ISSN 2664-4010 (Print) & ISSN 2664-6730 (Online)
South Asian Research Journal of Agriculture and Fisheries
Abbreviated Key Title: South Asian Res J Agri Fish

| Volume-8 | Issue-5 | Nov-Dec-2026 | **DOI: https://doi.org/10.36346/sarjaf.2026.v08i05.002**

Review Article

Silicate Solubilizing Microorganisms as Drivers of Soil Fertility and Plant Nutrition: Mechanisms, Plant Benefits and Critical Research Gaps

Vaishnavi S. Nalawade[1]*, Shrikumar V. Mahamuni[1]

[1]Department of Microbiology, Shardabai Pawar Mahila Arts, Commerce and Science College, (Affiliated to Savitribai Phule Pune University), Shardanagar, Malegaon Bk., Baramati, Dist. Pune, 413115, Maharashtra, India

***Corresponding Author:** Vaishnavi S. Nalawade
Department of Microbiology, Shardabai Pawar Mahila Arts, Commerce and Science College, (Affiliated to Savitribai Phule Pune University), Shardanagar, Malegaon Bk., Baramati, Dist. Pune, 413115, Maharashtra, India

Article History
Received: 18.09.2026
Accepted: 10.11.2026
Published: 14.11.2026

Abstract: The majority of silicon (Si) in soil is immobilized into poorly soluble silicate minerals, despite the fact that Si reinforces plant tissues, promotes growth, and aids crops in enduring biotic and abiotic stress. Silicate-solubilizing microorganisms (SSMs) are capable of releasing Si along with related cations such as K, Ca, and Mg in forms that can be taken up by roots. This review consolidates existing insights on SSM diversity, techniques utilized for their isolation and characterization, and the mechanisms believed to facilitate mineral dissolution: acidolysis via organic acids, ligand-promoted chelation, siderophore functions, cation exchange, enzymatic processes, and the role of exopolysaccharides and biofilms. We subsequently investigate the impact of SSMs on the supply of nutrients in the rhizosphere (P, K, Fe, and others), the balance of plant hormones, root growth, antioxidant protection, and resilience to pathogens, drought, metal, and salinity stress. Throughout, we assess the strength of the evidence and not only its direction. Three evidence gaps stand out: screening is dominated by plate halos that rarely quantify soluble Si; mechanisms are mostly inferred from correlations; and fungi, especially endophytic fungi, are far less studied than bacteria. Currently, the control of silicate dissolution through quorum sensing is a hypothesis rather than an established mechanism. We conclude with a prioritized research agenda that includes standardized assays, genetic and omics validation, endophytic and halotolerant strains, consortia, formulation, and multi-season field evaluations.

Keywords: Silicate-Solubilizing Microorganisms, Silicon Mobilization, Mineral Weathering, Endophytes, Rhizosphere Microbiology, Biofertilizers, Nutrient-Use Efficiency.

1. INTRODUCTION

Agricultural escalation over the preceding century has elevated food output significantly, but it has done so at an environmental cost. Long-term dependence on synthetic fertilizers and pesticides degrades soil, pollutes water and declines biodiversity, so production systems now need to stay productive while lowering their footprint. Plant-associated microbes are one of the most widely explored routes to this goal. The term plant growth-promoting rhizobacteria was introduced by Kloepper and Schroth (1978) for root-colonizing bacteria that improve plant performance, and later work has shown that such partnerships also help plants deal with biotic and abiotic stress.

Silicate minerals are a major reservoir of Si, K, Mg and Ca in soils. These elements enter the soil solution slowly, through weathering and dissolution. Silicon is not classed as an essential element for higher plants, but many studies link it to better growth, yield and disease resistance, and it is particularly important for high accumulators such as rice (Ma, 2004; Liang *et al.,* 2007). Silicon is generally regarded as a beneficial or quasi-essential element rather than universally essential for higher plants. Its benefits are especially evident in high-Si-accumulating species such as rice and may include improved structural support, reduced lodging and greater tolerance to selected biotic and abiotic stresses. The difficulty is that crustal Si occurs mainly in insoluble forms, which are released only through rock weathering or microbial activity (Sheng *et al.,*2008). Plants take up Si as monosilicic acid (H_4SiO_4), so the conversion of mineral Si into this form is the

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step that limits supply. Commercial Si fertilizers can supply it directly, but their cost restricts use, which has increased interest in microbial alternatives.

Silicate-solubilizing bacteria are a recognized subset of plant growth-promoting bacteria, found in soil, water, marine sediment and on mineral surfaces, although efficient strains appear to be uncommon (Naureen *et al.,* 2015; Vasanthi *et al.,* 2018). Genera such as *Bacillus*, *Pseudomonas* and *Enterobacter* are the most frequently reported.

Silicate-solubilizing microorganisms (SSMs) have attracted interest as potential biological agents for mobilizing mineral-bound Si. The field is closely related to the broader study of microbially mediated mineral weathering, in which bacteria and fungi alter mineral dissolution through chemical and physical interactions (Deshmukh *et al.,* 2017; Uroz *et al.,* 2009). Previous overviews have concentrated on bacteria and on isolation and screening. This review differs in three ways. First, it covers microorganisms generally and highlights the under-representation of fungi and endophytes. Second, it weighs the quality of the evidence for each proposed mechanism and plant benefit. Third, it ends with a structured list of knowledge gaps and the experiments that would close them.

