



Editorial: Special issue on silicon at the root-soil interface

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‘A greater awareness of the importance of Si in plants, especially on the part of experimental plant biologists, is bound to have beneficial synergistic effects beyond plant biology *per se*.’ (Epstein 1994).

Introduction

Studies concerning silicon (Si) in plants and soils have come of age. There was a time when papers on Si were rare events to be celebrated, but now it is impossible to keep up with the whole field. Emanuel Epstein, quoted above, had quite a lot to do with the explosion in research that has happened in the last quarter of a century. His major reviews (Epstein 1994, 1999) set the tone for much that has happened since. He was also correct that the work of plant biologists on Si has had beneficial effects well beyond plant biology. We have seen this impact in agriculture, archaeology, biogeochemistry, chemistry, food

science, soil science, and palaeoecology, to name a few key areas. Quite quickly after Epstein’s reviews, a published monograph on *Silicon in Agriculture* appeared (Datnoff et al., 2001) and an updated collection was published 14 years later (Liang et al. 2015).

There have been very many reviews of aspects of plant and soil Si research in the last few years, and we will cite just a few here, and other, more specific, ones in the sections below. For a review concentrating on agricultural aspects of this topic, particularly in North America, see Tubana et al. (2016). Coskun et al. (2019) very much followed on from the reviews of Epstein, and considered some of the key controversies currently surrounding Si research. A detailed account of Si uptake, transport and deposition is provided by Mandlik et al. (2020). Greger et al. (2018) reviewed how Si influences soil availability and uptake of other nutrients by plants. Finally, the interactions of Si with essential and beneficial elements are covered by Pavlovic et al. (2021).

Our Special Issue is the first to focus on Si in *Plant and Soil*, but it is far from the first special edition we have seen in international scientific journals. In recent years we have noted these in *Functional Ecology* (Cooke et al. 2016), the *Journal of Experimental Botany* (Tripathi et al. 2020), and *Frontiers in Plant Science* (Cooke and DeGabriel 2016; Deshmukh et al. 2017; Hodson et al. 2020). *Plants* have had several small special editions, the largest of which was edited by Jörg Schaller and colleagues and included a major review of Si cycling in the soil (Schaller et al.

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2021). In addition, the series of International Meetings on Phytolith Research (IMPR), which began in Madrid in 1996, have frequently produced proceedings, sometimes in books and not infrequently as special editions of journals. Zurro and Hodson (2018) documented all of these at the end of their paper under 'Further Readings'.

As befits a Special Issue in *Plant and Soil* we wanted to bring together a collection that focussed on the interface between the plant and the soil, and so particularly looking at the rhizosphere. We are grateful to the authors who provided the papers for our Special Issue, and they well illustrate the variety of work that is now being carried out on Si in plants and soils.

Silicon uptake and deposition

One of the areas that has made most progress since the classic review articles by Epstein is Si uptake. The seminal paper by Ma et al. (2006) on a Si transporter in rice roots was the first of many articles on such transporters, and we now have a much better idea of how Si is moved across plant membranes. For a recent review of this topic see Mitani-Ueno and Ma (2021). Most of the Si taken up by plants is eventually deposited as solid amorphous silica bodies, often known as phytoliths. There have been fewer advances in our understanding of the deposition process than of Si uptake. It is now clear that there are two main types of phytolith, those where deposition is in the cell lumen, and those where silica is laid down on a carbohydrate matrix in the cell wall (Hodson 2016; Kumar et al. 2017). But many questions remain concerning the control of Si deposition.

In our Special Issue we included two papers that fit in the broad area of Si uptake and deposition. Most of the work carried out in this area has been conducted on plants grown in strictly regulated laboratory conditions, and there is far less available for field-grown plants. Schaller et al. (2022) investigated silicification patterns in developing wheat leaves and sheaths over a growing season in Germany. When they were just formed, leaves had relatively low Si concentrations, but this increased with time. Silica bodies and trichomes were particularly important sites of deposition. The work of Lu et al. (2021) was also conducted under field conditions, but this time in the tropical

forest of Southern China. They investigated the effects of nitrogen addition on aboveground Si and phytolith concentrations in understory plants. Anthropogenic nitrogen deposition has enriched many areas of the world and has previously been shown to have modified the biogeochemical cycling of other elements. Lu et al. showed that nitrogen enrichment increased concentrations of silica and phytoliths in the leaves of understory plants, but had no effect on phytolith and plant available Si in the topsoil. We should point out that other workers (Johnson et al. 2021; Minden et al. 2021; Quigley et al. 2020) have found that increased soil nitrogen availability decreased shoot Si concentrations. Clearly more work is required in this area to explain the differences between these results.

