



Potential role of silicon (Si) to promote plant defense mechanism against insect Herbivores

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Abstract

Silicon (Si) played a major role in plant growth, mechanical strength and resistance to biotic and abiotic stresses. It has been recently identified that, Si relating to plant physiology, plant chemistry and gene regulation mechanism. Silicon has received great attention as a nutrient capable of providing some measure of defense for plants against insectpests, fungal pathogens and herbivores. The beneficial effects of Si are usually expressed more clearly in Si-accumulating plants under various abiotic and biotic stress conditions. On the basis of a study including two generalist insectfolivores and a phloem feeder have drawn attention to a putative distinction between the effects of plant Si in defending against folivores and phloem-feeding insects. Plant resistance to herbivores is a crucial component in integrated pest management. Silicon application to plants enhances resistance mechanism which is observed in most of the cases to herbivorous insects.

Keywords: silicon, insect pests, biotic and abiotic stresses, folivores, herbivores

Introduction

Silicon (Si) is the second most abundant element in earth crust. Availability of Si is not lacking in soil, but in plant available form is limiting. In soil solution, Si occurs mainly as monosilicic acid (H_4SiO_4) at concentrations ranging from 0.1 to 0.6 mM and is taken up by plants in this form. All terrestrial plants contain Si in their tissues although the content of Si varies considerably with the species, ranging from 0.1 to 10% Si on a dry weight basis (Ma and Takahashi, 2002) [19]. However, Si has not been recognized as an essential element for plant growth. The major reason is that there is no evidence to show that Si is involved in the metabolism of plant, which is one of the three criteria required for essentiality established by Arnon and Stout (1939) [1]. However, recently, Epstein and Bloom (2003) [4] have reconsidered this definition of essentiality and proposed a new definition of elements that are essential for plant growth: An element is essential if it fulfills either one or both of two criteria, viz. (1) the element is part of a molecule which is an intrinsic component of the structure or metabolism of the plant, and (2) the plant can be so severely deficient in the element that it exhibits abnormalities in growth, development, or reproduction, i.e. "performance," compared to plants with a lower deficiency. According to this new definition, Si is an essential element for higher plants because Si deficiency causes various abnormalities in the plant, as reported in a number of reviews (Ma and Takahashi, 2002) [19]. Several beneficial effects of Si have been reported, including increased photosynthetic activity, increased insect and disease resistance, reduced mineral toxicity, improvement of nutrient imbalance, and enhanced drought and frost tolerance.

Insect herbivores represent one class of biotic stressors that Si can provide some defence against; however, in comparison with plant diseases, their interaction with plant Si has been little explored. In particular, elucidation of the

mechanism (s) of Si-mediated plant resistance to insect herbivores has largely addressed the dominant hypothesis of a Si barrier providing mechanical resistance to insect feeding and/or plant penetration (Kvedaras and Keeping, 2007) [14]. Massey *et al.* (2006) [22] recently demonstrated that provision of Si increased abrasiveness of the leaves of four of five grass species studied, while changing the relative palatability of the grasses, deterring feeding, and reducing the growth rates and feeding efficiency of two generalist insect folivores, *Spodoptera exempta* (Lepidoptera) and *Schistocerca gregaria* (Orthoptera). It has been demonstrated that Si amendment to plants can afford substantial protection from herbivorous damage by enhancing plant resistance. Si amendment enhances plant resistance to herbivores through constitutive defense and/or induced defense. Enhanced constitutive defense is believed to be a result of increased rigidity and reduced digestibility of plant tissues due to additional amorphous silica deposition in Si amended plants (Massey and Hartley, 2009) [21]. Si-mediated resistance may also be realized through priming chemical defense in plants and augmented release of herbivore-induced plant volatiles that attract natural enemies of the attacking pests (Kvedaras, 2010) [14]. Herbivorous feeding usually induces a battery of chemical defense responses in plants, on which Si is reported to play a role. As one of the physiological responses to herbivory, malondialdehyde (MDA) usually experiences increase in concentration and has been extensively used as a biomarker of the degree of cell membrane damage. The rapid and transient production of reactive oxygen species (ROS) by the plant, particularly H_2O_2 , in the early phase of plant responses to biotic stress activates an array of plant defense mechanisms. Antioxidant enzymes, superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD), which are important in maintaining a balance of ROS, are shown to be activated more in Si-amended than in non-amended infested

plants (Ma, 2004) [18].

Silicon-induced chemical defenses in plants

While increased mechanical resistance is thought to be the major mechanism whereby Si defends plants against insect attack, there is increasing evidence of an active role for soluble Silicon. Gomes *et al.* (2005) [6] found that the plant’s defence system was activated by previous infestation with aphids, Si fertilization, or both, which negatively affected green aphid preference and population increase rate, while increasing activities of three enzymes involved in induced defence responses in plants (Karban and Baldwin, 1997) [10]. Si-induced resistance to the phloem feeder *Bemisia tabaci* (Hemiptera) in cucumber was identical in all parameters measured to that produced by benzothiadiazole (BTH), a synthetic analogue of the natural plant elicitor, salicylate (Correa *et al.*, 2005) [3].

