
48. Puppe D, Höhn A, Kaczorek D, Wanner M, Wehrhan M, Sommer M (2017) How big is the influence of biogenic silicon pools on short-term changes in water-soluble silicon in soils? Implications from a study of a 10-year-old soil–plant system. *Biogeosci* 14:5239–5252
49. Puppe D (2020) Review on protozoic silica and its role in silicon cycling. *Geoderma* 365:114224
50. Wu C, Zhang L, Mao L, Zhu L, Zhang Y, Jiang H, Zheng Y, Liu X (2022) Efficiency of four extraction methods to assess the bioavailability of oxyfluorfen to earthworms in soil amended with fresh and aged biochar. *Agriculture* 12:765
51. Farmer V, Lumsdon D (1994) An assessment of complex formation between aluminium and silicic acid in acidic solutions. *Geochim Cosmochim* 58:3331–3334
52. Jurkić LM, Cepanec I, Pavelić SK, Pavelić K (2013) Biological and therapeutic effects of ortho-silicic acid and some ortho-silicic acid-releasing compounds: New perspectives for therapy. *Nutr Metab* 10:1–12
53. Bechtold MF, Vest RD, Plambeck L Jr (1968) Silicic acid from tetraethyl silicate hydrolysis. Polymerization and properties. *J Ameri Chemi Soci* 90:4590–4598
54. Swedlund PJ, Miskelly GM, McQuillan AJ (2010) Silicic acid adsorption and oligomerization at the ferrihydrite– water interface: Interpretation of ATR-IR spectra based on a model surface structure. *Langmuir* 26:3394–3401
55. Coradin T, Lopez PJ (2003) Biogenic silica patterning: simple chemistry or subtle biology? *Chem Bio Chem* 4:251–259
56. Ke Y, Stroeve P (2005) Polymer-layered silicate and silica nanocomposites. (Elsevier).
57. Cornelis JT, Delvaux B (2016) Soil processes drive the biological silicon feedback loop. *Funct Ecol* 30:1298–1310
58. Vandevenne F, Barão L, Ronchi B, Govers G, Meire P, Kelly E, Struyf E (2015) Silicon pools in human impacted soils of temperate zones. *Global Biogeochem Cycles* 29:1439–1450
59. Haynes RJ (2019) What effect does liming have on silicon availability in agricultural soils? *Geoderma* 337:375–383
60. Sommer M, Kaczorek D, Kuzakov Y, Breuer J (2006) Silicon pools and fluxes in soils and landscapes—a review. *J Plant Nutri Soil Sci* 169:310–329
61. White AF, Vivit DV, Schulz MS, Bullen TD, Evett RR, Agarwal J (2012) Biogenic and pedogenic controls on Si distributions and cycling in grasslands of the Santa Cruz soil chronosequence, California. *Geochim Cosmochim* 94:72–94
62. Creevy KE, Austad SN, Hoffman JM, O'Neill DG, Promislow DE (2016) The companion dog as a model for the longevity dividend. *Cold Spring Harb Perspect Med* 6:a026633
63. Tubaña BS, Heckman JR (2015) In: Fabrício AR, Lawrence ED (eds) *Silicon in soils and plants*, Springer International Publishing Switzerland
64. Laruelle GG et al. (2009) Anthropogenic perturbations of the silicon cycle at the global scale: Key role of the land-ocean transition. *Global Biogeochem Cycles* 23
65. Brindavathy R (2022) In: Aydin B, Mostafa S (eds) *Mineral Formation by Microorganisms*, Springer, Cham
66. Fomina M, Skorochod I (2020) Microbial interaction with clay minerals and its environmental and biotechnological implications. *Minerals* 10:861
67. Li GL, Zhou CH, Fiore S, Yu WH (2019) Interactions between microorganisms and clay minerals: New insights and broader applications. *Appl Clay Sci* 177:91–113
68. Etesami H, Jeong BR (2021) Contribution of arbuscular mycorrhizal fungi, phosphate-solubilizing bacteria, and silicon to P uptake by plant: a review. *Front Plant Sci* 12:1355
69. Thies JE, Grossman JM (2006) In: Norman UF, Andrew SB, Erick F, Hans H, Olivier H, Mark L, Cheryl P, Jules P, Pedro S, Nteranya S, Janice T (eds) *Biological approaches to sustainable soil systems*. CRC Press, Boca Raton
70. Patrick S, Holding A (1985) The effect of bacteria on the solubilization of silica in diatom frustules. *J Appl Bacteriol* 59:7–16
71. Sheng M, Tang M, Chen H, Yang B, Zhang F, Huang Y (2008) Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. *Mycorrhiza* 18:287–296
72. Bist V, Niranjana A, Ranjan M, Lehri A, Seem K, Srivastava S (2020) Silicon-solubilizing media and its implication for characterization of bacteria to mitigate biotic stress. *Front plant sci* 11:28
73. Driks A (2002) Maximum shields: the assembly and function of the bacterial spore coat. *Trends Microb* 10:251–254
74. Liu W, Xu X, Wu X, Yang Q, Luo Y, Christie P (2006) Decomposition of silicate minerals by *Bacillus mucilaginosus* in liquid culture. *Environ Geochem Health* 28:133–140
75. Sumitha S et al (2018) Phyto-mediated photo catalysed green synthesis of silver nanoparticles using *Durio zibethinus* seed extract: antimicrobial and cytotoxic activity and photocatalytic applications. *Molecules* 23:3311
76. Shahbazi Y, Moosavy M-H (2019) Physico-mechanical and antimicrobial properties of quince seed mucilage supplemented with titanium dioxide and silicon oxide nanoparticles. *J Nanomed Res* 4:157–163