Silicon isotopes

There are four Si isotopes in the natural environment: the three stable isotopes, ^{28}Si , ^{29}Si , ^{30}Si , and the radioactive ^{32}Si . The relative abundances of the stable isotopes are 92.23% (^{28}Si), 4.67% (^{29}Si), and 3.10% (^{30}Si) on Earth. But isotopic fractionation events can occur which slightly change these abundances. Fractionation is defined as the relative partitioning of heavier and lighter isotopes between two coexisting phases in a system. Silicon isotopes have been much used by geochemists and those interested in using them as a proxy for environmental change, but there have been fewer investigations using these isotopes in higher plants (Leng et al. 2009). What is clear from studies with a variety of plants is that fractionation events occur as the isotopes are transported up the plant. The lighter isotopes are more reactive, and are incorporated into deposited silica lower down the plant, meaning that the heavier isotopes predominate towards the end of the transpiration stream. There is also a fractionation event as the isotopes are taken up into the root, and lighter isotopes seem to be preferred. Our Special Issue had one paper featuring Si isotopes, that by Zhou et al. (2022). The authors analysed Si isotopic fractionation in Si accumulators (rice, maize), intermediates (cucumber), and non-accumulators (tomato) grown in three different soils. All four species grown in any of the three soil types exhibited ^{28}Si enrichment relative to the soil solution, confirming previous work that suggested that plant roots preferentially take up lighter Si isotopes. Within

the shoot rice, maize and cucumber all showed the expected fractionation with heavier ^{30}Si accumulating in the upper parts, but tomato showed no such fractionation, suggesting that non-accumulators may differ in their Si transport mechanisms.

Silicon and stress

Since the seminal review by Liang et al. (2007) it has become more and more evident that Si has major roles to play in the amelioration of abiotic stresses. This has made the area one of the most popular in plant Si research, and it is therefore not surprising that seven of the papers submitted to our Special Issue concern stress in some way. None of our papers concerned biotic stresses, and we might perhaps have expected this bias in papers submitted to *Plant and Soil*, as most publications concerning grazing or plant pathogens will be on shoots, and relatively few on roots and the soil environment.

The effects of Si on the responses of plants to drought is an important area, reviewed by Chen et al. (2018), and four papers in our Special Issue investigated this topic. Markovich et al. (2022) investigated the effects of drought in sorghum Lsi1 mutant plants which take up 1/15th of the Si that wild type plants do. They observed little difference in mutant and wild type plants under non-stressed conditions, but that under drought stress the mutant plants showed early stomatal closure which caused reduced transpiration. This then led to decreased growth under stressed conditions in the mutant. In a different approach, Wade et al. (2022) investigated the effects of watering regime on a barley landrace and cultivar. The amount of water the plants received was more important than frequency of watering in decreasing plant growth. Lowered water availability decreased Si uptake. It seems that sustained decreases in rainfall have a greater effect on Si uptake by plants, rather than episodic droughts followed by heavy rainfall events. This may be important as it indicates the kind of conditions under which Si supply is maintained, with consequent benefits for resistance to biotic and abiotic stresses. Teixeira et al. (2022) studied the effects of Si fertigation treatments on maize growing under two soil water regimes (adequate and severe drought). The three fertigation treatments were: sodium and potassium silicate stabilized with

sorbitol; potassium silicate; and a control. Si fertigation increased Si uptake and growth of maize plants, even under drought conditions. Finally, Aktar and Ilyas (2022) investigated the effects of nanosilicab (a combination of a biofertiliser containing a number of bacterial strains and silicon dioxide nanoparticles), on wheat plants under control and drought conditions. Nanosilicab promoted the growth of wheat under all conditions, and was effective in relieving the effects of drought stress.