2. Silicon Pools, Soil Chemistry and Plant Acquisition

Silicon (Si) refers to the element; silicate minerals are minerals containing Si-O frameworks and associated cations; silica commonly refers to silicon dioxide (SiO_2); and dissolved plant-available Si is predominantly monosilicic acid (H_4SiO_4) at typical agricultural soil pH. These terms are not interchangeable. Microbial dissolution of a silicate mineral may release Si and other constituent elements, whereas dissolution of relatively pure quartz or amorphous silica has different kinetics and should not be treated as equivalent. Plant-available silicon depends on soil monosilicic acid (H_4SiO_4) dynamics, influenced by soil, climate and cropping systems, while the lack of standardized extraction methods and crop-specific critical limits restricts reliable fertilizer recommendations (Tubana, 2023). Soil silicon exists in multiple fractions, with amorphous Si representing the largest pool, while organic Si showed a significant positive correlation with plant-available Si. Rice Si uptake was influenced by occluded, mobile, amorphous and adsorbed Si pools, highlighting the importance of considering overall soil Si dynamics rather than plant-available Si alone (Pallavi & Prakash, 2019).

Dissolved Si reflects the balance between mineral dissolution and removal from solution. Mineral composition, crystallinity, particle size, pH, redox conditions, ionic strength, water availability, temperature and reactive Fe- and Al-oxide surfaces influence this balance. Organic matter and root exudates can modify mineral-surface reactions and microbial activity. Consequently, the same inoculant may show different effects in soils with contrasting mineralogy or pH. Increased total dissolved Si does not always translate into greater plant uptake if Si is re-adsorbed, polymerized, leached or unavailable during the crop's period of demand (Raturi *et al.,* 2021; Sharma *et al.,* 2023).

Plant Si acquisition is species- and genotype-dependent. Root uptake systems, transpiration, root architecture and tissue deposition influence the amount and distribution of Si in the plant. Studies evaluating SSMs should quantify both soil-solution Si and plant-tissue Si, and report crop species, growth stage, sampling procedure and analytical method. Total soil Si alone is an inadequate indicator of biological availability.

3. Diversity of Silicate-Solubilizing Microorganisms

Reported SSMs come mostly from the rhizosphere, weathered rock and mineral surfaces, and unusual niches such as earthworm guts and bryophyte surfaces (Table 1). Bacterial isolates dominate the literature. Fungal records are few and are concentrated in *Trichoderma* and *Aspergillus*, and the sources reviewed here did not yield well-documented examples from archaea. Endophytic SSMs, which live inside plant tissue and are therefore protected from competition in bulk soil, are almost unrepresented. These reports indicate functional diversity rather than a single taxonomic group specialized for Si mobilization. Mineral-weathering organisms have been recovered from rhizosphere soils, weathered rocks, agricultural soils and other mineral-associated habitats. Their ecological activity is likely shaped by carbon supply, mineral-surface attachment, competition and interactions with plant roots and other microorganisms (Uroz *et al.,* 2009; Raturi *et al.,* 2021).

Table 1: Examples of reported silicate-solubilizing microorganisms

Organism(s)	Source	Reference
Bacillus globisporus Q12	Weathered feldspar	Sheng *et al.,* 2008
Rhizobium tropici	Weathered rock	Wang *et al.,* 2015
Burkholderia eburnea CS4-2	Rice rhizosphere	Kang *et al.,* 2017
Bacillus sp.	Clay	Maleva *et al.,*2017
Aeromonas, *Bacillus*, *Cellvibrio*, *Ensifer*, *Flavobacterium*, *Microbacterium*, *Paracoccus*, *Pseudomonas*, *Rhizobium*, *Streptomyces*	Earthworm gut and surrounding soil	Hu *et al.,* 2018
B. flexus, *B. mucilaginosus*, *B. megaterium*, *P. fluorescens*	Soil	Vasanthi *et al.,* 2018
Rhizobium sp. IIRR-1	Rice rhizosphere	Chandrakala *et al.,* 2019

Organism(s)	Source	Reference
Kosakonia sp.	Rhizoids of the bryophyte *Hypnum plumaeforme* L.	Hu *et al.,* 2019
B. mucilaginosus	Rice rhizosphere	Vijayapriya *et al.,* 2019
Enterobacter ludwigii GAK2	Paddy soil	Lee *et al.,* 2019; Adhikari *et al.,* 2020[a]
Pseudomonas koreensis MU2	Rhizosphere	Adhikari *et al.,* 2020[b]
Pseudomonas sp., *B. amyloliquefaciens*, *Sphingobacterium* sp.	Rhizosphere soils	Bist *et al.,* 2020
Enterobacter sp.	Rubber field soil	Shabbir *et al.,* 2020[b]
Aspergillus niger BCC194, A. niger K0909, A. niger A1601, Trichoderma polysporum, T. viride, T. pseudokoningii, and Trichoderma spp,	Not reported	Santi, *et al.,* 2021
Pseudomonas, *Aeromonas*, *Bacillus* and *Enterobacter*	Rice rhizosphere	Cruz *et al.,* 2022
Bacillus sp., *Pseudomonas* spp., *Enterobacter* sp.	Pigweed	Das *et al.,* 2022
Bacillus paramycoides strain AR 2019-4	Groundnut rhizosphere	Ruban &Jeyaramraja, 2023
Bacillus amyloliquefaciens	Brinjal rhizosphere	Singh & Kumaresan, 2023
Bacillus tequilensis SKSSB09	Maize rhizosphere	Sukumar *et al.,*2023
Staphylococcus ureilyticus MV-1	Grape wine rhizosphere	Mahale, 2024
Penicillium limosum, Bipolaris sorokiniana	Soil	Mor *et al.,* 2024
Enterobacter sp., Serratia surfactantfaciens, and Klebsiella sp.	Maize rhizosphere	Maharjan *et al.,* 2025
Bacillus megaterium SKSSB18, B. subtilis SKSSB22, Enterobacter hormachei SSB04, B. paramycoides SSB029, B. velezensis SSB036, B. vallismortis SK070	Maize rhizosphere	Sukumar *et al.,* 2025
Etopseudomonas mendocina.	Rice field soil	Devi *et al.,* 2026
Pantoea ananatis ASEna, Pantoea dispersa E345Se, and Pseudomonas migulae DSb	Sugarcane	Kamyab & Motamedi, 2026.