77. Whitehead KA, Colligon J, Verran J (2005) Retention of microbial cells in substratum surface features of micrometer and sub-micrometer dimensions. *Colloids Surf, B* 41:129–138
78. Dasgupta N, Arora SK, Ramphal R (2000) fleN, a gene that regulates flagellar number in *Pseudomonas aeruginosa*. *J Bacteriol* 182:357–364
79. Ghorbani-Choghamarani A, Azadi G, Tahmasbi B, Hadizadeh-Hafshejani M, Abdi Z (2014) Phosphorus Sulfur Silicon Relat Elem 189:433–439
80. Yin L, Wang S, Tanaka K, Fujihara S, Itai A, Den X, Zhang S (2016) Silicon-mediated changes in polyamines participate in silicon-induced salt tolerance in *Sorghum bicolor* L. *Plant Cell Environ* 39:245–258
81. Zellner W, Datnoff L (2020) In: Youssef R, Patrick du J, Patrick B, Stefania De P, Giuseppe C (eds) *Silicon as a biostimulant in agriculture*, 1st edn. Burleigh Dodds Science Publishing
82. Bist N, Sircar A, Yadav K (2020) Holistic review of hybrid renewable energy in circular economy for valorization and management. *Environ Techn Innov* 20:101054
83. Dhiman P et al (2021) Fascinating role of silicon to combat salinity stress in plants: An updated overview. *Plant Physiol Biochem* 162:110–123
84. Armbruster CE, Hodges SA, Smith SN, Alteri CJ, Mobley HL (2014) Arginine promotes *Proteus mirabilis* motility and fitness by contributing to conservation of the proton gradient and proton motive force. *Microbiologyopen* 3:630–641
85. Shivaraj S, Mandlik R, Bhat JA, Raturi G, Elbaum R, Alexander L, Tripathi DK, Deshmukh R, Sonah H (2022) Outstanding questions on the beneficial role of silicon in crop plants. *Plant Cell Physiol* 63:4–18
86. Currie HA, Perry CC (2007) Silica in plants: biological, biochemical and chemical studies. *Annals Bot* 100:1383–1389

87. Neethirajan S, Gordon R, Wang L (2009) Potential of silica bodies (phytoliths) for nanotechnology. *Tren Biotechnol* 27:461–467
88. Dhiman G, Kumar V (2019) Seagull optimization algorithm: Theory and its applications for large-scale industrial engineering problems. *Knowl Based Syst* 165:169–196
89. Jensen DM, Morgan TR, Marcellin P, Pockros PJ, Reddy KR, Hadziyannis SJ, Ferenci P, Ackrill AM, Willems B (2006) Early identification of HCV genotype 1 patients responding to 24 weeks peginterferon α -2a (40 kD)/ribavirin therapy. *Hepatology* 43:954–960
90. Al-Karaki GN (2006) Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. *Sci Hortic* 109:1–7
91. Li H, Zhu Y, Hu Y, Han W, Gong H (2015) Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture. *Acta Physiol Plant* 37:1–9
92. Hafez EM, Osman HS, El-Razek UAA, Elbagory M, Omara AE-D, Eid MA, Gawayed SM (2021) Foliar-applied potassium silicate coupled with plant growth-promoting rhizobacteria improves growth, physiology, nutrient uptake and productivity of faba bean (*Vicia faba* L.) irrigated with saline water in salt-affected soil. *Plants* 10: 894
93. Ribeiro IDA, Volpiano CG, Vargas LK, Granada CE, Lisboa BB, Passaglia LMP (2020) Use of mineral weathering bacteria to enhance nutrient availability in crops: a review. *Front Plant Sci* 11:590774
94. Saad M, Abo-Koura HA (2018) Improvement of sorghum (*Sorghum bicolor* L. Moench) growth and yield under drought stress by inoculation with *Bacillus cereus* and foliar application of potassium silicate. *Environ Biodiv Soil Sec* 2:205–221
95. Tubana BS, Babu T, Datnoff LE (2016) A review of silicon in soils and plants and its role in US agriculture: history and future perspectives. *Soil Sci* 181:393–411
96. Barker W, Welch S, Chu S, Banfield J (1998) Experimental observations of the effects of bacteria on aluminosilicate weathering. *Am Min* 83:1551–1563
97. Raturi G, Sharma Y, Rana V, Thakral V, Myaka B, Salvi P, Singh M, Dhar H, Deshmukh R (2021) Exploration of silicate solubilizing bacteria for sustainable agriculture and silicon biogeochemical cycle. *Plant Physiol Biochem* 166:827–838
98. Drever JI (1994) The effect of land plants on weathering rates of silicate minerals. *Geochim Cosmochim* 58:2325–2332
99. Lambers H, Mougél C, Jaillard B, Hinsinger P (2009) Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. *Plant Soil* 321:83–115
100. Chen W, Luo L, He L-Y, Wang Q, Sheng X-F (2016) Distinct mineral weathering behaviors of the novel mineral-weathering strains *Rhizobium yantingense* H66 and *Rhizobium etli* CFN42. *Appl Environ Microbiol* 82:4090–4099
101. Wang RR, Wang Q, He LY, Qiu G, Sheng XF (2015) Isolation and the interaction between a mineral-weathering *Rhizobium tropici* Q34 and silicate minerals. *World J Microbiol Biotechnol* 31:747–753
102. Yanni YG, Rizk RY, Corich V, Squartini A, Ninke K, Philip-Hollingsworth S, Orgambide G, Bruijn FD, Stoltzfus J, Buckley D, Schmidt TM (1997) in *Opportunities for biological nitrogen fixation in rice and other non-legumes. Natural endophytic association between Rhizobium leguminosarum bv. trifolii and rice roots and assessment of its potential to promote rice growth.* (Springer) pp. 99–114.