The amelioration of metal and metalloid toxicity by Si has been another major topic of research in recent years (Bhat et al. 2019). Our Special Issue included two papers within this general topic area, both featuring cadmium as a toxic element. An et al. (2022) investigated cadmium toxicity in maize plants and its amelioration by Si. They found that Si treatment reduced the toxic effect of cadmium on the plants, and also decreased the amount of the element transported into the shoot and the grain. The authors showed that Si treatment reduced daily intake of metal and health risk index for humans. Taking another approach, Linam et al. (2022), working on rice, investigated the effects of Si amendments (rice husks and husk biochar) on cadmium and arsenic uptake. These treatments significantly increased soil pore water and plant Si. However, the Si amendments had little effect on cadmium or arsenic concentrations in the plants, which seemed more related to water availability.

There has been much more work on the ameliorative effects of Si on metal toxicity than on its effects on elemental deficiencies. However, Benslima et al. (2021) observed that Si could mitigate the adverse effects of potassium deficiency in barley plants. The beneficial effects of Si were not seen through increased shoot potassium concentration and phenolic compound accumulation, but were mainly due to increased growth and photosynthetic activity.

Silicon in the rhizosphere

Whilst the papers in the other sections of this editorial were relatively easy to categorise, those in this section were less so, but all of the processes investigated here start in the rhizosphere and in the soil. There have been several recent review papers covering this area (de Tombeur et al. 2021b; Katz et al.

2021; Schaller et al. 2021). We will now assess the five papers published in our Special Issue.

Limmer et al. (2022) investigated the effects of Si additions to soil on iron plaque formation in the roots of rice. They found that the treatments had minimal effects on plaque quantities, although there were some differences in the timing of plaque formation. Rice is a heavy Si accumulator, and a very important crop, and it is not surprising that quite a number of investigations in this Special Issue concerned this species. The work of Ning et al. (2021) focusses on intercropping between rice and water spinach. Intercropping considerably increased absorption of Si by rice. The authors went on to investigate the mechanisms behind this phenomenon, and found that an interspecific rhizosphere interaction appeared to induce the upregulation of Si transporter genes in rice roots (OsLsi1, OsLsi2) and stems (OsLsi6), and also stimulated rice roots to secrete more organic acids thereby increasing available soil Si. Recently, de Tombeur et al. (2021a) highlighted the effect of root exudates, and specifically organic acids, on soil Si availability.

Two of the papers in this section concern interactions between roots and microorganisms. Putra et al. (2022) investigated the effects of Si treatment on *Medicago truncatula* inoculated with rhizobial strains of *Ensifer meliloti*. Nodule number per plant was increased with improved Si supply. The concentrations of nodule flavonoid concentrations, of foliar nitrogenous compounds and foliar carbon (C) were all increased in the Si treatments, but foliar Si was not. Johnson et al. (2022) studied the effects of Si treatment on arbuscular mycorrhizal fungal colonisation in the grass *Brachypodium distachyon*. They included both a wild type and a mutant, Bdlsi1-1, which takes up very little Si. The fungi did not affect Si uptake, but increased soil Si led to greater plant growth and phosphorus (P) uptake. The colonisation of the roots by arbuscular mycorrhizal fungi was suppressed in wild type but not in Bdlsi1-1 mutants.

The final paper in this section (Nakamura et al. 2022) was somewhat different as it did not concern plant responses to Si treatments, but focussed on the effects of siliceous trichomes on decomposition of leaf material in the soil. The authors investigated the decomposition of leaves of two species, *Broussonetia papyrifera* and *Morus australis*, in mesh bags that either permitted the entry of meso- and macrofauna or did not. *B. papyrifera* leaves had greater trichome

densities than those of *M. australis*, and decomposed slower, but only in bags with a wide mesh size (5-mm) that allowed large decomposers to enter. It seems that siliceous trichomes reduced decomposition by the large decomposers and hints at effects of trichomes on C cycling in soil.

Silicon and carbon

Possibly the most controversial area of plant Si research at the moment is that concerning various aspects of the way Si interacts with C in plants and soils.

For many years, the dating of phytoliths using ^{14}C had seemed a reasonably reliable technique, but the work of Santos et al. (2018) has thrown some doubt on it. They have suggested that “old carbon” originating from plant uptake from the soil is affecting dating results. However, others are less keen on this idea, and this has led to a vigorous debate (Piperno 2016; Zuo and Lu 2019).

