



eXtra Botany

Special Issue Editorial

Silicon in plant biology: from past to present, and future challenges

Silicon (Si) is the second most abundant element in the Earth's crust after oxygen, and it has wide implications in plant biology. The effects of Si range from regulation of development to protection of plants from various types of stresses. In recent years, much progress has been made in research on the uptake of Si at the root surface, its loading into the xylem, and its transport to various tissues in Si-accumulating plants. However, much still remains to be discovered. For instance, there is currently no direct evidence for the participation of Si in plant metabolism, and little detail is known of the mechanisms by which Si functions in plants. In this special issue, we present a collection of papers that attempt to answer such questions, but we are still a long way from fully understanding the role of Si in plant biology.

Silicon research in past years

It has long been known that Si has beneficial effects on plants, and research in the early 20th century identified its potential for use as a plant growth supplement. Prior to that, [Lupton \(1880\)](#) noted its accumulation in wheat, corn, and grasses and suggested its presence was beneficial to the plants. [Sommer \(1926\)](#) demonstrated enhanced growth of rice and millet in the presence of Si, and found that seed heads of millet grown in its absence were more severely infected by pathogenic fungi. Beet production was found to increase by 44% in acid soils with high aluminum content when treated with calcium silicate slag as a liming agent as compared with calcium hydroxide ([Raleigh, 1939](#)), and it was also observed that roots became necrotic and were infected with fungus in the absence of Si. In the second half of the 20th century, several studies using either pot-grown plants or hydroponics documented positive effects of Si in increasing yields and improving plant resistance to biotic and abiotic stresses (e.g. [Woolley, 1957](#); [Bollard and Butler, 1966](#); [Lewin and Reimann, 1969](#)). [Jones and Handreck \(1967\)](#) provided a detailed account of the importance of Si in agriculture, and plant physiology and pathology; indeed, there was a discussion as to whether it should be included in the list of essential elements, if not for all plants in general then at least for certain species such as horsetail and sugarcane ([Chen and Lewin, 1969](#); [Fox and Silva, 1978](#)). The last decades of the

20th century through to the present time might be regarded as a 'golden era' of Si research. Several studies have demonstrated the importance of Si in crop resistance to pathogens, pests, and various kinds of abiotic stresses, and there has been a focus of research on Si management in sustainable crop production and its roles in plant life (e.g. [Epstein, 1994](#); [Birchall, 1995](#); [Hodson and Evans, 1995](#); [Datnoff *et al.*, 1997](#); [Hattori *et al.*, 2005](#); [Mitani and Ma, 2005](#)). This interest in Si is reflected by the increasing number of papers that have been published on the topic in recent decades ([Fig.1](#)). This has been driven by a desire to better understand its role in plants combined with the increasing availability of improved technical methods and approaches for its detailed study.

Recent progress and breakthroughs in silicon research

Recent decades have brought a considerable increase in our knowledge regarding the uptake and translocation of Si in plant tissues. The breakthrough discovery of the first Si transport-channel protein, Lsi1, in rice published by [Ma *et al.* \(2006\)](#) prompted a search for Si transport mechanisms in other plant species. Our knowledge of Si-uptake pathways has thus been considerably improved in the last 15 years, and this progress is reviewed by [Mandlik *et al.* \(2020\)](#) in this special issue. Silicon is taken up from the soil solution in the form of silicic acid ([Epstein, 1994](#)) and enters cells through channel-type membrane proteins called aquaporins ([Ma and Yamaji, 2015](#); [Deshmukh and Bélanger, 2016](#)). Recent novel findings have been made regarding aquaporins belonging to the nodulin 26-like intrinsic protein group III (NIP-III), which are considered to play a major role in plant Si uptake. [Deshmukh *et al.* \(2020\)](#) suggest that the aromatic/arginine (ar/R) selectivity filter of the NIP-IIIs does not need to be exclusively composed of the sequence Glycine-Serine-Glycine-Arginine (G-S-G-R), and some amino acids positions seem to be less conserved. However, they suggest that the change of NPA to NPV or an alternative motif structure does not play such an important role as has previously been believed. Instead, the spacing of 108 amino acids between two NPA motifs appears to be one of the most conserved and important features with respect to Si permeability. [Deshmukh *et al.* \(2020\)](#) also conduct a comprehensive genomic analysis of

