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Silicon in Agriculture

Availability, Uptake and Functionality Inside and Outside the Plant

Why total silicon in a soil or fertiliser is not the same as plant-available silicon, how crops take it up, and the evidence linking silicon supply to better performance under stress.

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1. Why Silicon Matters in Crop Production

Silicon (Si) occupies an unusual position in plant nutrition. It is not generally classified as an essential element for higher plants because its absence does not necessarily prevent completion of the plant life cycle; nevertheless, a substantial body of experimental evidence associates Si supply with improved plant performance, particularly under abiotic and biotic stress. The magnitude of these responses is highly context-dependent and varies with crop species and genotype, soil properties, Si source and formulation, application method, and the nature and intensity of the prevailing stress (Mandlik *et al*., 2020; Boutafda *et al*., 2026).

The abundance of Si in soil should not be confused with its availability to plants. Although Si is a major constituent of the Earth's crust and occurs extensively in silicate minerals and silica phases, plant acquisition depends principally on the much smaller dissolved Si pool. Under the moderately acidic-to-neutral conditions characteristic of many agricultural soils, this dissolved pool is dominated by orthosilicic acid [H_4SiO_4; $Si(OH)_4$], the principal form available for root uptake. Its concentration is dynamically controlled by mineral weathering and dissolution, adsorption–desorption reactions, polymerisation, soil pH, Fe and Al oxides, organic matter and biological processes. Consequently, a soil—or an applied Si material—may contain a high concentration of total Si without necessarily supplying a correspondingly high concentration of immediately plant-available Si (Haynes, 2014; Farooq and Dietz, 2015; Boutafda *et al*., 2026).

This distinction becomes particularly important when Si is applied agronomically. An applied Si source does not simply move quantitatively from fertilizer into the crop. Experimental evidence demonstrates that substantial quantities can remain associated with the soil. In a five-year field experiment on a highly weathered Gibbsihumox in Hawaii, for example, Khalid, Silva and Fox found that cumulative crop uptake accounted for only 12–21% of the applied Si from calcium silicate, while 14–28% was recovered by repeated extraction of the

soil profile and an estimated 57–72% remained in the soil in forms not readily displaced by the phosphate-containing extractant. No movement of applied Si below 30 cm was detected under the conditions of that experiment (Khalid *et al*., 1978). These values are specific to that source, soil, cropping sequence and experimental system and should not be interpreted as a universal Si recovery ratio.

Importantly, Si that has not been incorporated into plant tissue cannot automatically be regarded as agronomically inactive. Literature describes an ex planta component of Si functionality in which Si amendments can modify the soil and rhizosphere environment. Reported mechanisms include interactions between dissolved Si and soil mineral surfaces that can influence phosphorus availability, immobilization or reduced availability of potentially toxic elements such as Al, modification of soil acidity and ion-exchange processes, and changes in biological and microbial activity within the rhizosphere. However, these responses are strongly dependent on soil conditions and Si formulation, and causal relationships between Si-induced changes in the microbiome and subsequent improvements in plant performance remain incompletely established (Farooq and Dietz, 2015; Boutafda *et al*., 2026).

A second and mechanistically distinct pathway begins when dissolved Si reaches the root and enters the plant. In well-characterized Si-accumulating species, particularly rice, silicic acid can cross root-cell plasma membranes through specific transport systems. Lsi1 functions as an influx channel facilitating silicic-acid movement into root cells, while the complementary localization and function of the efflux transporter Lsi2 permits Si to leave these cells toward the stele. Si is subsequently transported toward the shoot in the xylem, while Lsi6 participates in xylem unloading and redistribution in aerial tissues. Thus, Si uptake should not be conceptualized simply as extracellular movement accompanying water: silicic acid can cross the plasma membrane, enter the symplast and subsequently be exported from living root cells (Ma *et al*., 2006; Ma and Yamaji, 2008; Zexer *et al*., 2023).

Where Si ultimately resides is equally important. Following transport to aerial tissues, soluble silicic acid can become concentrated and polymerised into hydrated amorphous silica associated predominantly with cell walls and other apoplastic structures. Earlier interpretations attributed silicification largely to passive concentration of silicic acid as water was lost through transpiration. More recent evidence indicates a more controlled process in

which cell-wall polymers and proteins can provide scaffolds for silica nucleation and polymerisation, thereby influencing both the location and extent of mineral deposition (Mandlik *et al*., 2020; Zexer *et al*., 2023). This distinction is fundamental: Si may pass through living cells during transport without its final functional location necessarily being intracellular.

Once associated with plant tissues, Si functionality is likewise unlikely to be explained by a single mechanism. Silicification can contribute to structural and physical properties of tissues, whereas Si treatment has also been associated with changes in physiological and biochemical responses to stress (Mandlik *et al*., 2020). Of particular interest is redox homeostasis. The recent integrated review by Boutafda *et al*. (2026) identifies regulation of water, ionic and redox homeostasis among the physiological responses associated with Si uptake and transport. At the same time, the authors emphasize an important unresolved question: observed redox responses cannot always be attributed to a direct biochemical action of Si because they may arise indirectly when Si modifies nutrition, rhizosphere conditions, soil chemistry or the severity of the original stress. This distinction between direct Si-mediated regulation and secondary consequences of stress alleviation is particularly important when interpreting antioxidant and redox responses.