103. Banfield JF, Hamers RJ (1997) Processes at minerals and surfaces with relevance to microorganisms and prebiotic synthesis. *Rev Mineral Geochem* 35:81–122
104. Dove MT, Keen DA, Hannon AC, Swainson IP (1997) Direct measurement of the Si–O bond length and orientational disorder in the high-temperature phase of cristobalite. *Phys Chem Miner* 24:311–317
105. Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plants. *Agron Sustain Dev* 34:455–472
106. Vayssiere J-L, Petit PX, Risler Y, Mignotte B (1994) Commitment to apoptosis is associated with changes in mitochondrial biogenesis and activity in cell lines conditionally immortalized with simian virus 40. *Proc Natl Acad Sci* 91:11752–11756
107. Yue H, Mo W, Li C, Zheng Y, Li H (2007) The salt stress relief and growth promotion effect of Rs-5 on cotton. *Plant Soil* 297:139–145
108. Etesami H (2018) Can interaction between silicon and plant growth promoting rhizobacteria benefit in alleviating abiotic and biotic stresses in crop plants? *Agri Ecosys Environ* 253:98–112
109. Raza T, Villalobos SdLS, Shehzad M, Imran S, da Silva DJH (2020) PGP Characterization of rhizobacteria associated with apple gourd (*Praecitrullus fistulosus* L.). *Pak J Agri Res* 33: 926
110. Torbeck RL, Saedi N (2016) Optimization of laser tattoo removal: optical clearing agents and multiple same-day treatments via the R0 and R20 methods. *Curr Dermatol Reps* 5:136–141
111. Meena V, Dotaniya M, Coumar V, Rajendiran S, Kundu S, Subba Rao A (2014) A case for silicon fertilization to improve crop yields in tropical soils. *Proceedings of the National Academy of Sciences, India Section B: Biol Sci* 84:505–518
112. Singh T, Singh P, Singh A (2021) Silicon significance in crop production: Special consideration to rice: An overview. *J Pharm Innov* 10:223–229
113. Shin J et al (2019) Bioresorbable pressure sensors protected with thermally grown silicon dioxide for the monitoring of chronic diseases and healing processes. *Nat Biomed Eng* 3:37–46
114. Gondil VS, Asif M, Bhalla TC (2017) Optimization of physico-chemical parameters influencing the production of prodigiosin from *Serratia nematodiphila* RL2 and exploring its antibacterial activity. *Biotech* 7:1–8
115. Al-Kumaim NH, Alhazmi AK, Mohammed F, Gazem NA, Shabbir MS, Fazea Y (2021) Exploring the impact of the COVID-19 pandemic on university students' learning life: An integrated conceptual motivational model for sustainable and healthy online learning. *Sustain* 13:2546
116. Lee K-E, Adhikari A, Kang S-M, You Y-H, Joo G-J, Kim J-H, Kim S-J, Lee I-J (2019) Isolation and characterization of the high silicate and phosphate solubilizing novel strain *Enterobacter ludwigii* GAK2 that promotes growth in rice plants. *Agron* 9:144
117. Adhikari A, Lee K-E, Khan MA, Kang S-M, Adhikari B, Imran M, Jan R, Kim K-M, Lee I-J (2020) Effect of silicate and phosphate solubilizing *Rhizobacterium Enterobacter ludwigii* GAK2 on *Oryza sativa* L. under cadmium stress. *J Microbiol Biotechnol* 30(1): 118–126
118. Mendoza-Arroyo GE, Chan-Bacab MJ, Aguila-Ramírez RN, Ortega-Morales BO, Canché Solís RE, Chab-Ruiz AO, Cob-Rivera KI, Dzib-Castillo B, Tun-Che RE, Camacho-Cab JC (2020) Inorganic phosphate solubilization by a novel isolated bacterial strain *Enterobacter* sp. ITCB-09 and its application potential as biofertilizer. *Agri* 10: 383
119. Liang Y, Wong J, Wei L (2005) Silicon-mediated enhancement of cadmium tolerance in maize (*Zea mays* L.) grown in cadmium contaminated soil. *Chemo* 58:475–483
120. Li Z, Delvaux B, Yans J, Dufour N, Houben D, Cornelis JT (2018) Phytolith-rich biochar increases cotton biomass and silicon-mineralomass in a highly weathered soil. *J Plant Nutri Soil Sci* 181:537–546
121. Mehrabanjoubani P, Abdolzadeh A, Sadeghipour HR, Aghdasi M (2015) Silicon affects transcellular and apoplastic uptake of some nutrients in plants. *Pedosphere* 25:192–201

122. Sakurai G, Satake A, Yamaji N, Mitani-Ueno N, Yokozawa M, Feugier FG, Ma JF (2015) In silico simulation modeling reveals the importance of the Casparian strip for efficient silicon uptake in rice roots. *Plant Cell Physiol* 56:631–639
123. Liang Y, Shen Q, Shen Z, Ma T (1996) Effects of silicon on salinity tolerance of two barley cultivars. *J Plant Nutri* 19:173–183
124. Jarvis S (1987) The uptake and transport of silicon by perennial ryegrass and wheat. *Plant Soil* 97:429–437
125. Savant NK, Korndörfer GH, Datnoff LE, Snyder GH (1999) Silicon nutrition and sugarcane production: a review. *J Plant Nutri* 22:1853–1903
126. Deshmukh R, Bélanger RR (2016) Molecular evolution of aquaporins and silicon influx in plants. *Funct Ecol* 30:1277–1285
127. Guntzer F, Keller C, Meunier J-D (2012) Benefits of plant silicon for crops: a review. *Agron Sustain Dev* 32:201–213
128. Shen D (1997) Microbial diversity and application of microbial products for agricultural purposes in China. *Agric Ecosyst Environ* 62:237–245
129. Kang S-M et al (2017) Isolation and characterization of a novel silicate-solubilizing bacterial strain *Burkholderia eburnea* CS4-2 that promotes growth of japonica rice (*Oryza sativa* L. cv. Dongjin). *Soil Sci Plant Nutri* 63:233–241
130. Batista BD, Singh BK (2021) Realities and hopes in the application of microbial tools in agriculture. *Microb Biotechnol* 14:1258–1268
131. Garg KK, Jain D, Rajpurohit D, Kushwaha HS, Daima HK, Stephen BJ, Singh A, Mohanty SR (2021) Agricultural significance of silica nanoparticles synthesized from a silica solubilizing bacteria. *Comments Inorg Chem* 1–17