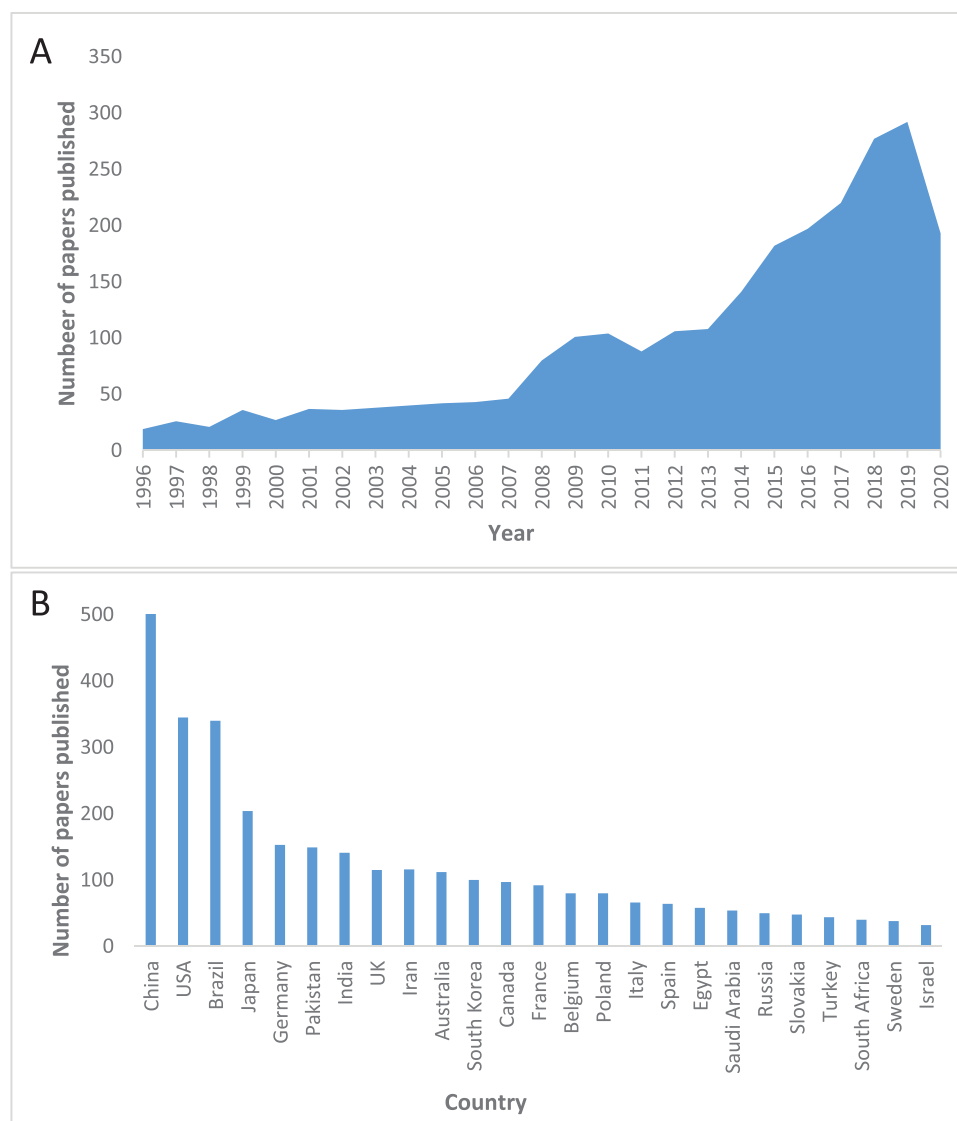


Fig. 1. The number of papers focused on Si research related to plants in the last 25 years (A) and their countries of origin according to corresponding author (B), as listed in the Web of Science (data from August 2020).

aquaporins from over a thousand plants species, which reveals that the evolution of NIP-IIIs as primary Si influx transporters dates back as early as 515 million years ago. This confirms previous assumptions that Si accumulation has been an important feature of land plants right from the time at which they left the aquatic environment. They also rule out the traditional accepted opinion that monocots generally take up more Si than dicots. Based on their results, species from several dicot families including the Cucurbitaceae, Fabaceae, and Ateraceae, accumulate considerably higher amount of Si compared with many monocots outside the Poaceae family.

In recent years, channels and proteins involved in Si membrane permeability have been recorded in many monocot as well as dicot species (e.g. Yamaji *et al.*, 2012; Bokor *et al.*, 2019; Zellner *et al.*, 2019). In this special issue, Noronha *et al.* (2020) report that there is an active Si uptake transport system in a species of agricultural importance, namely grapevine. They find that *VvNIP2;1* is mostly expressed in roots and also in green berries, it is localized in the plasma membrane, and it

codes for functional aquaporin that is able to transport Si as well as arsenite. It has been a matter of debate as to how silicic acid is transported within plants, but it is believed that Si is transported via the xylem to the aerial parts. In common with other compounds and elements, Si needs to cross (so-called) apoplasmic barriers (mostly Casparian bands and suberin lamellae) to enter the central cylinder and xylem veins. In this regard, it has been shown that Si can influence the deposition of lignin and suberin within the root exo- and endodermis and thereby modify plant metal(loid) uptake (e.g. Vaculik *et al.*, 2020). However, Kreszies *et al.* (2020) note that controversies exist, as both enhanced as well as delayed formation of root apoplasmic barriers in response to Si have been described in the literature. In their own experiments with barley grown under control and osmotic stress conditions, they found no direct effect of Si and suggest that enhanced stress tolerance of plants after Si treatment is due to other responses. Silicon is deposited as amorphous silica in various organs and cells (Mandlik *et al.*, 2020). With regards to the roots, the endodermis has been