Si amendment to rice (*Oryza sativa*) plants impacts multiple plant defense responses induced by a phloem-feeder, the brown planthopper (*Nilaparvatalugens*, BPH). Si amendment improved silicification of leaf sheaths that BPH feed on. Si addition suppressed the increase of malondialdehyde concentration while encouraged increase of H₂O₂ concentration in plants attacked by BPH. Higher activities of catalase and superoxide dismutase were recorded in Si-amended than in non-amended BPH-infested plants. BPH infestation activated synthases for secondary metabolites, polyphenol oxidase and phenyl-lalanine ammonia-lyase, and β-1, 3-glucanase, but the activation was greater in Si-amended than in non-amended plants. Taken together, our findings demonstrate that Si amendment interacts with BPH infestation in the induction of plant defense responses and consequently, to confer enhanced rice plant resistance (Lang *et al.*, 2017) [17]. Polyphenol oxidase (PPO) and phenyl-lalanine ammonia-lyase (PAL), catalyzing the synthesis of herbivore resistant secondary metabolites (lignin and phenols) (Fig-1), show changes in activities similar to the antioxidant enzymes in response to Si amendment and herbivorous attack, although recent reports indicate a positive relationship between root herbivore performance and root phenolic concentrations (Johnson and Nielsen, 2012) [9].

Effect of Silicon on plant herbivores

Silicon suppresses insect pests such as stem borer, brown planthopper, rice green leafhopper, and white backed planthopper, and non-insect pests such as leaf spider and mites (Savant *et al.*, 1997) [26]. Stems attacked by the rice stem borer were found to contain a lower amount of Si (Sasamoto, 1961) [25]. Borers feeding on Si-fertilized rice or highly siliceous rice varieties showed typical effects of antibiosis, such as decreased survival, and in some cases worn mandibles indicating reduced feeding efficiency due to Si (Ukwungwu and Odebiyi, 1985) [29]. Setamou *et al.* (1993) found that Si applied to maize reduced larval survival, percentage pupation and adult emergence in *Sesamia calamistis* (Lepidoptera). Recently, Keeping and Meyer (2002, 2006) [13] showed that treatment of sugarcane with Si significantly reduced survival of *Eldanasaccharina* (Lepidoptera) larvae, while further studies found that Si treatment reduced the growth rate of individual *E. saccharina* larvae and delayed penetration of the sugarcane stalk by third instar larvae (Kvedaras *et al.*, 2007) [15].

Brazilian researchers recently found that the adverse effects

of plant Si on phloem feeders, *Schizaphis graminum* (Aphididae) had reduced preference for, and lower longevity and fecundity on, leaves from wheat plants fertilized with sodium silicate solution. Reduced preference of *S. graminum* for Si-treated sorghum and of *Rhopalosiphum maidis* (Aphididae) for Si-treated maize was recorded by Moraes *et al.* (2005) [3]. As epidermal resistance of wheat to stylet penetration and ability of *Sc. graminum* to reach the phloem vessels was not affected by silicon application, a mechanical barrier of opaline Si in the leaf epidermal cells was not supported. However, Si application did induce aphids to withdraw their stylets more frequently, resulting in decreased probing time (Goussain *et al.*, 2005) [6].

Two hypotheses for the Si-enhanced resistance to diseases and pests have been proposed. One is that Si deposited on the tissue surface acts as a physical barrier (Fig-2). It prevents physical penetration and / or makes the plant cells less susceptible to enzymatic degradation by fungal pathogens. This mechanism is supported by the positive correlation between the Si content and the degree of suppression of diseases and pests. The other one is that Si functions as a signal to induce the production of phytoalexin (Cherif *et al.*, 1994) [2].

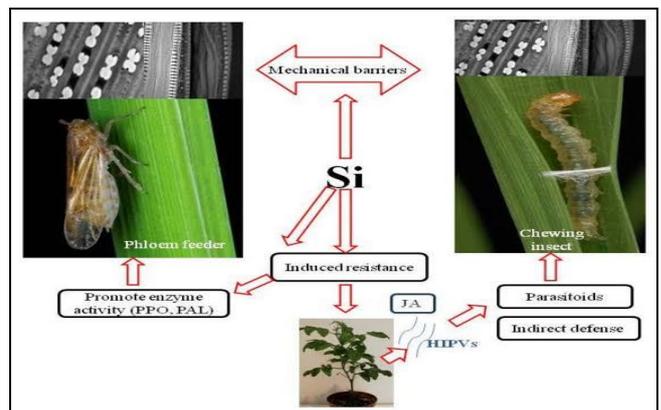


Fig 1: Silicon mediated mechanisms of plant resistance to insect pests. (PPO) polyphenol oxidase, (PAL) phenylalanine ammonia lyase, (HIPVs) herbivore-induced plant volatiles, (JA) jasmonatephytohormone (Fadi and Maria, 2018) [5].