Accordingly, understanding Si in agriculture requires moving beyond the simplified question of whether Si is “taken up” by the crop. The more relevant framework is to consider Si as operating across a soil–rhizosphere–plant continuum, with potentially functional pools both outside and inside the plant. The applied material must first generate or contribute to an available Si pool; part of this Si may interact with the soil and rhizosphere, part may be acquired by roots, and absorbed Si may subsequently cross cell membranes, enter the vascular transport system, redistribute among tissues and ultimately remain soluble or become incorporated into silica-rich structures. These processes occur simultaneously rather than as mutually exclusive mechanisms (Boutafda *et al*., 2026).

The objective of this paper is therefore to examine the availability, uptake and functionality of Si both outside and inside the plant, with particular emphasis on the mechanistic transitions between these compartments. The analysis addresses four linked questions: what fraction of an applied Si source can become plant available; what functions may occur in the soil and rhizosphere without Si entering the plant; how available Si crosses root-cell

membranes and is transported, localized and deposited within plant tissues; and how these processes relate to structural, physiological and redox responses.

2. Silicon Availability and Functionality Outside the Plant

2.1. From Applied Si to Plant-Available Si

Although silicon is one of the most abundant elements in soils, the majority of soil Si is not immediately available for plant uptake. It occurs in a wide range of forms, including quartz, silicate and aluminosilicate minerals, clay minerals, amorphous silica and biogenic silica. Consequently, total soil Si concentration is a poor indicator of the amount of Si that a crop can acquire. For root uptake, the relevant pool is primarily dissolved monosilicic or orthosilicic acid, H_4SiO_4 [$Si(OH)_4$], which is considered the principal plant-available form of Si (Haynes, 2014; Farooq and Dietz, 2015; Laane, 2018; Puppe and Sommer, 2018; Boutafda *et al*., 2026).

The same distinction must be applied to Si fertilizers and amendments. The amount of total Si contained in a product should not be considered equivalent to the amount of immediately plant-available Si that it provides. Agricultural Si sources can differ substantially in their chemical form, solubility, dissolution rate and interaction with the soil environment. These sources include soluble silicates such as potassium and sodium silicate; calcium silicate and other silicate minerals; monosilicic or orthosilicic acid formulations, including stabilized silicic acid; amorphous and biogenic silica sources such as rice husks, rice-husk ash and diatomaceous earth; and colloidal or nano-silica formulations (Laane, 2018; Puppe and Sommer, 2018).

Diatomaceous earth is particularly useful for illustrating the distinction between total Si and plant-available Si. It consists of siliceous diatom frustules and represents a biogenic amorphous Si source. Although biogenic amorphous silica can be more reactive than many crystalline silicate minerals, this does not imply that all biogenic silica sources are readily plant available. In the experimental comparison of Duboc *et al*. (2019), the tested diatomaceous earth did not release substantial amounts of Si. Its agronomic value therefore depends on the actual dissolution behaviour of the specific material under soil conditions rather than on its classification as amorphous silica alone (Puppe and Sommer, 2018; Duboc *et al*., 2019).

The transformation from an applied solid Si source to plant-available Si can therefore be represented conceptually as:

Si-containing solid → dissolution → dissolved H_4SiO_4 → root-available Si

Once present in solution, however, Si does not necessarily remain as free monosilicic acid. Dissolved Si can adsorb onto soil mineral surfaces, particularly Fe- and Al-containing oxides and hydroxides, and can subsequently return to solution through desorption. Monosilicic acid can also undergo condensation, forming oligomeric and progressively more polymerized Si species. Continued condensation and aggregation can ultimately result in colloidal or solid amorphous silica. These processes continuously redistribute Si between forms with different degrees of immediate availability (Farooq and Dietz, 2015; Laane, 2018).

The plant-available Si pool should therefore be considered dynamic rather than fixed. Mineral dissolution and desorption can replenish dissolved H_4SiO_4, while adsorption, polymerisation, mineral formation and leaching can decrease or redistribute it. Soil pH, mineralogy, Fe and Al oxides, organic matter, water movement and biological activity all influence these processes and therefore affect the concentration and persistence of dissolved Si around the root (Haynes, 2014; Farooq and Dietz, 2015; Boutafda *et al*., 2026).

This distinction also prevents an important misconception regarding colloidal and nano-silica. A material having a particle size in the nanometre range should not automatically be described as plant available simply because the particles are very small. A 50-nm SiO_2 particle, for example, is chemically and physically different from an individual molecule of H_4SiO_4. The established root-uptake pathway involves molecular silicic acid rather than the transport of such particles through the conventional Si transporters. Nano- or colloidal silica may nevertheless contribute to Si nutrition if it releases dissolved silicic acid, while additional uptake mechanisms have been proposed particularly for foliar-applied nanoparticles. The extent and importance of direct particulate uptake remain less clearly established than the conventional uptake of dissolved monosilicic acid (Laane, 2018; Puppe and Sommer, 2018).