Burkholderia eburnea CS4-2 was reported to solubilize silicate, produce indole-3-acetic acid (IAA), and increase Si deposition and growth attributes in rice when used with an insoluble Si source (Kang *et al.,*2017). *Enterobacter ludwigii* GAK2 was reported to solubilize both silicate and phosphate and to improve rice growth; a subsequent study examined its effects under cadmium stress (Lee *et al.,*2019; Adhikari *et al.,*2020[a]). These are proof-of-concept examples, but results should not be generalized to all strains within the respective genera.

Biosafety is a separate criterion from taxonomic identity and functional performance. Some taxa reported as plant-beneficial also contain opportunistic or plant/animal pathogenic members. Identification to genus or species level is insufficient to establish suitability for agricultural release. Candidate strains require strain-level genome analysis, screening for virulence and antimicrobial-resistance determinants, pathogenicity assessment, environmental persistence studies and compliance with applicable biosafety requirements.

4. Isolation, Screening and Characterization

4.1 Isolation

Si fertilization improves productivity and suppresses some fungal diseases, but production and application costs limit its use. Biological alternatives rely on organisms that occur naturally in cultivated soil, soil amendments and rock surfaces, but their distribution is patchy, so enrichment is normally needed. A typical workflow runs from sample collection (rhizosphere, rhizoplane, endosphere, irrigation water, mineral ores) through serial dilution and enrichment to purification, functional screening and taxonomic identification. Media are usually amended with an insoluble silicate such as magnesium trisilicate, and formulations in use include silica agar, modified Bunt and Rovira medium and Aleksandrov-type medium (Naureen *et al.,*2015; Bist *et al.,*2020; Ruban & Jeyaramraja, 2023).

4.2 Plate Screening and Its Limits

A clear zone around a colony is the usual first indicator, expressed as the solubilization index (halo diameter divided by colony diameter). Plate assays have two well-known weaknesses. A halo caused by silicate dissolution can look like one caused by phosphate solubilization, and the halo also reflects pH change and diffusion rate, not the amount of Si released. Adding a pH indicator such as bromocresol purple helps separate acid production from other effects (Maharjan *et al.,* 2025, Sukumar *et al.,* 2023). Realistic substrates, including aluminosilicates, rice husk and diatomaceous earth, are

also used to judge how an isolate behaves on materials closer to field conditions (Cai, *et al.,* 2013; Santi, 2020; Santi & Goenadi, 2017).

4.3 Characterization

Strains are described by colony and cell morphology, Gram reaction and spore formation (Collins *et al.,*1995), and by biochemical traits such as catalase, urease, nitrate reduction, citrate use and carbohydrate fermentation. Growth across temperature and pH ranges is tested as well, and some strains are reported to grow from about 4°C to 45°C (Santi and Goenadi, 2017; Sulizah *et al.,*2018; Vasanthi *et al.,* 2018). Identification is by 16S rRNA gene sequencing for bacteria and ITS for fungi. Plant growth-promoting traits are then quantified, for example IAA by GC–MS (Kang *et al.,* 2017; Vasanthi *et al.,* 2018), organic acids by GC–MS or HPLC (Lee *et al.,* 2019), and soluble silica and acids in culture by ICP-AES and HPLC (Santi & Goenadi, 2017).

Functional characterization should include growth under relevant pH, temperature and salinity conditions; organic-acid and siderophore profiles; EPS production; mineral-surface attachment; and persistence in target soil. Plant assays should progress from controlled growth systems to non-sterile soil pots, greenhouse trials and replicated multi-location field experiments. Each stage should use pre-defined primary outcomes and transparent statistical analysis.

4.4 Critical Appraisal

Most papers stop at a halo and an isolate name. Three improvements would raise the value of future work: direct quantification of soluble Si in broth (molybdenum blue or ICP) with time-course sampling; abiotic controls in which sterile medium is acidified to the same pH with the same acids, so that microbial-specific effects can be separated from simple acidity; and verification on the mineral surface by SEM-EDX, XRD or FTIR.

5. Mechanisms of Silicate Solubilization

Biological weathering of silicates is the combined result of several processes acting at the mineral-cell interface (Table 2). Organic acid production is the best supported mechanism. Santi (2020) reported acetic, citric and oxalic acids from *Trichoderma polysporum* and *Aspergillus niger* in association with silicate dissolution, and Hu *et al.,* (2021) found that *Paenibacillus mucilaginosus* accelerated biotite weathering, with GC-MS of the culture filtrate showing acids such as propanoic, acetic, butanoic and glycolic. Fumaric, succinic, maleic, gluconic and tartaric acids have also been reported (Bist *et al.,* 2020; Sukumar *et al.,* 2023), and 2-keto-gluconic acid, polysaccharides and enzymes are listed among the agents involved (Naureen *et al.,* 2015).