Another area of controversy concerns C sequestration in phytoliths in soils, an idea that was first suggested by Parr and Sullivan (2005). Their calculations suggested that the amount of C sequestered in this way could be substantial on a global scale, and this could have importance in mitigating climate change. For some years this idea was largely uncontested, but then calculations of Reyerson et al. (2016) and others from this group, suggested that C sequestration in phytoliths is insignificant globally. The main problems have been the difficulties in determining the “true” concentration of C in phytoliths, and how quickly phytoliths dissolve over time. A major debate ensued which was documented by Hodson (2019), who suggested a number of topics that need to be addressed to help resolve the dispute. However, there are still papers being published which tend to ignore the issues that have been raised, and make bold statements about the efficacy of C sequestration in phytoliths (e.g. Song et al. 2022). It is worth noting that the recent 6th Assessment Report of the IPCC, Working Group 3, on mitigation of climate change considered C sequestration in soils in some depth, but did not mention phytoliths once (IPCC 2022). Some in the phytolith/ plant Si community may be certain of the importance of C sequestration in phytoliths, but the wider scientific world has yet to be convinced.

The final area in this section that we will cover is trade-offs between Si and C, and so-called substitution of one element for the other. The idea was first suggested by Raven (1983) as he calculated that using Si for structural support should be energetically favourable over using C compounds. However, it has only been in the last 12 years, since Schoelynck et al. (2010) promoted the idea, that this area has taken off to become a popular area of plant Si research. Even just within this Special Issue these trade-offs are mentioned by Johnson et al. (2022), Putra et al. (2022), Schaller et al. (2022), and Wade et al. (2022) in the context of their quite varied research topics. However, one paper, Hodson and Guppy (2022) had a specific focus on this subject, and pointed out some potential problems that need to be considered. In particular, the authors were concerned that we needed to relate Si and C trade-offs, often observed from whole organ analyses, to Si and C distributions at the cellular level. Moreover, they were worried about some of the language being used to describe this phenomenon, and with the use of the word “strategy” in a manner bordering on teleology.

Silicon fertilisers

As scientists have realised how significant Si is in plant nutrition the deployment of Si fertilisers has been increasing in many parts of the world and for a wide range of crops. Two reviews that have given significant coverage of Si fertilisers are those by Artyszak (2018) and Puppe and Sommer (2018). One of the key issues in Si fertiliser research in the context of plant nutrition concerns the availability and release of Si from the many, and increasingly various, products available on the market. An approved test was released to measure Si availability from solid products in 2013 (Sebastian et al. 2013) using a 5-day alkaline-salt extraction, but within two years questions were raised around how closely that test reflected plant recovery of Si from the applied products (Zellner et al. 2015). Many of the papers in our Special Issue applied some type of Si treatment, including three that we have already mentioned where the emphasis was more on the plant responses: one study concerning the effects of nanosilica on drought stress in wheat (Akhtar and Ilyas 2022); work on Si fertigation in maize (Teixeira et al. 2022); and Linam et al. (2022) who studied rice

husk and charred husk amendments and their impacts on cadmium and arsenic uptake in rice. Difference in Si availability from various products was demonstrated by Linam et al. (2022) where the highest Si concentration product was less soluble than untreated husks. There were, however, two papers where the focus was more specifically on the fertilisers themselves. Both of these papers concerned interactions with P availability. Gunnarsen et al. (2022) investigated the effects of glacial rock flour (GRF) amendments on P availability in an acidic tropical soil. The authors found that GRF did not improve P availability in the soil, but the Si released from the fertiliser did improve stress tolerance and wheat plant yield.

Finally, Rezakhani et al. (2022), working on wheat, examined the effect of Si fertiliser alone or in combination with phosphate-solubilising bacteria (PSB) on plant uptake of P and Si when grown in a calcareous soil with low available P. When treatments included both Si and PSB strains, increased shoot uptake of Si and P and wheat biomass was observed as compared to the control and treatments where either Si or PSB were applied alone. It is heartening to see innovation in product design that recognises that both microbes and plants play a role in releasing Si from soil and fertiliser products, and we hope that future rhizosphere research increases our understanding of ways to improve the startlingly poor solubility of many of the Si sources available on the market currently.