132. Hendry KR, Marron AO, Vincent F, Conley DJ, Gehlen M, Ibarbalz FM, Quéguiner B, Bowler C (2018) Competition between silicifiers and non-silicifiers in the past and present ocean and its evolutionary impacts. *Front Mar Sci* 5:22
133. Rezakhani L, Motesharezadeh B, Tehrani MM, Etesami H, Mirseyed Hosseini H (2020) Effect of silicon and phosphate-solubilizing bacteria on improved phosphorus (P) uptake is not specific to insoluble P-fertilized sorghum (*Sorghum bicolor* L.) plants. *J Plant Growth Regul* 39:239–253
134. Bharti V, Dotaniya M, Shukla S, Yadav V (2017) In: Jay SS, Gamini S (eds) *Agro-environmental sustainability*, 1st edn. Springer, Cham
135. Sindhu V, Chatterjee R, Santhoshkumar G, Sinha T (2020) Enrichment of Organic Manures and Their Utilization in Vegetable Crops. *Curr J App Sci Technol* 39:10–24
136. Pratheesh P, Lal S, Tuvikene R, Manickam S, Sudheer S (2020) In: Ali AR, Ajar NY, Neelam Y (eds) *New and future developments in microbial biotechnology and bioengineering*, 1st edn. Elsevier, Amsterdam, Netherlands
137. Raza T, Khan MY, Nadeem SM, Imran S, Qureshi KN, Mushtaq MN, Sohaib M, Schmalenberger A, Eash NS (2021) Biological management of selected weeds of wheat through co-application of allelopathic rhizobacteria and sorghum extract. *Biol Cont* 164:104775
138. Rajput VD et al (2021) Effects of silicon and silicon-based nanoparticles on rhizosphere microbiome, plant stress and growth. *Biology* 10:791
139. Raza T, Qureshi KN, Imran S, Eash NS, Bortone I (2021) Associated health risks from heavy metal-laden effluent into point drainage channels in Faisalabad. *Pakistan Pak J Agri Res* 34(3):487–494
140. Verma KK et al (2020) Interactive role of silicon and plant-rhizobacteria mitigating abiotic stresses: A new approach for sustainable agriculture and climate change. *Plants* 9:1055
141. Kumar A, Patel JS, Bahadur I, and Meena VS (2016) In: Vijay SM, Bihari RM, Jay PV, Ram SM (eds). *Potassium solubilizing microorganisms for sustainable agriculture*, 1st edn. Springer, India
142. Kumawat N, Kumar R, Khandkar U, Yadav R, Saurabh K, Mishra J, Dotaniya M, and Hans H (2019) In: Bhoopander G, Ram P, Qiang-Sheng W, Ajit V (eds) *Biofertilizers for sustainable agriculture and environment*, 1st edn. Springer, Cham
143. Shah AA, Yasin NA, Akram K, Ahmad A, Khan WU, Akram W, Akbar M (2021) Ameliorative role of *Bacillus subtilis* FBL-10 and silicon against lead induced stress in *Solanum melongena*. *Plant Physiol Biochem* 158:486–496
144. Paulraj P, Balakrishnan K, Rajendran RRMV, Alagappan B (2021) Investigation on recent research of mechanical properties of natural fiber reinforced polymer (NFRP) materials. *Mater Plast* 58:100–118
145. Dollinger J, Schacht VJ, Gaus C, Grant S (2018) Effect of surfactant application practices on the vertical transport potential of hydrophobic pesticides in agrosystems. *Chemosphere* 209:78–87
146. Zhou J, Sun Y, Xiao H, Ma Q, Si L, Ni L, Wu L (2021) Silicon uptake and translocation in low-silica rice mutants investigated by isotope fractionation. *Agron J* 113:2732–2741
147. Brindavathy R, Dhara N, Rajasundari K (2012) Biodissolution of silica by silicon bacteria in sugarcane rhizosphere. *Res J Agr Sci* 3:1042–1044
148. Chaiwong N, Rerkasem B, Pusadee T, Prom-u-thai C (2021) Silicon application improves caryopsis development and yield in rice. *J Sci Food Agric* 101:220–228
149. Bocharnikova E, Loginov S, Matychenkov V, Storozhenko P (2010) Silicon fertilizer efficiency *Russ Agric Sci* 36:446–448
150. Shamim M, Kumar M, Pal AK, Kumar RR, and Jha V (2019) In: Shamim M, Kumar M, Pal AK, Kumar RR, Jha V (eds) *Biofertilizers and biopesticides in sustainable agriculture*, 1st edn. Apple Academic Press
151. Van der Weijden CH, Middelburg JJ, Van Ganns P (1989) Early diagenetic silica precipitation, in relation to redox boundaries and bacterial metabolism, in late Cretaceous Chalk of the Maastrichtian type locality. *Geol Mijnb* 68: 263–270
152. Matthey M (1992) The production of organic acids. *Crit Rev Biotechnol* 12:87–132
153. Vandevivere P, Welch S, Ullman W, Kirchman DL (1994) Enhanced dissolution of silicate minerals by bacteria at near-neutral pH. *Microb Ecol* 27:241–251
154. Machado RMA, Serralheiro RP (2017) Soil salinity: effect on vegetable crop growth. *Management practices to prevent and mitigate soil salinization. Sci Hort* 3: 30
155. Nanayakkara U, Uddin W, Datnoff L (2008) Application of silicon sources increases silicon accumulation in perennial ryegrass turf on two soil types. *Plant Soil* 303:83–94
156. Kalia A and Kaur H in *Nanoscience for sustainable agriculture* (2019). In: Ramesh N P, Nidhi C, Chittaranjan K (eds) *Nanobiofertilizers*, 1st edn. Springer, Chem
157. Kannan N, Raj SA (1998) Occurrence of silicate solubilizing bacteria in rice ecosystem. *Madras Agri J* 85:47–49
158. Shivaraj S, Mandlik R, Bhat JA, Raturi G, Elbaum R, Alexander L, Tripathi DK, Deshmukh R, Sonah H (2021) Outstanding questions on the beneficial role of silicon in crop plants. *Plant Cell Physiol* 63(1):4–18
159. Schwab F, Zhai G, Kern M, Turner A, Schnoor JL, Wiesner MR (2016) Barriers, pathways and processes for uptake, translocation and accumulation of nanomaterials in plants—Critical review. *Nanotoxicology* 10:257–278
160. Li L, Luo Y, Li R, Zhou Q, Peijnenburg WJ, Yin N, Yang J, Tu C, Zhang Y (2020) Effective uptake of submicrometre plastics by crop plants via a crack-entry mode. *Nat Sustain* 3:929–937