Thus, when comparing Si sources, the relevant question is not simply how much total Si is applied, but how much of that Si can enter and maintain the dissolved plant-available pool

over time. A highly soluble source may provide Si rapidly, whereas a less soluble amorphous or mineral source may contribute more gradually and potentially persist as a residual soil Si pool. For this reason, equal application rates expressed as total Si should not automatically be expected to produce equivalent Si availability, plant uptake or agronomic responses.

2.2. Functionality in the Soil and Rhizosphere

However, Si that remains outside the plant should not automatically be considered inactive. One important example is the interaction between Si and phosphorus. Silicic acid and phosphate can compete for sorption sites on soil mineral surfaces, particularly Fe- and Al-containing phases, so Si addition can alter P adsorption–desorption equilibria and, under suitable conditions, increase P availability. However, this response is not universal and depends on soil chemistry, Si and P concentrations, pH and fertilizer form. A recent meta-analysis of 15 Si–P co-fertilization studies reported an overall relative increase in plant P uptake of 52%, although responses varied substantially among crops and experimental systems (Mückschel *et al*., 2025). Therefore, Si should not simply be described as universally "displacing" phosphate from soil.

Si can also influence the behavior of potentially toxic elements. Reported mechanisms include adsorption, complexation and precipitation or coprecipitation reactions that can reduce the mobility and bioavailability of certain metals. In acidic soils, silicate amendments may additionally influence pH, base saturation and exchangeable acidity, potentially reducing Al stress and improving the chemical environment surrounding roots. These effects demonstrate an important principle: part of the agronomic response to Si can originate from modification of the root environment rather than from Si that has already entered plant tissue (Farooq and Dietz, 2015; Boutafda *et al*., 2026).

The rhizosphere adds a biological component to this process. Microorganisms associated with mineral surfaces and roots can participate in silicate weathering and Si mobilization through mechanisms including biofilm formation, production of organic acids and localized modification of pH. Silicate-solubilizing microorganisms include genera such as *Bacillus, Pseudomonas* and *Burkholderia*. Boutafda *et al*. (2026) summarize published evidence that B. subtilis can contribute to silicate dissolution through biofilm-associated and pH-mediated mechanisms.

The interaction is potentially bidirectional. Si amendments can modify soil pH, nutrient availability, aggregation, metal speciation and root performance, all of which can alter microbial habitats and community composition. Nevertheless, the causal relationship between changes in the microbiome, increased Si mobilization, greater plant Si uptake and improved crop performance remains incompletely resolved. Microbial changes associated with Si application should therefore not automatically be interpreted as evidence that those changes are responsible for the agronomic response (Boutafda *et al*., 2026).

Taken together, these processes indicate that an applied Si source can follow several pathways before plant uptake. Some Si may dissolve and contribute directly to the H_4SiO_4 pool available to roots; some may remain associated with soil minerals or poorly soluble phases; some may participate in interactions affecting nutrients or potentially toxic elements; and microbial activity may influence its subsequent mobilization. Therefore, the fraction of applied Si that does not immediately enter the plant cannot automatically be classified as lost or non-functional. Its potential contribution must instead be considered within the chemistry and biology of the soil–rhizosphere system before addressing the next stage: uptake across the root and transport within the plant.

3. Silicon Uptake, Transport and Localization Inside the Plant

3.1. Root Uptake and Membrane Transport

Once Si is present in the soil solution as plant-available silicic acid, the next stage is its transfer across the root and into the vascular system. This process has been characterized most extensively in rice, although homologous Si transporters have subsequently been identified in other species, including maize, barley and wheat. Differences in transporter presence, localization and activity contribute substantially to the large differences in Si accumulation observed among plant species (Ma and Yamaji, 2008; Kaur and Greger, 2019).

A major advance in understanding this process came from the identification of the rice transporter Lsi1 by Ma *et al*. (2006). Lsi1 is an influx transporter belonging to the nodulin-26-like intrinsic protein (NIP) family of aquaporins and facilitates the passage of uncharged silicic acid across the plasma membrane into root cells. The subsequent identification of Lsi2 demonstrated the complementary mechanism required to move Si toward the vascular system. Lsi2 functions as an efflux transporter, exporting silicic acid from root cells toward

the apoplast and ultimately facilitating radial movement toward the stele (Ma *et al*., 2006; Ma *et al*., 2007; Ma and Yamaji, 2008).

In rice, Lsi1 and Lsi2 are located on opposite sides of cells in the exodermis and endodermis. This polar localization creates a directional transport system. Silicic acid enters through Lsi1 on the distal side of the cell and leaves through Lsi2 on the proximal side, allowing Si to progress toward the stele. This arrangement is particularly important because the Casparian strips of the exodermis and endodermis restrict unrestricted apoplastic movement toward the vascular tissue (Ma *et al*., 2006; Ma *et al*., 2007; Ma and Yamaji, 2008).