Conclusions and future prospects

We were very pleased to gather such a diverse and internationally representative set of papers for this Special Issue. Our authors listed their addresses as in Australia, Brazil, China, Denmark, Germany, Iran, Israel, Japan, Pakistan, Spain, Switzerland, Tunisia, United Kingdom, United States of America, and Uruguay. So, it appears that research on Si in plants and soils is now happening on every continent, with the possible exception of Antarctica. The assembled papers also represent the very wide range of topics that are now being worked on, far wider than we had even envisaged at the time of Epstein’s first review in 1994. Perhaps not too surprisingly, given the importance of Si for grasses and cereals, 13 of the 18 papers focussed on these species, including four on wheat and three on rice. Three papers featured dicot species,

one looked at both cereals and dicots, and one had no species focus. Katz (2014) called for more Si studies on plants other than grasses, but obviously the bias is still there.

Clearly more progress has been made in some areas than others. So, we have a much better knowledge of Si transport in plants than we did 25 years ago, but studies of Si deposition have lagged some way behind. It is now well recognised that Si has major roles to play in the alleviation of stress in plants. We are only just beginning to understand some of the processes Si is involved in at the plant-soil interface in the rhizosphere. The whole topic of the way Si and C interrelate in plants has grown both in importance and in controversy in recent years. Fertilisers containing Si are increasing in significance, and a number of our papers reflected this, and studies on rhizosphere mobilisation of Si in soil and fertilisers will hopefully increase accordingly.

Looking forward, the future for research on Si in plants and soils looks bright. The growing recognition of the importance of Si in agriculture, and the links with many other fields, particularly archaeology and palaeoecology, will ensure that this is the case. The interdisciplinary nature of much of the work on Si makes it a very exciting area, even if it is almost impossible to keep up with everything that is happening!

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References

- Akhtar N, Ilyas N (2022) Role of nanosilicab to boost the activities of metabolites in *Triticum aestivum* facing drought stress. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05285-1>
- An T, Gao Y, Kuang Q, Wu Y, uz Zaman Q, Zhang Y, Xu B, Chen Y (2022) Effect of silicon on morpho-physiological attributes, yield and cadmium accumulation in two maize genotypes with contrasting root system size and health risk assessment. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05384-7>
- Artyszak A (2018) Effect of silicon fertilization on crop yield quantity and quality— a literature review in Europe. *Plants* 7(3):54. <https://doi.org/10.3390/plants7030054>
- Benslimam W, Zorrig W, Bagues M, Abdely C, Hafsi C (2021) Silicon mitigates potassium deficiency in *Hordeum vulgare* by improving growth and photosynthetic activity but not through polyphenol accumulation and the related antioxidant potential. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05188-1>
- Bhat JA, Shivaraj SM, Singh P, Navadagi DB, Tripathi DK, Dash PK, Solanke AU, Sonah H, Deshmukh R (2019) Role of silicon in mitigation of heavy metal stresses in crop plants. *Plants* 8:71. <https://doi.org/10.3390/plant8030071>
- Chen D, Wang S, Yin L, Deng X (2018) How does silicon mediate plant water uptake and loss under water deficiency? *Front Plant Sci* 9:281. <https://doi.org/10.3389/fpls.2018.00281>
- Cooke J, DeGabriel JL (2016) Editorial: Plant silicon interactions between organisms and the implications for ecosystems. *Front Plant Sci* 7:1001. <https://doi.org/10.3389/fpls.2016.01001>
- Cooke J, DeGabriel JL, Hartley SE (2016) Editorial. The ecology of plant silicon: geoscience to genes. *Funct Ecol* 30:1270–1276. <https://doi.org/10.1111/1365-2435.12711>
- Coskun D, Deshmukh R, Sonah H, Menzies JG, Reynolds O, Ma JF, Kronzucker HJ, Bélanger RR (2019) The controversies of silicon's role in plant biology. *New Phytol* 221:67–85. <https://doi.org/10.1111/nph.15343>
- Datnoff LE, Snyder GH, Korndörfer GH (eds) (2001) Silicon in agriculture. *Studies in plant science* 8. Elsevier, Amsterdam. ISBN: 9780444502629
- de Tombeur F, Cornelis J-T, Lambers H (2021a) Silicon mobilisation by root-released carboxylates. *Trends Plant Sci* 26:1116–1125. <https://doi.org/10.1016/j.tplants.2021.07.003>
- de Tombeur F, Roux P, Cornelis JT (2021b) Silicon dynamics through the lens of soil-plant-animal interactions: perspectives for agricultural practices. *Plant Soil* 467:1–28. <https://doi.org/10.1007/s11104-021-05076-8>
- Deshmukh RK, Ma JF, Bélanger RR (2017) Editorial: Role of silicon in plants. *Front Plant Sci* 8:1858. <https://doi.org/10.3389/fpls.2017.01858>
- Epstein E (1994) The anomaly of silicon in plant biology. *Proc Natl Acad Sci USA* 91:11–17. <https://doi.org/10.1073/pnas.91.1.11>
- Epstein E (1999) Silicon. *Annu Rev Plant Physiol Plant Mol Biol* 50:641–664. <https://doi.org/10.1146/annurev.arplant.50.1.641>
- Greger M, Landberg T, Vaculík M (2018) Silicon influences soil availability and accumulation of mineral nutrients in various plant species. *Plants* 7(2):41. <https://doi.org/10.3390/plants7020041>
- Gunnarsen KC, Schjoerring JK, Gómez-Muñoz B, de Neergaard A, Jensen LS (2022) Can silicon in glacial rock flour enhance phosphorus availability in acidic tropical soil? *Plant Soil*. <https://doi.org/10.1007/s11104-022-05399-0>