161. Limmer MA, Wise P, Dykes GE, Seyfferth AL (2018) Silicon decreases dimethylarsinic acid concentration in rice

- grain and mitigates straighthead disorder. *Environ Sci Technol* 52:4809–4816
162. Lovisolo C, Hartung W, Schubert A (2002) Whole-plant hydraulic conductance and root-to-shoot flow of abscisic acid are independently affected by water stress in grapevines. *Funct Plant Biol* 29:1349–1356
 163. Marafon AC, Endres L (2013) Silicon: fertilization and nutrition in higher plants. *Embrapa Tabuleiros Costeiros-Artigo em periódico indexado (ALICE)*. *Rev Cienc Agrar* 56(4): 380–388
 164. Mandlik R, Thakral V, Raturi G, Shinde S, Nikolić M, Tripathi DK, Sonah H, Deshmukh R (2020) Significance of silicon uptake, transport, and deposition in plants. *J Exp Bot* 71:6703–6718
 165. Motomura H, Fujii T, Suzuki M (2006) Silica deposition in abaxial epidermis before the opening of leaf blades of *Pleioblastus chino* (Poaceae, Bambusoideae). *Ann Bot* 97:513–519
 166. Kumar S, Elbaum R (2018) Interplay between silica deposition and viability during the life span of sorghum silica cells. *New Phytol* 217:1137–1145
 167. Nassif N, Livage J (2011) From diatoms to silica-based biohybrids. *Chem Soc Rev* 40:849–859
 168. Zhou K-G et al (2018) Electrically controlled water permeation through graphene oxide membranes. *Nature* 559:236–240
 169. Harley A, Gilkes R (2000) Factors influencing the release of plant nutrient elements from silicate rock powders: a geochemical overview. *Nutr Cycl Agroecosystems* 56:11–36
 170. Manning DA (2010) Mineral sources of potassium for plant nutrition. A review *Agron Sustain Dev* 30:281–294
 171. Anda M, Shamshuddin J, Fauziah C (2015) Improving chemical properties of a highly weathered soil using finely ground basalt rocks. *CATENA* 124:147–161
 172. Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. *Ann Rev Plant Biol* 52:527
 173. Aoki M, Fujii K, Kitayama K (2012) Environmental control of root exudation of low-molecular weight organic acids in tropical rainforests. *Ecosyst* 15:1194–1203
 174. Vives-Peris V, de Ollas C, Gómez-Cadenas A (2020) Pérez-Clemente RMJPCr. Root exudates: from plant to rhizosphere and beyond. *Plant Cell Repr* 39:3–17
 175. Richter DdB, Oh N-H, Fimmen R, and Jackson J (2007) In: Zoe GC, Julie LW (eds) *The rhizosphere*, Elsevier, Academic Press
 176. Bennett P, Rogers J, Choi W, Hiebert F (2001) Silicates, silicate weathering, and microbial ecology. *Geomicrobiol J* 18:3–19
 177. Samuels T, Bryce C, Landenmark H, Marie-Loudon C, Nicholson N, Stevens AH, Cockell C (2020) Microbial weathering of minerals and rocks in natural environments. *Biogeochemical cycles: Environ Ecol Stat* 59–79
 178. Ranalli G, Zanardini E, and Sorlini C (2009) Biodeterioration—including cultural heritage.
 179. Zhu Y, Duan G, Chen B, Peng X, Chen Z, Sun G (2014) Mineral weathering and element cycling in soil-microorganism-plant system. *Sci China Earth Sci* 57:888–896
 180. Smith KS, Ferry JG (2000) Prokaryotic carbonic anhydrases. *FEMS Microbiol Rev* 24:335–366
 181. Xiao L, Hao J, Wang W, Lian B, Shang G, Yang Y, Liu C, Wang S (2014) The up-regulation of carbonic anhydrase genes of *Bacillus mucilaginosus* under soluble Ca²⁺ deficiency and the heterologously expressed enzyme promotes calcite dissolution. *Geomicrobiol J* 31:632–641
 182. Adeleke R, Nwangburuka C, Oboirien B (2017) Origins, roles and fate of organic acids in soils: A review. *S Afr J Bot* 108:393–406
 183. Torres MA, West AJ, Nealson K (2014) Microbial acceleration of olivine dissolution via siderophore production. *Procedia Environ Sci* 10:118–122
 184. Uroz S, Calvaruso C, Turpault M-P, Frey-Klett P (2009) Mineral weathering by bacteria: ecology, actors and mechanisms. *Trends Microbiol* 17:378–387
 185. Zavarzina DG et al (2016) Oxidative biotransformation of biotite and glauconite by alkaliphilic anaerobes: the effect of Fe oxidation on the weathering of phyllosilicates. *Chem Geol* 439:98–109
 186. Chandrakala C, Voleti S, Bandappa S, Sunil Kumar N, Latha P (2019) Silicate solubilization and plant growth promoting potential of *Rhizobium* sp. isolated from rice rhizosphere. *SILICON* 11:2895–2906
 187. Hu L, Xia M, Lin X, Xu C, Li W, Wang J, Zeng R, Song Y (2018) Earthworm gut bacteria increase silicon bioavailability and acquisition by maize. *Soil Biol Biochem* 125:215–221
 188. Sauer D, Saccone L, Conley DJ, Herrmann L, Sommer M (2006) Review of methodologies for extracting plant-available and amorphous Si from soils and aquatic sediments. *Biogeochem* 80:89–108
 189. Belton DJ, Deschaume O, Perry CC (2012) An overview of the fundamentals of the chemistry of silica with relevance to biosilicification and technological advances. *The FEBS J* 279:1710–1720
 190. Perry CC, Keeling-Tucker T (1998) Aspects of the bioinorganic chemistry of silicon in conjunction with the biometals calcium, iron and aluminium. *J Inorg Biochem* 69:181–191
 191. Wonisch H, Gérard F, Dietzel M, Jaffrain J, Nestroy O, Boudot J-P (2008) Occurrence of polymerized silicic acid and aluminum species in two forest soil solutions with different acidity. *Geoderma* 144:435–445
 192. Cornelis J-T, Delvaux B, Cardinal D, André L, Ranger J, Opfergelt S (2010) Tracing mechanisms controlling the release of dissolved silicon in forest soil solutions using Si isotopes and Ge/Si ratios. *Geochim Cosmochim Acta* 74:3913–3924
 193. Matichenkov V and Bocharnikov E in *Studies in plant science* (2001). The relationship between silicon and soil physical and chemical properties. (Elsevier) pp. 209–219.