The pathway can therefore be represented schematically as:

soil solution → Lsi1 → root-cell symplast → Lsi2 → apoplast/stele → xylem.

Thus, root uptake of Si involves transmembrane passage of molecular silicic acid through living cells; this transient symplastic transport should be distinguished from the predominantly apoplastic localization of much of the Si that is subsequently deposited in plant tissues.

The efficiency and anatomical organization of this transport system are not identical among species. In barley and maize, for example, Si influx and efflux transporters have different cellular localization patterns from those found in rice (Chiba *et al*., 2009; Mitani *et al*., 2009a,b). This helps explain why identical concentrations of plant-available Si around the roots cannot be expected to result in identical Si uptake among crops.

The established Lsi transport pathway also concerns molecular silicic acid rather than solid silica particles. Consequently, the presence of nano- or colloidal SiO_2 in the root environment should not automatically be interpreted as direct availability to these transporters. Such materials can contribute to the conventional uptake pathway when they generate dissolved silicic acid.

3.2. Root-to-Shoot Transport and Tissue Localization

After reaching the stele, Si is loaded into the xylem and transported toward aerial tissues. Xylem loading can be highly effective in Si-accumulating plants. Mitani *et al*. (2005), for example, measured a xylem-sap Si concentration of approximately 6 mM in rice within 30 minutes of exposure to a nutrient solution containing only 0.5 mM Si, increasing to

approximately 18 mM after a further 8.5 hours. These results demonstrate rapid concentration of Si into the xylem against a concentration gradient (Mitani *et al*., 2005).

Although Lsi1 and Lsi2 explain major steps in radial root transport, the complete molecular machinery linking radial transport to Si loading into the xylem has not yet been fully resolved. Thus, there remains an important mechanistic gap between radial transport through the root and long-distance xylem transport (Mandlik *et al*., 2020).

Once in the xylem, silicic acid moves toward the shoot predominantly with the transpiration stream. In aerial tissues, Lsi6 participates in unloading silicic acid from the xylem into surrounding tissues. In rice stem nodes, Si redistribution is more complex: Lsi6 acts together with the efflux transporters Lsi2 and Lsi3 to mediate intervascular transfer and preferentially distribute Si toward tissues such as the flag leaf and panicle (Yamaji *et al*., 2008; Yamaji and Ma, 2009). Consequently, transpiration provides an important physical driver of long-distance Si movement, whereas transporter-mediated unloading and intervascular transfer influence its final distribution among shoot organs.

The overall pathway can therefore be summarized as:

root uptake → radial cellular transport → stele → xylem → transpiration-driven long-distance transport → xylem unloading → distribution among shoot tissues.

The final distribution of Si is strongly associated with transpiration. Older leaves commonly accumulate more Si than younger leaves, and highly transpiring organs tend to receive greater Si deposition (Henriet *et al*., 2006). Nevertheless, transport and deposition should not be considered entirely passive processes because specific transporters influence where Si is unloaded and redistributed within aerial tissues (Yamaji *et al*., 2008; Yamaji and Ma, 2009).

An important distinction is that Si can occur in both the symplast and the apoplast, but evidence indicates that much of the Si transported through aerial tissues is associated with the apoplastic solution and that substantial final deposition occurs in cell walls and other extracellular structures (Zexer *et al*., 2023). Therefore, saying that Si has been “absorbed by the plant” does not necessarily mean that the Si ultimately remains within the cytoplasm of living cells.

3.3. Polymerisation and Silica Deposition

As silicic acid is transported into aerial tissues, increasing local concentrations can promote condensation and polymerisation, ultimately producing hydrated amorphous silica, commonly represented as $SiO_2 \cdot nH_2O$. The resulting biogenic silica deposits can occur as phytoliths and other silica-rich structures in epidermal cell walls, specialized silica cells, trichomes, tissues beneath the cuticle and other plant structures (Sangster *et al*., 2001; Zexer *et al*., 2023).

The association between Si transport and transpiration historically led to a predominantly passive model of silica deposition: water is lost from the tissue, silicic acid becomes progressively concentrated, and supersaturation eventually results in polymerisation and precipitation. The relationship between transpiration and Si accumulation remains important, and classical studies demonstrated substantial Si deposition in epidermal tissues and increasing deposition as leaves age (Yoshida *et al*., 1962; Sangster, 1970).

However, the spatial pattern of silicification cannot be explained by evaporation and supersaturation alone. Evidence from genetically and anatomically controlled deposition sites indicates that biological matrices—including cell-wall polymers and proteins—can influence silicic-acid concentration, nucleation and subsequent silica polymerisation. Silicification can occur at specific cellular locations, and cell-wall components can provide matrices that influence nucleation and polymerisation. For example, experimental work has demonstrated genetic control over silica deposition in wheat awns (Peleg *et al*., 2010), while callose has been shown to be necessary for silica deposition at the base of Arabidopsis leaf trichomes (Kulich *et al*., 2018). More recently, cellulose-associated organization of biological silica has been demonstrated in rice tissues (Nakamura *et al*., 2021). These findings support the concept that organic polymers and cellular structures can control where and how silica forms.