- Hodson MJ (2016) The development of phytoliths in plants and its influence on their chemistry and isotopic composition. Implications for palaeoecology and archaeology. *J Archaeol Sci* 68:62–69. <https://doi.org/10.1016/j.jas.2015.09.002>
- Hodson MJ (2019) The relative importance of cell wall and lumen phytoliths in carbon sequestration in soil: A hypothesis. *Front Earth Sci* 7:167. <https://doi.org/10.3389/feart.2019.00167>
- Hodson MJ, Guppy CN (2022) Some thoughts on silicon and carbon trade-offs in plants. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05394-5>
- Hodson MJ, Song Z, Ball TB, Elbaum R, Struyf E (2020) Editorial: Frontiers in phytolith research. *Front Plant Sci* 11:454. <https://doi.org/10.3389/fpls.2020.00454>
- IPCC (2022) Climate Change 2022: Mitigation of climate change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on climate change [P.R. Shukla, J. Skea, R. Slade, A. Al Khourdajie, R. van Diemen, D. McCollum, M. Pathak, S. Some, P. Vyas, R. Fradera, M. Belkacemi, A. Hasija, G. Lisboa, S. Luz, J. Malley, (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA. <https://doi.org/10.1017/9781009157926>
- Johnson SN, Waterman JM, Wuhrer R, Rowe RC, Hall CR, Cibils-Stewart X (2021) Siliceous and non-nutritious: Nitrogen limitation increases anti-herbivore silicon defences in a model grass. *J Ecol* 109:3767–3778. <https://doi.org/10.1111/1365-2745.13755>
- Johnson SN, Powell JR, Frew A, Cibils-Stewart X (2022) Silicon accumulation suppresses arbuscular mycorrhizal fungal colonisation in the model grass *Brachypodium distachyon* *Plant Soil*. <https://doi.org/10.1007/s11104-022-05463-9>
- Katz O (2014) Beyond grasses: The potential benefits of studying silicon accumulation in non-grass species. *Front Plant Sci* 5(376):376. <https://doi.org/10.3389/fpls.2014.00376>
- Katz O, Puppe D, Kaczorek D, Prakash NB, Schaller J (2021) Silicon in the soil–plant continuum: Intricate feedback mechanisms within ecosystems. *Plants* 10:652. <https://doi.org/10.3390/plants10040652>
- Kumar S, Soukup M, Elbaum R (2017) Silicification in grasses: Variation between different cell types. *Front Plant Sci* 8. <https://doi.org/10.3389/fpls.2017.00438>
- Leng MJ, Swann GEA, Hodson MJ, Tyler JJ, Patwardhan SV, Sloane HJ (2009) The potential use of silicon isotope composition of biogenic silica as a proxy for environmental change. *Silicon* 1:65–77. <https://doi.org/10.1007/s12633-009-9014-2>
- Liang Y, Sun W, Yong-Guan Z, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: A review. *Env Pollut* 147:422–428. <https://doi.org/10.1016/j.envpol.2006.06.008>
- Liang Y, Nikolic M, Bélanger R, Gong H, Song A (eds) (2015) Silicon in agriculture. From theory to practice. Springer, Dordrecht. <https://doi.org/10.1007/978-94-017-9978-2>
- Limmer MA, Thomas J, Seyfferth AL (2022) The effect of silicon on the kinetics of rice root iron plaque formation. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05414-4>
- Linam F, Limmer MA, Tappero R, Seyfferth AL (2022) Rice husk and charred husk amendments increase porewater and plant Si but water management determines grain As and Cd concentration. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05350-3>