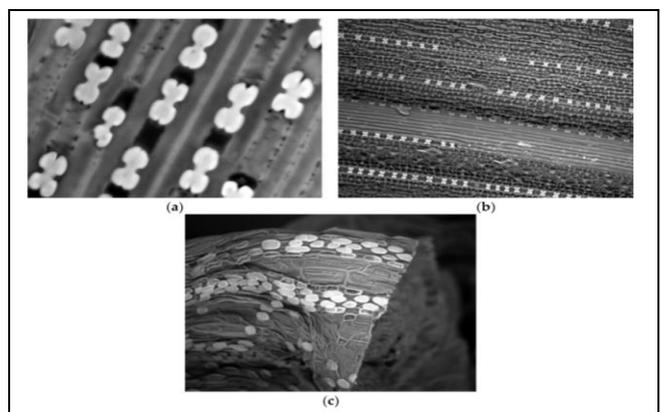


Fig 2: Scanning electron micrographs of maize (a); rice (b); and wheat (c) sheath surfaces showing silica cell form and deposition. (Fadi and Maria, 2018) [5]

Plant defense study through “OMICS” Technologies

To understand properly, how the application/amendment of Silicon to plants can improve the defense mechanism, plant

as a whole must be considered through global analysis of the major responsive components of the DNA, RNA, proteins, and metabolites which are then holistically viewed using bioinformatics (Figure 3). While system-wide analysis has long been applied to plants, their application to analyzing plant defense has been limited (Duceppe *et al.*, 2012; Timbo *et al.*, 2014) and analyzing silicon's role even more so. Transcriptome analysis represents the only -omic analysis of silicon's effects, with a study on challenged *A. thaliana* showing silicon treatment causes a decrease in primary metabolism that allows a more efficient defense response. Silicon's role in defense against herbivores remains vastly under studied by-omics method logies which would reveal the role of, as yet, untargeted molecules, including proteins and metabolites, through global analysis.

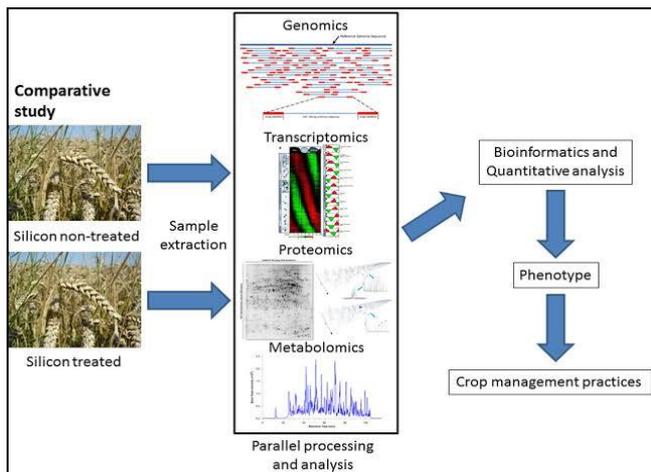


Fig 3

Figure 3: The workflow for the application of-omics technology to quantify phenotypic changes in plants due to silicon treatment. In a comparative study, parallel samples are grown under laboratory conditions or in the field with one subject to silicon treatment. After the application of appropriate sample extraction techniques to obtain mRNA (Transcriptomics), proteins (Proteomics) or metabolites (Metabolomics) in an unbiased and comprehensive manner, the samples are subjected to parallel analysis to obtain a comprehensive dataset of the transcriptome, proteome, and metabolome. These datasets are then analyzed in bioinformatic pipelines to identify the components and quantify the differences in abundance of specific mRNAs, proteins or metabolites, which can then be related to phenotypic changes in the plant, such as resistance to a herbivore or pathogen. This information can then be utilized in crop management practices (Olivia *et al.*, 2016) [24].

Conclusions

Silicon is likely to be as important in resistance to phloem (and xylem) feeding insects as in resistance to folivores (or to borers). It is obvious that most of the effects of Si were expressed through Si deposition on the leaves, stems, and hulls. The more Si accumulated in the shoots, the larger the effect. However, Si accumulation in the shoot varies considerably with the plant species and most plants are unable to accumulate high levels Si in the shoots. The difference in Si accumulation was attributed to the ability of the roots to take up Si. Therefore, although Si is abundant in soil, since most plants especially dicots are unable to take up

a large amount of Si from soil, they do not benefit from Si. One approach to enhance the resistance of plants to multiple stresses, is to genetically modify the Si uptake ability (Jian, 2004) [8]. Despite past efforts to raise awareness of the importance of Si coupled with selected recent findings on its role in gene regulation in plant development and defence, many plant scientists remain indifferent to or unaware of the potential roles of this interesting and unique element. So it is necessary to properly understand the physiological and molecular role of silicon in plants through multidisciplinary studies for the development of durable resistance in plants. Modern approaches of transcriptomics, proteomics, metabolomics, and transgenic mutants will serve as powerful tools for dissecting the underlying mechanism/s involved in silicon and plant defense. In an era when sustainable pest management is receiving more attention than ever before, due largely to restrictions or the withdrawal of toxic pesticides, because of their negative impacts on human and environmental health, silicon treatment should be more widely considered and tested as a pest management option.

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