Zexer *et al*. (2023) synthesize this evidence into a model in which cell-wall polymers and proteins act as scaffolds for silica formation. In this model, organic structures can concentrate or stabilize silicic acid, promote its initial condensation and provide sites for subsequent silica polymerisation. Silicification therefore reflects an interaction between Si chemistry, water transport and biological control rather than simply passive precipitation following evaporation.

Most solid silica deposition occurs in association with the apoplast and cell-wall system. For example, silica has been observed in specific layers of primary cell walls and at the interface between the plasma membrane and cell wall, while the protoplast itself can remain free of solid silica. Nevertheless, Si can exist in both symplastic and apoplastic compartments before deposition (Zexer *et al*., 2023).

Accordingly, Si inside the plant should not be treated as a single functional pool. During uptake and transport, Si occurs principally as soluble silicic acid and can pass through both symplastic and apoplastic compartments. Following concentration and polymerisation, much of this Si becomes immobilized as hydrated amorphous silica associated predominantly with cell walls and other apoplastic structures. These two states—mobile soluble Si and deposited silica—should be distinguished because their localization, mobility and likely modes of action differ.

4. Functionality of Silicon Inside the Plant

4.1. Structural and Physical Functionality

Once Si has been transported to aerial tissues and deposited as hydrated amorphous silica, an important part of its functionality is physical and structural. Silica deposition occurs particularly in epidermal tissues, cell walls, specialized silica cells, trichomes and beneath the cuticle. These deposits can increase tissue rigidity and mechanical strength and contribute to maintaining leaf architecture (Haynes, 2017; Zexer *et al*., 2023).

In grasses and other Si-accumulating crops, silicification can strengthen stems and leaves and contribute to greater resistance to bending and lodging. The combination of silica with structural components of the cell wall can reinforce tissues without requiring Si to remain metabolically active within the cytoplasm. In this sense, polymerised silica acts principally as a structural material rather than as a conventional nutrient participating directly in metabolic reactions (Haynes, 2017; Zexer *et al*., 2023).

Silica deposition can also contribute to plant protection against biotic stress. Increased silicification of epidermal tissues can create a harder physical barrier that makes penetration by fungal pathogens more difficult and can increase the mechanical resistance of tissues to chewing and piercing insects. In herbivores, highly silicified tissues can also reduce palatability and feeding efficiency and increase wear of feeding structures. However, the

protective effect of Si against pathogens and herbivores cannot be explained entirely by this physical-barrier mechanism, because Si is also associated with inducible biochemical defence responses, which are discussed below (Haynes, 2017).

Silica deposition can additionally contribute to plant water relations through structural effects on epidermal tissues and leaf architecture. However, improved drought tolerance following Si supply cannot be attributed solely to a physical reduction in water loss, because Si-associated responses also involve physiological processes affecting water uptake, stomatal behaviour, hydraulic conductance and osmotic adjustment (Haynes, 2017; Boutafda *et al*., 2026).

Thus, deposited silica can be regarded as a relatively stable structural component of the plant, contributing principally to mechanical reinforcement, maintenance of tissue architecture and physical protection. These effects should be distinguished from those occurring while Si is associated with physiological and biochemical responses.

4.2. Physiological and Biochemical Functionality

The effects associated with Si inside the plant are not restricted to deposited silica. Numerous studies reviewed in the literature report physiological and biochemical changes following Si supply, particularly when plants are exposed to drought, salinity, nutrient imbalance, metal toxicity, pathogens or herbivores. These responses include changes in water relations, ionic balance, photosynthetic performance, defence signalling and stress-related metabolism (Haynes, 2017; Mandlik *et al*., 2020; Boutafda *et al*., 2026).

Under water deficit, Si-treated plants have frequently shown improved plant water status. Reported responses include greater relative water content, maintenance of stomatal function, changes in root hydraulic conductance and improved osmotic adjustment. Accumulation of compatible solutes such as proline, glycine betaine and soluble sugars has also been reported in Si-treated plants under dehydration stress. Together, these responses can help maintain cellular turgor and photosynthetic activity during periods of limited water availability. A recent review emphasizes, however, that these responses vary with genotype, stress intensity and growing conditions (Haynes, 2017; Puppe and Sommer, 2018; Boutafda *et al*., 2026).

Si can also contribute to ionic homeostasis under salinity. Reported responses include reduced Na^+ accumulation in aerial tissues, greater retention or exclusion of Na^+ in roots and improved maintenance of the K^+/Na^+ ratio. Maintaining this balance is physiologically important because excessive Na^+ disrupts enzyme activity, membrane function and cellular metabolism, while K^+ is required for numerous metabolic and osmotic processes. The mechanisms involved appear to include both structural restriction of uncontrolled ion movement and regulation of ion-transport systems (Boutafda *et al*., 2026).