- Lu X, Qin Z, Lambers H, Tang S, Kaal J, Hou E, Kuang Y (2021) Nitrogen addition increases aboveground silicon and phytolith concentrations in understory plants of a tropical forest. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05236-w>
- Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M (2006) A silicon transporter in rice. *Nature* 440:688–691. <https://doi.org/10.1038/nature04590>
- Mandlik R, Thakral V, Raturi G, Shinde S, Nikolić M, Tripathi DK, Sonah H, Deshmukh R (2020) Significance of silicon uptake, transport, and deposition in plants. *J Exp Bot* 71:6703–6718. <https://doi.org/10.1093/jxb/eraa301>
- Markovich O, Zexer N, Negin B, Zait Y, Blum S, Ben-Gal A, Elbaum R (2022) Low Si combined with drought causes reduced transpiration in sorghum Lsi1 mutant. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05298-4>
- Minden V, Schaller J, Olde Venterink H (2021) Plants increase silicon content as a response to nitrogen or phosphorus limitation: a case study with *Holcus lanatus* *Plant Soil* 462:95–108. <https://doi.org/10.1007/s11104-020-04667-1>
- Mitani-Ueno N, Ma JF (2021) Linking transport system of silicon with its accumulation in different plant species. *Soil Sci Plant Nutr* 67(1):10–17. <https://doi.org/10.1080/00380768.2020.1845972>
- Nakamura R, Amada G, Kajino H, Morisato K, Kanamori K, Hasegawa M (2022) Silicious trichomes as a trait that may slow down leaf decomposition by soil meso- and macrofauna. *Plant Soil* 471:289–299. <https://doi.org/10.1007/s11104-021-05223-1>
- Ning C, Wang L, Liu R, Pan T, Cai Y, Tian J, Luo S, Cai K (2021) Plant-mediated rhizospheric interactions in rice and water spinach intercropping enhance Si uptake by rice. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05199-y>
- Parr JF, Sullivan LA (2005) Soil carbon sequestration in phytoliths. *Soil Biol Biochem* 37:117–124. <https://doi.org/10.1016/j.soilbio.2004.06.013>
- Pavlovic J, Kostic L, Bosnic P, Kirkby EA, Nikolic M (2021) Interactions of silicon with essential and beneficial elements in plants. *Front Plant Sci* 12:697592. <https://doi.org/10.3389/fpls.2021.697592>
- Piperno DR (2016) Phytolith radiocarbon dating in archaeological and paleoecological research: a case study of phytoliths from modern Neotropical plants and a review of the previous dating evidence. *J Archaeol Sci* 68:54–61. <https://doi.org/10.1016/j.jas.2015.06.002>
- Puppe D, Sommer M (2018) Experiments, uptake mechanisms, and functioning of silicon foliar fertilization. A review focusing on maize, rice, and wheat. *Adv Agron* 152:1–49. <https://doi.org/10.1016/bs.agron.2018.07.003>
- Putra R, Waterman JM, Mathesius U, Wojtalewicz D, Powell JR, Hartley SE, Johnson SN (2022) Benefits of silicon-enhanced root nodulation in a model legume are contingent upon rhizobial efficacy. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05358-9>
- Quigley KM, Griffith DM, Anderson TM (2020) Soil nutrients and precipitation are major drivers of global patterns of