 194. Lucas Y and Chauvel A (1992) Soil formation in tropically weathered terrains. *Regolith exploration geochemistry in tropical and subtropical terrains..* 57–77
 195. Savant NK, Datnoff LE, Snyder GH (1997) Depletion of plant-available silicon in soils: A possible cause of declining rice yields. *Commun Soil Sci Plant Anal* 28:1245–1252
 196. El-Tayeb M (2005) Response of barley grains to the interactive effect of salinity and salicylic acid. *Plant Growth Regul* 45:215–224
 197. Gunes A, Inal A, Bagci E, Coban S, Sahin O (2007) Silicon increases boron tolerance and reduces oxidative damage of wheat grown in soil with excess boron. *Biol Plant* 51:571–574
 198. Roboredo MC, Pessoa AA (2013) A branch-and-cut algorithm for the discrete (r|p)-centroid problem. *Eur J Oper Res* 224:101–109
 199. Rains D, Epstein E, Zasoski R, Aslam M (2006) Active silicon uptake by wheat. *Plant Soil* 280:223–228
 200. Meena H, Meena RS (2017) Assessment of sowing environments and bio-regulators as adaptation choice for clusterbean productivity in response to current climatic scenario. *Bangladesh J Bot* 46:241–244
 201. Mali M, Aery CN (2008) Silicon effects on nodule growth, dry-matter production, and mineral nutrition of cowpea (*Vigna unguiculata*). *J Plant Nutr Soil Sci* 171:835–840
 202. Desplanques V, Cary L, Mouret J-C, Trolard F, Bourrie G, Grauby O, Meunier J-D (2006) Silicon transfers in a rice field in Camargue (France). *J Geochem Explor* 88:190–193
 203. Pei Z, Ming D, Liu D, Wan G, Geng X, Gong H, Zhou W (2010) Silicon improves the tolerance to water-deficit stress induced by polyethylene glycol in wheat (*Triticum aestivum* L.) seedlings. *J Plant Growth Reg* 29:106–115

204. Ma J, Takahashi E (1990) Effect of silicon on the growth and phosphorus uptake of rice. *Plant soil* 126:115–119
205. Alzahrani Y, Kuşvuran A, Alharby HF, Kuşvuran S, Rady MM (2018) The defensive role of silicon in wheat against stress conditions induced by drought, salinity or cadmium. *Ecotoxicol Environ Saf* 154:187–196
206. Schaller J, Brackhage C, Bäucker E, Dudel EG (2013) UV-screening of grasses by plant silica layer? *J Biosci* 38:413–416
207. Rizwan M, Ali S, Ibrahim M, Farid M, Adrees M, Bharwana SA, Zia-ur-Rehman M, Qayyum MF, Abbas F (2015) Mechanisms of silicon-mediated alleviation of drought and salt stress in plants: a review. *Environ Sci Pollu Res* 22:15416–15431
208. Zhu Z, Wei G, Li J, Qian Q, Yu J (2004) Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). *Plant Sci* 167:527–533
209. Massey FP, Smith MJ, Lambin X, Hartley SE (2008) Are silica defences in grasses driving vole population cycles? *Biol Lett* 4:419–422
210. Massey FP, Hartley SE (2009) Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. *J Animal Ecol* 78:281–291
211. Ning D, Song A, Fan F, Li Z, Liang Y (2014) Effects of slag-based silicon fertilizer on rice growth and brown-spot resistance. *Plosone* 9:e102681
212. Schaller J, Puppe D, Kaczorek D, Ellerbrock R, Sommer M (2021) Silicon Cycling in Soils Revisited *Plants* 10(2):295
213. Katz O, Puppe D, Kaczorek D, Prakash NB, Schaller J (2021) Silicon in the soil-plant continuum: intricate feedback mechanisms within ecosystems. *Plants* 10(4):652
214. Pico LBO, Zhang C, Vyn TJ (2021) The central role of ear nitrogen uptake in maize endosperm cell and kernel weight determination during the lag period. *Field Crops Res* 273:108285
215. Cassman KG, Dobermann A (2022) Nitrogen and the future of agriculture: 20 years on. *Ambio* 51:17–24
216. Li C, Wang X, Guo Z, Huang N, Hou S, He G, Batchelor WD, Siddique KH, Wang Z, Zhang D (2022) Optimizing nitrogen fertilizer inputs and plant populations for greener wheat production with high yields and high efficiency in dryland areas. *Field Crops Res* 276:108374
217. Nayak HS et al (2022) Rice yield gaps and nitrogen-use efficiency in the Northwestern Indo-Gangetic Plains of India: Evidence based insights from heterogeneous farmers' practices. *Field Crops Res* 275:108328
218. Burke WJ, Jayne TS, Snapp SS (2022) Nitrogen efficiency by soil quality and management regimes on Malawi farms: Can fertilizer use remain profitable? *World Develop* 152:105792
219. Min J, Sun H, Kronzucker HJ, Wang Y, Shi W (2021) Comprehensive assessment of the effects of nitrification inhibitor application on reactive nitrogen loss in intensive vegetable production systems. *Agri Ecosys Environ* 307:107227
220. Gou T, Yang L, Hu W, Chen X, Zhu Y, Guo J, Gong H (2020) Silicon improves the growth of cucumber under excess nitrate stress by enhancing nitrogen assimilation and chlorophyll synthesis. *Plant Physiol Bioch* 152:53–61
221. Schaller J, Brackhage C, Gessner M, Bäucker E, Gert Dudel E (2012) Silicon supply modifies C: N: P stoichiometry and growth of *Phragmites australis*. *Plant Biol* 14:392–396
222. Barreto RF, Júnior AAS, Maggio MA, de Mello PR (2017) Silicon alleviates ammonium toxicity in cauliflower and in broccoli. *Scient Hort* 225:743–750
223. Cooke J, Leishman MR (2016) Consistent alleviation of abiotic stress with silicon addition: a meta-analysis. *Func Ecol* 30:1340–1357