Under metal and metalloid stress, Si can reduce the amount of toxic element reaching metabolically sensitive tissues. Inside the plant, reported mechanisms include increased binding of metals to cell-wall components, retention within roots, reduced root-to-shoot translocation and, in some cases, enhanced vacuolar sequestration. These effects can indirectly preserve nutrient acquisition and cellular metabolism by reducing the physiological damage caused by toxic elements. The relative importance of these mechanisms depends strongly on the element, its chemical speciation, the crop and the growing environment (Boutafda *et al*., 2026).

Si supply has also been associated with maintenance of photosynthetic performance under stress. Reported effects include preservation of chlorophyll, chloroplast structure, stomatal conductance and photosynthesis-related proteins or gene expression. Under pathogen challenge, for example, experimental studies summarized by Haynes (2017) reported Si-associated changes in photosynthesis and photorespiration that helped maintain photosynthetic function in infected plants.

Biotic resistance provides particularly strong evidence that Si functionality cannot be explained exclusively by the formation of a passive silica barrier. Experimental studies reviewed by Haynes (2017) have reported changes in defence-related gene expression, proteins and hormone-signalling pathways involving salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). These observations have contributed to the hypothesis that Si can prime plant defence, allowing a stronger or more rapid defence response following pathogen attack. The exact mechanism by which Si participates in this signalling remains unresolved, and responses differ among plant–pathogen systems (Haynes, 2017).

Taken together, these observations indicate that Si-associated physiological functionality is highly context dependent. Si should not be described as directly performing each of these

biochemical processes. In many cases, it remains difficult to separate a direct effect of Si on signalling or metabolism from an indirect effect resulting from reduced stress intensity, improved water status, better ionic balance or decreased exposure to toxic elements. This distinction is particularly important when considering Si effects on cellular redox regulation.

4.3. Silicon and Plant Redox Homeostasis

Redox homeostasis describes the plant's ability to maintain a controlled balance between the generation of reactive oxygen species (ROS) and the biochemical systems responsible for their utilization, regulation and removal. ROS such as superoxide ($O_2\bullet^-$) and hydrogen peroxide (H_2O_2) are naturally produced during plant metabolism and also function as signalling molecules. Under severe environmental or biological stress, however, ROS production can exceed the capacity of the plant's antioxidant and repair systems, resulting in oxidative stress and damage to membranes, proteins and nucleic acids (Boutafda *et al*., 2026).

Si supply under stress is frequently associated with changes in the enzymatic antioxidant system. Reported responses include increased activities of superoxide dismutase (SOD), catalase (CAT), peroxidases and enzymes involved in the ascorbate–glutathione cycle. SOD converts superoxide into H_2O_2, while catalase and peroxidase systems subsequently participate in controlling H_2O_2 concentrations. Si treatment has also been associated with improved maintenance of the non-enzymatic antioxidants ascorbate and glutathione and with more favourable ratios between their reduced and oxidized forms, including AsA/DHA and GSH/GSSG (Boutafda *et al*., 2026).

These changes are important because the objective of the antioxidant system is not to eliminate ROS completely. Controlled ROS production is required for normal cellular signalling and defence. Redox homeostasis therefore represents the ability to prevent excessive ROS accumulation while retaining their physiological signalling functions.

Improved redox regulation in Si-treated plants is frequently accompanied by lower indicators of oxidative damage. One commonly measured marker is malondialdehyde (MDA), which is generated during lipid peroxidation and is therefore used as an indicator of oxidative damage to cellular membranes. Lower MDA concentrations and reduced

membrane damage reported in Si-treated stressed plants are consistent with improved control of oxidative stress (Boutafda *et al*., 2026).

However, Si should not be described as a conventional antioxidant that directly reacts with and neutralizes ROS. The available evidence supports a more complex mechanism. Si may influence antioxidant and defence signalling systems, but it can also improve redox status indirectly by reducing the primary stress responsible for excessive ROS generation. For example, improved water status under drought, reduced Na^+ accumulation under salinity or reduced exposure to toxic metals can decrease the oxidative pressure experienced by the cell before antioxidant detoxification is required (Boutafda *et al*., 2026).

This distinction also explains why increased antioxidant-enzyme activity should not automatically be interpreted as the only indicator of improved Si-mediated redox performance. If Si substantially reduces the original stress, the plant may produce less ROS and consequently require less antioxidant-enzyme activity. The relevant outcome is therefore the overall redox condition of the plant—including ROS accumulation, antioxidant status and oxidative damage—rather than an increase in any single antioxidant enzyme.

The available evidence consequently supports a model in which Si-associated redox protection may operate through several interacting processes:

primary stress alleviation → reduced excessive ROS generation
Si-associated modulation of antioxidant systems → improved ROS regulation
reduced oxidative pressure + antioxidant regulation → lower oxidative damage → improved cellular function.