The proposed sequence is: acids lower the local pH and supply protons; their anions chelate Al, Fe, Ca and Mg in the lattice, destabilizing it; cations are exchanged at the surface; and Si is released as silicic acid. Some bacteria also produce carbonic anhydrase, which could raise bicarbonate availability and promote dissolution (Liu *et al.,* 2006). Extracellular polysaccharides and cell-wall components can adhere to mineral surfaces and concentrate acids and chelators at the point of attack. Siderophores can mobilize Fe held in silicate minerals and disrupt thin Fe-oxide layers, which exposes the underlying mineral (Berghe *et al.,* 2021; Dong *et al.,* 2022).

5.1 Proton-Promoted Dissolution and Organic Acids

Microbial respiration and metabolism can release protons or acidic metabolites, lowering pH near a mineral surface. Organic acids such as gluconic, citric and oxalic acids may contribute through proton-promoted dissolution and metal complexation. The effect depends on acid identity, concentration, dissociation constants, mineral composition and buffering capacity. A fall in bulk-medium pH is suggestive but does not prove silicate dissolution. Quantification of dissolved Si and relevant cations is required.

5.2 Ligand-Promoted Dissolution and Siderophores

Organic ligands and siderophores bind mineral-associated cations, particularly Fe and Al, and can destabilize mineral surfaces or remove secondary coatings. This pathway can operate alongside acidification. Siderophore production should not automatically be interpreted as direct Si solubilization: effects may arise indirectly through removal of Fe-bearing phases or alteration of surface chemistry. Ligand-deficient mutants or suitable chemical controls would strengthen causal interpretation.

5.3 EPS, Biofilms and Mineral-Surface Attachment

Extracellular polymeric substances (EPS) and biofilms can promote attachment to mineral particles and create microsites in which pH, ligand concentration and redox conditions differ from the bulk solution. EPS may bind cations, retain metabolites and influence dissolution or secondary mineral formation. However, EPS detection is not proof of enhanced Si release. Studies should compare attached and planktonic cells, characterize EPS composition and quantify dissolved Si (Breitenbach *et al.,* 2022; Dubey *et al.,* 2025).

5.4 Redox, Physical Effects and Enzyme-Associated Processes

Microbial redox activity can alter the solubility of redox-sensitive elements associated with minerals and influence weathering indirectly. Fungal hyphae may improve contact with mineral surfaces and generate localized chemical gradients. Carbonic anhydrase and other enzymes have been discussed in mineral transformation, but a direct, generalizable enzymatic pathway for silicate dissolution is not established across SSM taxa. Claims that a specific enzyme directly converts insoluble silicate to plant-available Si require purified-enzyme or genetic evidence and abiotic controls (Deshmukh *et al.,* 2017).

Table 2: Proposed mechanisms of microbial silicate dissolution

Mechanism	Description	Strength of evidence	Reference
Acidolysis	Organic acids lower pH and release protons	Strong	Bist *et al.,* 2020; Sukumar *et al.,* 2023
Chelation / ligand exchange	Acid anions and siderophores bind Al, Fe, Ca, Mg and weaken the lattice	Moderate	Etesami & Glick, 2023; Berghe *et al.,* 2021
Enzymatic (carbonic anhydrase)	Hydration of CO_2 gives bicarbonate that attacks the mineral	Limited	Liu *et al.,* 2006
EPS and cell-surface contact	Polysaccharides adhere to the mineral and concentrate reactants	Limited; mostly inferred	Breitenbach *et al.,* 2022; Dubey *et al.,* 2025
Environmental modulation	pH, temperature, salinity and nutrients alter all of the above	Moderate	Deshmukh *et al.,* 2017; Hu *et al.,* 2021; Sukumar *et al.,* 2023

A critical reading of this literature shows that the evidence is largely correlational. Acid production and Si release rise together, but few studies use purified acids, cell-free filtrates or deletion mutants to show that a specific compound is responsible. Enzymatic and EPS contributions are mostly proposed from general weathering literature and have not been separated experimentally in SSMs. Fungal systems, in which oxalic and citric acid secretion is well known in other mineral-weathering contexts, offer an obvious test bed.

6. Environmental Factors Affecting Solubilization

SSM activity is controlled by interacting variables rather than a universal optimum. Soil pH affects microbial growth, acid dissociation, mineral surface charge and Si speciation. Temperature and moisture influence metabolism and diffusion. Carbon availability can stimulate organic-acid production, but excessive readily metabolizable carbon may also cause rapid acidification, oxygen depletion or competition with indigenous organisms. Nitrogen and phosphorus regulate biomass production and metabolic allocation. Oxygen status matters where respiration or redox transformations contribute to mineral weathering.

Salinity deserves particular attention in irrigated and salt-affected agroecosystems. Halotolerant isolates may remain metabolically active under elevated ionic strength, but salt tolerance alone does not demonstrate silicate-solubilizing efficacy in saline soil. Na^+, Ca^{2+} and other ions can alter mineral equilibria and Si adsorption. Salt-tolerant candidates should therefore be tested across realistic salinity gradients using the target soil and crop, rather than selected solely on growth in NaCl-amended broth.