224. Pascual MB, Echevarria V, Gonzalo MJ, Hernández-Apaolaza L (2016) Silicon addition to soybean (*Glycine max* L.) plants alleviate zinc deficiency. *Plant Physiol Biochem* 108:132–138
225. Deus ACF, de Mello PR, de Cássia Félix Alvarez R, de Oliveira RLL, Felisberto G, (2020) Role of silicon and salicylic acid in the mitigation of nitrogen deficiency stress in rice plants. *SILICON* 12:997–1005
226. Mabagala F, Geng Y, Cao G, Wang L, Wang M, Zhang M (2020) Effect of silicon on crop yield, and nitrogen use efficiency applied under straw return treatments. *Appl Ecol Environ Res* 18:5577–5590
227. Láiné P, Haddad C, Arkoun M, Yvin J-C, Etienne P (2019) Silicon promotes agronomic performance in Brassica napus cultivated under field conditions with two nitrogen fertilizer inputs. *Plants* 8:137
228. Neu S, Schaller J, Dudel EG (2017) Silicon availability modifies nutrient use efficiency and content, C: N: P stoichiometry, and productivity of winter wheat (*Triticum aestivum* L.). *Sci Rep* 7:1–8
229. Pál M, Kovács V, Szalai G, Soós V, Ma X, Liu H, Mei H, Janda T (2014) Salicylic acid and abiotic stress responses in rice. *J Agron Crop Sci* 200:1–11
230. Detmann KC, Araújo WL, Martins SC, Sanglard LM, Reis JV, Detmann E, Rodrigues FÁ, Nunes-Nesi A, Fernie AR, DaMatta FM (2012) Silicon nutrition increases grain yield, which, in turn, exerts a feed-forward stimulation of photosynthetic rates via enhanced mesophyll conductance and alters primary metabolism in rice. *New Phytol* 196:752–762
231. Soratto RP, Fernandes AM, Pilon C, Souza MR (2019) Phosphorus and silicon effects on growth, yield, and phosphorus forms in potato plants. *J Plant Nutr* 42:218–233
232. Owino-Gerroh C, Gascho G (2005) Effect of silicon on low pH soil phosphorus sorption and on uptake and growth of maize. *Commun Soil Sci Plant Anal* 35:2369–2378
233. Zhang Y, Liang Y, Zhao X, Jin X, Hou L, Shi Y, Ahammed GJ (2019) Silicon compensates phosphorus deficit-induced growth inhibition by improving photosynthetic capacity, antioxidant potential, and nutrient homeostasis in tomato. *Agron* 9:733
234. Hu AY, Xu SN, Qin DN, Li W, Zhao XQ (2020) Role of silicon in mediating phosphorus imbalance in plants. *Plants* 10:51
235. Schaller J, Puppe D, Kaczorek D, Ellerbrock R, Sommer M (2021) Silicon cycling in soils revisited. *Plants* 10: 295
236. Dunne EJ and Reddy K (2005) Phosphorus biogeochemistry of wetlands in agricultural watersheds. Nutrient management in agricultural watersheds: a wetland solution. Wageningen, The Netherlands: Wageningen Academic Publishers: 105–119
237. Xia Z, He Y, Yu L, Lv R, Korpelainen H, Li C (2020) Sex-specific strategies of phosphorus (P) acquisition in *Populus cathayana* as affected by soil P availability and distribution. *New Phytol* 225:782–792
238. Pavlovic J, Kostic L, Bosnic P, Kirkby EA, Nikolic M (2021) Interactions of silicon with essential and beneficial elements in plants. *Front Plant Sci* 12:1224
239. Rajan S (1975) Phosphate adsorption and the displacement of structural silicon in an allophane clay. *J Soil Sci* 26:250–256
240. Knorr K-H, Lischeid G, Blodau C (2009) Dynamics of redox processes in a minerotrophic fen exposed to a water table manipulation. *Geoderma* 153:379–392
241. Schaller J, Faucherre S, Joss H, Obst M, Goeckede M, Planer-Friedrich B, Peiffer S, Gildeder B, Elberling B (2019) Silicon increases the phosphorus availability of Arctic soils. *Sci Rep* 9:1–11
242. Sigg L, Stumm W (1981) The interaction of anions and weak acids with the hydrous goethite (α -FeOOH) surface. *Colloids Surf* 2:101–117
243. Reithmaier G-MS, Knorr K-H, Arnhold S, Planer-Friedrich B, Schaller J (2017) Enhanced silicon availability leads to increased methane production, nutrient and toxicant mobility in peatlands. *Sci Rep* 7:1–8

244. Yang X, Post WM, Thornton PE, Jain A (2013) The distribution of soil phosphorus for global biogeochemical modeling. *Biogeochem* 10:2525–2537
245. Dong Q, Fang J, Huang F, Cai K (2019) Silicon amendment reduces soil Cd availability and Cd uptake of two Pennisetum species. *Int J Environ Res Public Health* 16:1624
246. Di Nasso NN, Angelini L, Bonari E (2010) Influence of fertilisation and harvest time on fuel quality of giant reed (*Arundo donax* L.) in central Italy. *Eur J Agron* 32:219–227
247. Hu AY, Che J, Shao JF, Yokosho K, Zhao XQ, Shen RF, Ma JF (2018) Silicon accumulated in the shoots results in down-regulation of phosphorus transporter gene expression and decrease of phosphorus uptake in rice. *Plant Soil* 423:317–325
248. Guo W, Hou Y-L, Wang S-G, Zhu Y-G (2005) Effect of silicate on the growth and arsenate uptake by rice (*Oryza sativa* L.) seedlings in solution culture. *Plant Soil* 272:173–181
249. Kostic L, Nikolic N, Bosnic D, Samardzic J, Nikolic M (2017) Silicon increases phosphorus (P) uptake by wheat under low P acid soil conditions. *Plant Soil* 419:447–455
250. Chen J, Zhang N-N, Pan Q, Lin X-Y, Shangguan Z, Zhang J-H, Wei G-H (2020) Hydrogen sulphide alleviates iron deficiency by promoting iron availability and plant hormone levels in Glycine max seedlings. *BMC Plant Biol* 20:1–22
251. Dhankhar R, Gupta S, Gulati P (2022) Insights on plant–microbe interactions in soil in relation to iron dynamics. *Vegetos*: 1–18