identified as a site of elevated deposition in various species, and particularly in sorghum (e.g. [Lux et al., 2020](#)). This special issue includes a series of studies describing the mechanisms of Si phytolith formation and silica precipitation in sorghum roots and leaves. [Soukup et al. \(2020\)](#) find that the process of Si phytolith deposition within the root endodermis is strictly associated with living and fully metabolic active cells, whilst [Zexer and Elbaum \(2020\)](#) suggest that polymerization of silicic acid occurs only at specific locations in the tangential endodermis cell walls where modification of lignin is present in the form of a lack of ferulic acid. Finally, [Kumar et al. \(2020\)](#) describe a unique protein in sorghum leaves that is responsible for silica precipitation, which they name as Siliplant1 (Slp1). They find that Slp1 is present in developing silica cells and that it is transported to the cell wall during silicification.

The ameliorative effects of Si on metal toxicity are a well-known phenomenon, and many papers documenting its positive role have been previously published. Much research has focused on Al, which follows Si as the third most abundant element in the Earth's crust ([Epstein, 1994](#)). In this special issue, [Hodson and Evans \(2020\)](#) review the last quarter-century of research in plant Si–Al interactions, providing an update to their review on the same topic that was published in this journal 25 years ago ([Hodson and Evans, 1995](#)). As they note, our knowledge has greatly improved in certain areas, especially in our understanding of Si and Al uptake and transport mechanisms at the molecular level, and some hypothesis regarding the amelioration of Al toxicity by binding with Si in the apoplast have now been confirmed. However, a comprehensive understanding of a number of processes is still lacking, and the authors question why so little effort has been made in investigating the amelioration of Al toxicity in edible plants. The interactions of Si with other metals as well as metalloids is also the focus of another review by [Vaculik et al. \(2020\)](#). Whilst some elements already interact with Si in the soil and in the rhizosphere, important mitigation processes also occur on various levels inside the plant. Co-deposition in the apoplast, as occurs with Al, has also been documented for cadmium. [Vaculik et al. \(2020\)](#) identify a number of gaps in our knowledge that need to be addressed if we are to properly understand how Si-based mechanisms alleviate metal(loid) toxicity. More broadly, [Ahanger et al. \(2020\)](#) review the role of Si in stress tolerance in affecting the synthesis of plant defense enzymes and in the integration of secondary metabolites.

Another beneficial application of Si might be its use in increasing resistance against various pathogens and herbivores. It is well known that plants that actively take up relatively high levels of Si are more resistant to pests and diseases. In their review in this special issue, [Singh et al. \(2020\)](#) consider both direct aspects of resistance to plant herbivory that are induced by Si, such as strengthening mechanical protection and the synthesis of antioxidant enzymes, and indirect modes of resistance, such as the release of volatiles and alterations in the synthesis of defense-related hormones. A better understanding of the role of Si in host–pathogen interactions is clearly desirable. [Rasoolzadeh et al. \(2020\)](#) show that Si might help to create an unfavorable environment for pathogens in the apoplast and it probably interferes with host-recognition and/or limits

receptor–effector interactions, leading to an incompatible interaction between the pathogen and the host. We currently live in an era in which more environmentally friendly solutions are sought for agricultural problems, and in this context Si might provide a good tool for the improvement of resistance to pests and diseases, not only in cereals but also in other crop species.

Perspectives and future challenges for silicon in plant biology

Whilst the papers included in this special issue highlight our current knowledge about the uptake, translocation, deposition, and functioning of Si in plants, there are still many questions that remain to be answered, some of which are very fundamental. For instance, we do not know or have only limited knowledge about how Si is loaded into the xylem or the identity of the transporter that pumps Si to silica cells, and at a basic level we do not really know how Si provides such versatile benefits to plants. To date, there have been no reports showing an active role of Si in any biochemical and metabolic pathway that can define the benefits that the plant receives from supplementation with Si. Similarly, we have only limited information regarding the optimum quantities of Si that are needed for better plant growth at individual developmental stages. Hundreds of studies have reported beneficial effects of supplying Si to poor Si-accumulator species, which is hard to explain with our current level of understanding. As well as our lack of knowledge about the structural and functional characteristics of Si transport proteins, other unanswered questions include the role of Si in interactions with signaling molecules under normal as well as stress conditions, its impact on the uptake of nutrients, its influence on the photosynthetic machinery, and its role in the integration of phytohormones. A better understanding of Si biology will provide benefits in many different fields, including agriculture, industrial applications, and ecology. Collaborative research through organizations such as the Society for Silicon in Agriculture and Related Disciplines (ISSAG) should be encouraged to achieve this aim.

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