A major limitation is the frequent use of single-factor laboratory assays to infer field performance. A more informative approach combines factorial experiments testing pH, moisture, mineral substrate, carbon supply and salinity, followed by validation in non-sterile soils. Soil texture, mineralogy, baseline plant-available Si and buffering capacity should be reported as core experimental descriptors.

Solubilization in the field is shaped by the microbe's physiology and the chemistry of the soil together (Table 3). Because the supporting studies in this area frequently measure growth or acid output and not Si release, the statements below should be read as expectations to be tested, not settled results.

Table 3: Environmental factors that may influence silicate solubilization

Factor	Expected influence	Reference
Soil pH	Acidic conditions favour acid-mediated dissolution; in alkaline soils, other mechanisms (chelation, EPS) may matter more	Bist *et al.,* 2020
Temperature	Moderate temperatures favour organic acid and enzyme production; extremes inhibit activity	Hu *et al.,* 2021
Moisture	Adequate moisture supports growth and secretion; waterlogging or drought restricts activity	Naureen *et al.,* 2015

Factor	Expected influence	Reference
Carbon, N and P supply	Carbon sources drive acid production; N and P support biomass and enzymes	Sukumar *et al.,* 2023
Oxygen	Aerobic acid production is best documented; anaerobic solubilization by fermentation is plausible but poorly evidenced	Sukumar *et al.,* 2023

Salinity should be added as an important variable, because salt-tolerant SSMs could be especially useful in salt-affected soils

7. SSM-Mediated Nutrient Acquisition and Plant Performance

The most direct proposed benefit of SSM inoculation is increased release of dissolved Si from a defined silicate substrate. If roots acquire this Si, downstream effects may include improved tissue silicification, structural strength and stress tolerance. The response depends on crop genotype and Si-uptake capacity. The effect of Si on phosphorus availability is context-dependent: dissolved silicate may compete with phosphate for sorption sites on Fe- and Al-oxide surfaces in some soils, but the direction and magnitude depend on soil chemistry. It is inappropriate to claim that SSMs universally increase P availability.

Mineral weathering can release K, Ca, Mg and Fe from particular substrates. However, release from a mineral does not necessarily mean sustained plant availability. Ions may be re-adsorbed, precipitated, leached or immobilized by microorganisms. The contribution of SSMs to K nutrition should be assessed using a defined K-bearing mineral, exchangeable and solution K measurements, plant K uptake and mineral-only controls.

SSMs may possess traits independent of Si mobilization, including IAA production, ACC deaminase activity, siderophore production, phosphate solubilization and pathogen antagonism. These traits can influence root architecture, nutrient acquisition and stress responses. They should be measured as co-occurring plant-growth-promoting traits, not automatically attributed to silicate dissolution. GAK2 illustrates this issue because it was reported to solubilize both Si and P and to produce phytohormone-related metabolites (Adhikari *et al.,* 2020[b]; Lee *et al.,* 2019). SSMs usually carry more than one plant-beneficial trait, so their effect on nutrition is rarely due to Si release alone.

Siderophores

Siderophores are high-affinity iron chelators. Besides improving Fe supply in Fe-poor soils, they take part in ligand exchange with Al^{3+}, Ca^{2+} and Fe^{3+} in silicate minerals (Ahmed and Holmström, 2014). Production is tested on chrome azurol S agar, where an orange or yellow halo indicates activity (Schwyn and Neilands, 1987; Shabbir *et al.,* 2020[a]).

Auxin (IAA)

IAA from SSMs promotes root elongation, lateral roots and root hairs, increasing the volume of soil explored. It may also affect expression of nutrient transporters (Spaepen *et al.,* 2007; Chopra *et al.,* 2021). Enterobacter strains producing IAA have been reported to improve maize root length, height and biomass [ref. needed].

ACC Deaminase

Bacteria with this enzyme break down ACC, the precursor of ethylene, into ammonia and α-ketobutyrate, which relieves ethylene-induced inhibition of root growth under stress (Glick, 2014; Chandrakala *et al.,* 2019). Healthier roots in turn improve nutrient uptake and microbial colonization.

Phosphorus

Organic acids (citric, oxalic, gluconic) and phosphatases from SSMs release phosphate from mineral and organic sources (Richardson *et al.,* 2009; Sharma *et al.,* 2013; Vassilev *et al.,* 2006).

Potassium

Potassium is abundant in soil but largely mineral-bound, and acid secretion by SSMs can release it (Sharma *et al.,* 2013; Maathuis, 2009). Si and P also interact: silicate can displace adsorbed phosphate and increase P availability in low-P soils (Patra & Neue, 2010).

Many papers describe SSMs as "silicate-solubilizing" while actually measuring K or P release. Because phosphate and potassium solubilizers dissolve the same minerals by the same acids, an isolate should only be called a silicate solubilizer if soluble Si is measured directly.

8. Silicon, SSMs, and Plant Stress Tolerance

8.1 Biotic Stress

Silicon-deficient plants are more prone to insect attack, fungal disease and bacterial invasion. Silica deposition makes tissue harder to digest and can wear insect mouthparts (Massey and Hartley, 2009). Si-related protection has been reported against blast, sheath blight and brown spot in rice, and against powdery mildew in wheat, barley and cucumber.