252. Xing Y (2020), Universitäts- und Landesbibliothek Bonn.
253. Chowdhury NR, Das R, Joardar M, Ghosh S, Bhowmick S, Roychowdhury T (2018) Arsenic accumulation in paddy plants at different phases of pre-monsoon cultivation. *Chemosphere* 210:987–997
254. Carrasco-Gil S, Rodríguez-Menéndez S, Fernández B, Pereiro R, de la Fuente V, Hernandez-Apaolaza L (2018) Silicon induced Fe deficiency affects Fe, Mn, Cu and Zn distribution in rice (*Oryza sativa* L.) growth in calcareous conditions. *Plant Physiol Biochem* 125:153–163
255. Martín-Esquinas A, Hernández-Apaolaza L (2021) Rice responses to silicon addition at different Fe status and growth pH. Evaluation of ploidy changes. *Plant Physiol Biochem* 163:296–307
256. Dauqan EM, Abdullah A (2017) Medicinal and functional values of thyme (*Thymus vulgaris* L.) herb. *J Applied Biol Biotech* 5:017–022
257. Yang Z-X, Yu S-Z, Lin Y-C, Zhang W-J, Wang Y, Wang R-G, Xu S-X, Yang T-Z, Xue G (2020) Activation of potassium released from soil by root-secreted organic acids in different varieties of tobacco (*Nicotiana tabacum*). *Funct Plant Biol* 47:318–326
258. Ahanger MA, Tomar NS, Tittal M, Argal S, Agarwal R (2017) Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. *Physiol Mol Biol Plants* 23:731–744
259. Manishankar P, Wang N, Köster P, Alatar AA, Kudla J (2018) Calcium signaling during salt stress and in the regulation of ion homeostasis. *J Exp Bot* 69:4215–4226
260. Garg N, Bhandari P (2016) Silicon nutrition and mycorrhizal inoculations improve growth, nutrient status, K⁺/Na⁺ ratio and yield of *Cicer arietinum* L. genotypes under salinity stress. *Plant Growth Reg* 78:371–387
261. Thorne SJ, Hartley SE, Maathuis FJ (2020) Is silicon a panacea for alleviating drought and salt stress in crops? *Front Plant Sci* 11:1221
262. Yan G, Fan X, Zheng W, Gao Z, Yin C, Li T, Liang Y (2021) Silicon alleviates salt stress-induced potassium deficiency by promoting potassium uptake and translocation in rice (*Oryza sativa* L.). *J Plant Physiol* 258: 153379
263. Hajiboland R, Cherghvareh L, Dashtebani F (2017) Effect of silicon supplementation on wheat plants under salt stress. *J Plant Process Fun* 5
264. Adams WW, Stewart JJ, Polutcho SK, Demmig-Adams B (2018). In *The Leaf: A Platform for Performing Photosynthesis*. Leaf vasculature and the upper limit of photosynthesis. (Springer) pp. 27–54.
265. Daras G, Rigas S, Tsitsekian D, Iacovides TA, Hatzopoulos P (2015) Potassium transporter TRH1 subunits assemble regulating root-hair elongation autonomously from the cell fate determination pathway. *Plant Sci* 231:131–137
266. Véry A-A, Nieves-Cordones M, Daly M, Khan I, Fizames C, Sentenac H (2014) Molecular biology of K⁺ transport across the plant cell membrane: what do we learn from comparison between plant species? *J Plant Physiol* 171:748–769
267. Barreto RF, Maier BR, de Mello PR, de Moraes TCB, Felisberto G (2022) Silicon attenuates potassium and sulfur deficiency by increasing nutrient use efficiency in basil plants. *Sci Hortic* 291:110616
268. Araújo WBS, Teixeira GCM, de Mello PR, Rocha AMS (2022) Silicon mitigates nutritional stress of nitrogen, phosphorus, and calcium deficiency in two forages plants. *Sci Rep* 12:1–11
269. dos Santos Sarah MM, de Mello PR, de Souza Júnior JP, Teixeira GCM, dos Santos Duarte JC, de Medeiros RLS (2021) Silicon supplied via foliar application and root to attenuate potassium deficiency in common bean plants. *Sci Rep* 11:1–13
270. Silva JLFd and Prado RdM (2021) Elucidating the action mechanisms of silicon in the mitigation of phosphorus deficiency and enhancement of its response in sorghum plants. *J Plant Nut* 44: 2572–2582
271. Sales AC, Campos CNS, de Souza Junior JP, da Silva DL, Oliveira KS, de Mello PR, Teodoro LPR, Teodoro PE (2021) Silicon mitigates nutritional stress in quinoa (*Chenopodium quinoa* Willd.). *Sci Rep* 11:1–16
272. Syed A, Raza T, Bhatti TT, Eash NS (2022) Climate Impacts on the agricultural sector of Pakistan: Risks and solutions. *Environ Challenges* 6:100433
273. Khan KS, Qadir MF, Ahmad A, Naveed M, Raza T, Ditta A (2022). Efficacy of Different Endophytic Bacterial Strains in Enhancing Growth, Yield, and Physiological and Biochemical Attributes of *Linum usitatissimum* L. *J Soil Sci Plant Nutr* 1–12
274. Kim YH, Khan AL, Kim DH, Lee SY, Kim KM, Waqas, M, Jung HY, Shin JH, Kim JG, Lee, IJ (2014). Silicon mitigates heavy metal stress by regulating P-type heavy metal ATPases, *Oryza sativa* low silicon genes, and endogenous phytohormones. *BMC Plant Biol* 14: 1–13.
275. Schaller J, Puppe D (2021) Heat improves silicon availability in mineral soils. *Geoderma* 386:114909
276. Guntzer F, Keller C, Poulton PR, McGrath SP, Meunier JD (2012) Long-Term removal of wheat straw decreases soil amorphous silica at Broadbalk, Rothamsted. *Plant Soil* 352:173–184
277. Klotzbücher T, Treptow C, Kaiser K, Klotzbücher A, Mikutta R (2020) Sorption competition with natural organic matter as mechanism controlling silicon mobility in soil. *Sci Rep* 10:11225

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