At present, the relative contribution of direct Si-associated regulation of antioxidant and signalling pathways versus indirect improvement resulting from alleviation of the original stress remains incompletely resolved. This uncertainty should be retained when interpreting Si-associated redox responses rather than assuming that they result from a direct intracellular biochemical action of Si (Boutafda *et al*., 2026).

5. Fate and Recovery of Applied Silicon: How Much Actually Enters the Plant?

A central question in the agronomic use of silicon is how much of the Si applied to a crop actually enters the plant. This distinction is important because the amount of Si contained in a fertilizer, the fraction released from that fertilizer, the concentration of dissolved plant-

available silicic acid in the soil solution, and the amount ultimately accumulated by the crop are not equivalent. The available literature indicates that only a fraction of applied Si may be recovered in plant biomass, while a substantial proportion can remain in the soil in forms with very different degrees of availability (Khalid *et al*., 1978; Haynes, 2014).

The clearest quantitative evidence comes from the long-term field experiment of Khalid *et al*. (1978), who followed the fate of calcium silicate applied to a tropical soil during five years of cropping. The cropping sequence included sugarcane, ratoon sugarcane, maize and repeated harvests of kikuyu grass. Despite this prolonged period of cropping, cumulative plant uptake accounted for only approximately 12–21% of the applied Si. A further 14–28% was recovered as extractable residual Si in the soil, while approximately 57–72% remained in forms that were not readily recovered by the extraction procedure used. The study also found no significant movement of the applied Si below 30 cm under the experimental conditions (Khalid *et al*., 1978).

These results provide a useful quantitative illustration of Si partitioning after application. Across the experimental treatments, crop uptake accounted for 12–21% of applied Si, repeated soil extraction recovered a further 14–28%, and the remaining 57–72% was estimated to persist in forms not readily displaced by the extraction procedure. These ranges should not be combined as a single fixed mass balance or interpreted as universal Si fertilizer-recovery coefficients, because they varied with the experimental conditions. They apply specifically to the calcium-silicate source, soil, pH treatments, cropping sequence, experimental duration and analytical methodology used by Khalid *et al*. (1978).

The chemical nature of the Si source strongly influences what proportion of total Si can eventually become available to the plant. Haynes *et al*. (2013) demonstrated this clearly by comparing several Si-containing materials using chemical extraction, soil incubation and uptake by two successive rice crops. Fly ash, for example, contained approximately 29% total Si but had negligible extractable Si and did not significantly increase rice Si uptake. In contrast, several slags with lower total Si concentrations substantially increased extractable soil Si and plant Si uptake (Haynes *et al*., 2013).

Therefore, the relevant sequence is not simply:

fertilizer Si → plant Si

but rather:

total Si applied → fertilizer dissolution → dissolved Si → plant-available silicic acid → root uptake → plant accumulation.

At each stage, only part of the preceding Si pool may progress to the next. Silicon released into the soil solution can be taken up by roots, but it can also undergo adsorption and desorption reactions with soil surfaces, interact with Fe and Al phases, be incorporated into secondary solid phases, or remain within a soil Si reservoir capable of subsequently replenishing the soil solution (Haynes, 2014).

This distinction is especially important because total Si content is not synonymous with plant availability. Haynes (2014) describes soil Si availability as the result of a dynamic equilibrium involving mineral dissolution, adsorption and desorption, leaching, phytogenic Si cycling and soil chemical conditions, particularly pH. Soil solution Si is predominantly present as monomeric silicic acid, H_4SiO_4, which represents the form relevant to conventional root uptake (Haynes, 2014).

The importance of fertilizer chemistry was further demonstrated by Duboc *et al*. (2019), who compared chemically diverse potential Si sources, including mineral and industrial materials, wheat straw, biochars, ash and diatomaceous earth. Plant availability differed markedly among these materials. Wheat-straw biochars and ash exhibited Si solubility and availability equivalent to or marginally greater than the original wheat straw, whereas the diatomaceous earth evaluated in the experiment did not release substantial amounts of Si (Duboc *et al*., 2019).

The diatomaceous-earth result is particularly informative. Diatomaceous earth contains amorphous biogenic silica originating from diatom frustules, but its Si content or its classification as amorphous silica does not by itself demonstrate that this Si will rapidly become plant available. Duboc *et al*. (2019) therefore provide experimental evidence for an important principle: the agronomic value of a Si source cannot be predicted simply from its total Si concentration or from the general chemical description of the silica it contains. Actual dissolution under soil conditions is critical.

The same study also highlights a methodological problem in determining how much fertilizer Si is genuinely available. Different chemical extraction procedures gave different

estimates of Si availability. Duboc *et al*. (2019) found that resin extraction and their ferrihydrite-based “Iron Bag” sink method were better predictors of plant Si availability than several conventional extraction methods. Haynes *et al*. (2013) similarly concluded that the usefulness of chemical extraction depends on the type of Si material being evaluated (Haynes *et al*., 2013; Duboc *et al*., 2019).