Beyond a physical barrier, Si primes defence: higher activities of peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase and chitinase were seen in cucumber infected with *Pythium* (Yang *et al.,* 2003) and in wheat infected with *Blumeria graminis* (Cai *et al.,* 2008). Fawe *et al.,* (2001) linked Si-enhanced powdery mildew resistance in cucumber to accumulation of flavonoid phytoalexins, including rhamnetin. Silicon also precipitates metals, regulates defensive and metabolic genes, and activates plants' antioxidant systems (Tubana, *et al.,* 2026).

Some SSMs add direct antagonism. *Serratia marcescens* and *Pseudomonas aeruginosa* from rice fields promoted growth and reduced sheath blight caused by *Rhizoctonia solani* (Ng *et al.,* 2016); *Enterobacter* sp. reduced rubber root rot (Shabbir *et al.,* 2020[a]); *B. tequilensis* inhibited *Fusarium oxysporum* in vitro (Sukumar *et al.,* 2023); and engineered *B. mucilaginosus* was reported to limit grey mould in tobacco (Vijayapriya *et al.,* 2019).

It remains unclear how much of the protection is due to Si itself, how much to microbial antagonism, and how much to induced resistance, because most studies do not include treatments that separate these factors. In addition, *S. marcescens* and *P. aeruginosa* can be opportunistic pathogens, so biosafety screening should precede any field release.

8.2 Abiotic Stress

Si supply improves plant water status under drought and raises the activity of superoxide dismutase, catalase and glutathione reductase, while lowering hydrogen peroxide and sustaining pigments, soluble protein and CO_2 assimilation (Gong *et al.,* 2005). SSM inoculation has been reported to improve water-use efficiency in maize under moderate drought, with a smaller benefit under severe drought, possibly because dry substrate limits inoculant function. Bacteria from wild *Chenopodium* growing in rock crevices in Ladakh solubilized phosphate, potassium and zinc, produced siderophores and tolerated variable temperature and salinity (Das *et al.,* 2022). Under cadmium stress, *E. ludwigii* GAK2 lowered cadmium content and improved rice growth (Adhikari *et al.,* 2020[a]). In soybean under salt stress, *P. koreensis* MU2 raised gibberellin and organic acid levels, strengthened antioxidant defense and improved root and shoot growth and chlorophyll (Adhikari *et al.,* 2020[b]). High silica solubilizers *Pantoea ananatis* ASEna, *Pantoea dispersa* E345Se, and *Pseudomonas migulae* DSb, isolates from sugarcane exhibited tolerance to heat, salinity, drought, and pH stresses in sugarcane (Kamyab & Motamedi, 2026).

The abiotic stress literature rests on a handful of strains and crops (rice, soybean, maize). Antioxidant and osmolyte responses are usually reported as outcomes, without testing whether Si uptake mediates them. Heavy metal effects are also ambiguous: dissolution of silicates could release metals bound in minerals, but Si and microbial activity can also immobilize metals in the rhizosphere and reduce plant uptake. The direction depends on the metal, mineral and soil, and should be stated for each case.

9. Crop Responses and Agricultural Application

9.1 Evidence from Crops

SSM-based inoculants have increased growth, nutrient content and yield in cereals, legumes and vegetables in several studies (Das & Kim, 2024). Rice inoculated with *E. ludwigii* showed higher Si and P content than controls (Lee *et al.,* 2019), and *B. eburnea* CS4-2 solubilized silicate and may improve Si uptake in rice (Kang *et al.,* 2017). Si and P supplementation increased rice grain production in work by Patra and Neue (2010). *B. mucilaginosus* released K^+ and SiO_2 from mica, produced organic acids and polysaccharides, and promoted tobacco growth in greenhouse and field trials (Liu *et al.,* 2006). Deng *et al.* (2021) linked silica supply with better nutrient use in sugarcane.

9.2 Halotolerant Strains

Salt-affected soils are a priority target, because salinity restricts both microbial activity and plant growth. Strains able to tolerate high salt and still release Si, such as *P. koreensis* MU2 (Adhikari *et al.,* 2020[b]) and the stress-adapted isolates of Das *et al.* (2022) are promising starting material. However, most halotolerance data are from tolerance assays in vitro. Few studies combine salt tolerance, quantified Si release and plant benefit in a single saline soil.

9.3 Practical Constraints

Adoption is held back by formulation, shelf life, survival in non-sterile soil and variable field performance. Pot trials are common, whereas multi-season field trials in contrasting soils are rare. Reports usually do not include soluble-Si fertilizer or heat-killed inoculum controls, so the extra benefit of living SSMs over Si alone is seldom shown. Despite its established roles in plant defence and metabolic regulation, limited standardized soil testing and fertilizer calibration restrict the wider adoption of silicon fertilization also (Tubana *et al.,* 2026).

10. Quorum Sensing and SSMs: A Hypothesis Awaiting Evidence

The source draft devoted substantial space to quorum sensing (QS), including signal classes, agricultural applications and proposed genetic manipulation. QS is an established form of cell-density-dependent communication in many bacteria and can regulate biofilm formation, motility, secretion and other group behaviours. However, evidence that

QS directly regulates silicate dissolution in SSMs remains limited and should not be presented as an established mechanism without strain-specific experimental data.