- grass leaf silicification. *Ecology* 101:e03006. <https://doi.org/10.1002/ecy.3006>
- Raven JA (1983) The transport and function of silicon in plants. *Biol Rev* 58:179–207. <https://doi.org/10.1111/j.1469-185X.1983.tb00385.x>
- Reyerson PE, Alexandre A, Harutyunyan A, Corbineau R, De La Martinez HA, Badeck F, Cattivelli L, Santos GM (2016) Unambiguous evidence of old soil carbon in grass biosilica particles. *Biogeosciences* 13:1269–1286. <https://doi.org/10.5194/bg-13-1269-2016>
- Rezakhani L, Moteszarehadeh B, Tehrani MM, Etesami H, Hosseini HM (2022) The effect of silicon fertilization and phosphate-solubilizing bacteria on chemical forms of silicon and phosphorus uptake by wheat plant in a calcareous soil. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05274-4>
- Santos GM, Masion A, Alexandre A (2018) When the carbon being dated is not what you think it is: Insights from phytolith carbon research. *Quat Sci Rev* 197:162–174. <https://doi.org/10.1016/j.quascirev.2018.08.007>
- Schaller J, Puppe D, Kaczorek D, Ellerbrock R, Sommer M (2021) Silicon cycling in soils revisited. *Plants* 10(2):295. <https://doi.org/10.3390/plants10020295>
- Schaller J, Puppe D, Busse J, Paasch S, Katz O, Brunner E, Kaczorek D, Sommer M (2022) Silicification patterns in wheat leaves related to ontogeny and soil silicon availability under field conditions. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05385-6>
- Schoelynck J, Bal K, Backx H, Okruszko T, Meire P, Struyf E (2010) Silica uptake in aquatic and wetland macrophytes: a strategic choice between silica, lignin and cellulose? *New Phyt* 186:385–391. <https://doi.org/10.1111/j.1469-8137.2009.03176.x>
- Sebastian D, Rodrigues H, Kinsey C, Korndörfer G, Pereira H, Buck G, Datnoff L, Miranda S, Provance-Bowley M (2013) A 5-day method for determination of soluble silicon concentrations in nonliquid fertilizer materials using a sodium carbonate-ammonium nitrate extractant followed by visible spectroscopy with heteropoly blue analysis: single-laboratory validation. *J AOAC Int* 96(2):251–259. <https://doi.org/10.5740/jaoacint.12-243>
- Song Z, Wu Y, Yang Y, Zhang X, Van Zwieten L, Bolan N, Li Z, Liu H, Hao Q, Yu C, Sun X, Song A, Wang W, Liu C, Wang H (2022) High potential of stable carbon sequestration in phytoliths of China's grasslands. *Glob Chang Biol* 28:2736–2750. <https://doi.org/10.1111/gcb.16092>
- Teixeira GCM, de Mello Prado R, de Oliveira LT, de Castro Souza JV, Rocha AMS (2022) Silicon fertilization with appropriate source reduces water requirement of maize under water deficit. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05446-w>
- Tripathi DK, Singh VP, Lux A, Vaculik M (2020) Silicon in plant biology: from past to present, and future challenges. *J Exp Bot* 71:6699–6702. <https://doi.org/10.1093/jxb/eraa448>
- Tubana BS, Babu T, Datnoff LE (2016) A review of silicon in soils and plants and its role in US agriculture: history and future perspectives. *Soil Sci* 181:393–411. <https://doi.org/10.1097/SS.0000000000000179>
- Wade RN, Donaldson SM, Karley AJ, Johnson SN, Hartley SE (2022) Uptake of silicon in barley under contrasting drought regimes. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05400-w>
- Zellner W, Friedrich RL, Kim S, Sturtz D, Frantz J, Altland J, Krause C (2015) Continuing assessment of the 5-day sodium carbonate-ammonium nitrate extraction assay as an indicator test for silicon fertilizers. *J AOAC Int* 98(4):890–895. <https://doi.org/10.5740/jaoacint.14-205>
- Zhou J, Tang S, Pan W, Xiao H, Ma Q, Sun Y, Xu M, Liu M, Wu L (2022) Silicon isotope fractionation dynamics during uptake and translocation by various crop species under three soil types. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05264-6>
- Zuo X, Lu H (2019) Phytolith radiocarbon dating: A review of previous studies in China and the current state of the debate. *Front Plant Sci* 10:1302. <https://doi.org/10.3389/fpls.2019.01302>
- Zurro D, Hodson MJ (2018) Phytoliths in European archaeological research. In: Smith C (ed.) *Encyclopedia of Global Archaeology*. Springer International Publishing AG, New York. https://doi.org/10.1007/978-3-319-51726-1_3355-1

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