This creates an important distinction between Si that is not absorbed by the plant and Si that is agronomically inactive. The two categories should not automatically be considered equivalent. Silicon remaining outside the plant can potentially participate in the soil Si cycle through dissolution, adsorption–desorption and interactions with mineral surfaces, while phytogenic Si returned through plant residues can contribute to replenishment of the soil Si pool (Haynes, 2014). Conversely, Si retained within highly resistant mineral or silica phases may contribute very little plant-available silicic acid during the relevant crop cycle (Haynes, 2014; Duboc *et al*., 2019).

The soil should therefore be considered a dynamic Si reservoir rather than simply the medium through which fertilizer Si must pass before entering the plant. Root uptake continuously removes silicic acid from the soil solution, while fertilizer dissolution, mineral weathering, desorption and dissolution of biogenic Si can replenish it. At the same time, adsorption, leaching and incorporation into less soluble forms can decrease the immediately available pool (Haynes, 2014).

Phytogenic Si cycling adds another dimension to this process. Plants accumulate Si and subsequently deposit much of it as amorphous silica or phytoliths. When plant material decomposes, this biogenic silica can return to the soil and contribute to the Si cycle. In natural ecosystems, this recycling can be an important determinant of soil-solution Si concentrations. Agricultural harvesting disrupts this cycle because Si contained in harvested biomass is exported from the field, progressively contributing to soil desilication, particularly in high-Si-accumulating cropping systems (Haynes, 2014).

Consequently, a low percentage of applied Si recovered in plant biomass should not automatically be interpreted as evidence that all unrecovered Si has been lost or is agronomically inactive. At least three fractions should conceptually be distinguished: Si that has entered the plant; Si that remains outside the plant in sufficiently reactive forms to contribute to current or future plant-available Si pools; and Si retained in forms whose

dissolution is too slow to make a meaningful contribution during the agronomic period under consideration. Importantly, the presence of residual Si in soil does not by itself demonstrate that this residual fraction will subsequently become plant available (Khalid *et al*., 1978; Haynes, 2014; Duboc *et al*., 2019).

However, the current evidence does not allow universal percentages to be assigned to these three fractions. Recovery will depend on crop species and its Si-uptake capacity, fertilizer source and dissolution rate, application rate, soil mineralogy, pH, water regime, weathering status, crop duration and the analytical method used to define “available” or “residual” Si (Haynes *et al*., 2013; Haynes, 2014; Duboc *et al*., 2019).

The fate of applied Si is therefore better represented as a set of competing pathways:

applied Si → dissolution → dissolved plant-available Si → plant uptake
applied Si/dissolved Si → reactive soil Si pools → possible later release
applied Si/dissolved Si → slowly available or strongly retained forms

From an agronomic perspective, this distinction is critical. The efficiency of a Si fertilizer should not be evaluated solely from its total Si content or from the percentage recovered in plant biomass during the first crop. A more meaningful assessment must consider its capacity to release plant-available silicic acid, the proportion actually taken up by the crop, and the persistence and potential future availability of the Si remaining in the soil (Khalid *et al*., 1978; Haynes *et al*., 2013; Haynes, 2014; Duboc *et al*., 2019).

This interpretation also establishes an important limit to our present knowledge. Existing studies demonstrate that substantial amounts of applied Si can remain outside the plant, but the long-term biological and agronomic functionality of these different residual Si pools is much less well quantified than plant uptake itself. This distinction is important for interpreting fertilizer efficiency and represents a key area for further investigation.

6. Conclusions

The evidence reviewed in this article supports the interpretation of silicon as a beneficial element whose agronomic functionality cannot be understood solely from the amount of Si accumulated within plant tissues. Its effects occur across the soil–plant continuum and depend strongly on Si source, chemical form, availability, crop species and environmental conditions.

Outside the plant, Si participates in a dynamic soil system involving dissolution, adsorption–desorption, interactions with mineral surfaces, nutrient availability and biological processes. Consequently, Si that is not immediately absorbed by roots should not automatically be considered inactive or lost. Part of this residual Si may remain within reactive or slowly available soil pools capable of contributing to subsequent Si availability, although the long-term biological functionality of these pools remains insufficiently quantified.

Inside the plant, Si is taken up predominantly as soluble silicic acid and transported before a substantial fraction becomes deposited as hydrated amorphous silica. Deposited Si contributes to structural reinforcement and physical protection, while Si supply is also associated with broader physiological responses involving water relations, ionic balance, stress signalling, defence and redox homeostasis. Importantly, these physiological effects should not automatically be interpreted as direct biochemical actions of the Si molecule, since several may result indirectly from the alleviation of the original stress.

Ultimately, silicon is better understood not as a conventional nutrient with a simple application–uptake–response relationship, but as an element operating dynamically across the soil–microbiome–plant system. This broader perspective may explain why relatively modest plant recovery of applied Si can coexist with significant agronomic responses and provides a more appropriate framework for evaluating different Si technologies and application strategies.

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