Quorum sensing (QS) lets microbial populations coordinate behavior as density rises. Known signals include N-acyl-homoserine lactones (AHLs) in Gram-negative bacteria, autoinducing peptides in Gram-positive bacteria, autoinducer-2 across both groups, γ-butyrolactones in *Streptomyces*, and farnesol in *Candida albicans*, and QS regulates biofilm formation, virulence factors and secondary metabolite production. Because acid secretion, enzyme release and biofilm formation all contribute to weathering, it is reasonable to propose that QS influences silicate solubilization (Naureen *et al.,* 2015), and that plant root exudates could modulate this signaling (Chandrakala *et al.,* 2019).

However, in the sources reviewed we did not find studies showing that disrupting or supplementing a defined QS signal changes silicate dissolution in an SSM. The suggested applications, which include engineered signaling circuits, QS inhibitors, QS-matched consortia and manipulation of pH or nutrients to trigger QS (LaSarre & Federle, 2013), are therefore speculative. Challenges include the complexity of soil communities, the diversity and instability of signal molecules in soil, environmental stress interfering with signaling, and the difficulty of scaling laboratory observations. Studies using AHL-quenching enzymes, QS-deficient mutants and signal quantification in the rhizosphere would show whether this line of work is worth pursuing.

A credible QS–silicate-weathering study would identify the signal molecule, demonstrate its production under mineral-solubilizing conditions, detect the relevant synthase/receptor system, and show that disruption of the QS pathway changes Si release independently of effects on growth. Complementation or signal-addition experiments would strengthen causal inference. Transcriptomics or reporter assays could connect QS activation to acid production, ligand secretion, EPS formation or mineral attachment. Until such evidence is available, QS should be framed as a promising but unvalidated research direction.

11. Formulation, Field Translation and Biosafety

Translation from laboratory isolate to agricultural product requires more than high in-vitro solubilization. A viable formulation must retain cell number and functional activity during storage, transport and application. Carrier selection, moisture, pH, temperature tolerance, compatibility with fertilizers and pesticides, shelf life and application method all require optimization. Compatibility with the target mineral source and irrigation-water chemistry should also be assessed.

Field performance depends on indigenous microbial competition, soil texture and mineralogy, crop genotype, climate, management history and timing of inoculation. Trials should compare inoculant alone, mineral amendment alone and their combination, alongside standard fertilizer practice. Multi-season testing is needed to determine whether repeated inoculation is necessary and whether treatments change soil Si pools or other nutrient balances over time. Economic analysis should include production and application costs, yield response and stability across sites.

Biosafety and regulatory evaluation are essential. Strain-level identification, whole-genome screening for virulence and antimicrobial-resistance determinants, phenotypic safety testing, non-target effects and environmental persistence should precede field release. A genus name or prior use in another application is not adequate evidence of safety. Claims of reduced fertilizer requirement should be supported by nutrient-budget and fertilizer-substitution trials.

12. Critical Research Gaps

Table 4: Gaps, why they matter and how to address them

Gap	Why it matters	Suggested approach
No standard assay for solubilization	Halo indices and K/P release cannot be compared or tied to Si supply	Report soluble Si (molybdenum blue/ICP) over time, with abiotic acid and cell-free filtrate controls
Mechanisms inferred, not demonstrated	Cannot rationally improve strains	Organic acid profiling plus knockout mutants, transcriptomics or proteomics; SEM-EDX, XRD and FTIR on mineral surfaces
Incomplete nutrient/environmental accounting	Mobilized elements may be re-adsorbed, precipitated, leached or become toxic.	Use Si and co-released-metal mass balances; monitor leaching, plant accumulation and soil-health indicators.
Bacterial bias; few fungi and almost no endophytes	Fungi secrete large amounts of oxalic and citric acid, and endophytes may colonize more reliably	Screen fungal and endophytic collections; demonstrate endophytic colonization and re-isolation; compare with bacteria on the same mineral

Gap	Why it matters	Suggested approach
Plant benefit not separated from Si effect	Unclear whether microbes add value over Si fertilizer	Factorial designs: control, mineral alone, microbe alone, microbe + mineral, soluble Si, heat-killed microbe; measure plant Si
Insufficient soil-to-plant linkage	In-vitro Si release is often treated as evidence of improved plant Si nutrition.	Measure soil-solution H_4SiO_4, tissue Si, biomass and yield in the same experiment.
Crop/genotype dependence	Plant Si uptake differs substantially among species and genotypes.	Compare contrasting Si accumulators and cultivars; quantify uptake kinetics and tissue distribution.
Narrow range of crops and stresses	Results may not transfer	Test dicots and monocots; combined stresses; salt and drought in realistic soils
Limited field validation	Pot data overestimate performance Pot results may not persist in non-sterile soils or across environments.	Multi-location, multi-season trials with soil microbiome monitoring
Formulation and shelf life	Limits commercialization	Carriers, spore-based and consortium formulations; storage and survival data
Biosafety and regulation	Some reported strains are opportunistic pathogens or strains carrying undesirable genes.	Pathogenicity screening- whole-genome safety screening, phenotypic assays, risk assessment and regulatory-grade identification
Quorum sensing role unproven	Applications are speculative	Mutants, quenching enzymes and signal measurement and QS genes identification in SSMs
Contradictory metal effects	Remediation claims are uncertain	Metal-specific studies with speciation and plant uptake data

13. Proposed Experimental Framework

A practical research programme can be organized into five stages (Figure 1).

- First, select candidate isolates using a mineral-specific quantitative assay rather than halo formation alone.
- Second, characterize the mineral substrate and identify metabolites and cellular traits associated with Si release.
- Third, test causality using pH-matched abiotic controls, cell-free supernatants, washed-cell suspensions and, where feasible, genetic perturbation.
- Fourth, establish plant relevance using a factorial design that separates inoculum, mineral amendment and soluble-Si effects.
- Fifth, validate the best candidates in non-sterile soils and multi-location field trials while monitoring persistence, yield, nutrient uptake, economics and biosafety.

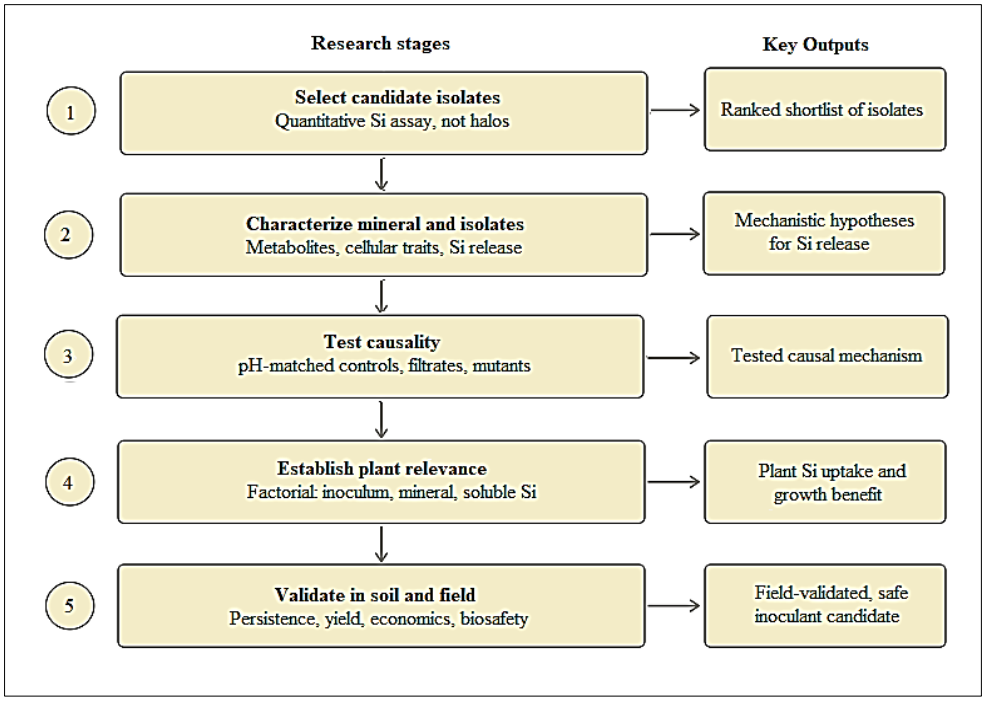


Figure 1: Research programme for developing SSM inoculants

A minimum greenhouse design may include: T1, uninoculated control; T2, silicate source alone; T3, SSM inoculum alone; T4, SSM plus silicate source; and T5, soluble-Si reference where appropriate. If the candidate also solubilizes phosphate or produces growth regulators, additional treatments or mechanistic controls are needed to distinguish those contributions. Primary endpoints should be defined before experimentation and should include dissolved Si in soil solution, plant-tissue Si, biomass and a crop-relevant yield component.

14. Future Research Directions

Several lines of work follow from these gaps.

1. **Standardize Methods-** A consensus protocol for quantifying soluble Si, including controls for pH and for abiotic acid, would make strains comparable across laboratories.
2. **Explore New Sources-** Pristine soils, extreme habitats and plant endosphere communities could hold strains with distinctive capabilities (Uroz *et al.,* 2009).
3. **Resolve Mechanisms.** Combining chemistry (acids, chelators), genetics and omics would show which pathways matter and could guide targeted improvement (Sheng and He, 2006; Vandevivere *et al.,* 1994).
4. **Link Environment to Function-** Systematic study of pH, temperature, moisture, nutrients and salinity effects on abundance, diversity and activity should lead to condition-specific inoculants (Uroz *et al.,* 2009).
5. **Test across Crops and Systems-** Plant-specific responses in growth, nutrient uptake, yield and stress resilience should be tested, ideally with Si content as a measured variable (Malboobi *et al.,* 2009).
6. **Scale to The Field-** Long-term trials should assess productivity, soil health and effects on resident microbial communities in different agro-ecosystems.
7. **Test Consortia-** Mixtures of SSMs with P-, N- and K-mobilizing or biocontrol microbes may be more robust than single isolates, but need compatibility testing.
8. **Evaluate Quorum Sensing Rigorously-** Pursue QS only where mutant or signal-quenching data show a role in solubilization (Miller & Bassler, 2001).
9. **Integrate with Sustainable Practice-** Combining SSMs with conservation agriculture, organic amendments and precision application may increase benefit (Lal, 2004; Tilman *et al.,* 2002).

15. CONCLUSIONS

Silicate-solubilizing microorganisms offer a plausible, low-input way to increase Si and cation supply to crops and to improve stress tolerance. The strongest evidence concerns organic-acid-based dissolution and growth benefits in a few model crops. The weakest concerns the true Si contribution of the microbes, the roles of enzymes, EPS and quorum sensing, performance of fungi and endophytes, and reliability in the field. Progress will depend on standardized quantification of Si release, mechanistic validation, properly controlled plant experiments, and field trials with biosafety assessment. Meeting these requirements would move the field from isolate screening toward dependable, mineral-specific and crop-specific bio-inputs.

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