Crop Protection 104 (2018) 21–34

Contents lists available at ScienceDirect

Crop Protection

journal homepage: www.elsevier.com/locate/cropro

Silicon mitigates biotic stresses in crop plants: A review

Hafiz Faiq Bakhat[a,*], Najma Bibi[a], Zahida Zia[a], Sunaina Abbas[a], Hafiz Mohkum Hammad[a], Shah Fahad[b,e,**], Muhammad Rizwan Ashraf[c], Ghulam Mustafa Shah[a], Faiz Rabbani[a], Shafqat Saeed[d]

[a] Department of Environmental Sciences, COMSATS Institute of Information Technology, Vehari 61100, Pakistan
[b] Department of Agriculture, University of Swabi, Khyber Pakhtunkhwa, Pakistan
[c] Department of Entomology, University of Agriculture Faisalabad (Burewala/Vehari-sub Campus), Pakistan
[d] Department of Entomology, Muhammad Nawaz Shareef University of Agriculture, Multan, Pakistan
[e] College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei, China

ARTICLE INFO

Keywords:
Silicon
Pest
Plants
Physical defense
Chemical defense
Pesticide
Integrated strategy

ABSTRACT

Silicon (Si) is the second most abundant element in the lithosphere. Soils commonly contain as much as 30% Si, the majority of which is found in minerals and rocks. In plants, the element Si is recognized as a “beneficial quasi-essential” mineral nutrient. It is taken up by the plant roots and trans-located to aerial parts through transpiration streams. Naturally, its accumulation in aerial parts augments its polymerization in the intercellular spaces and beneath the cuticles creates a barrier against pathogen attack. Moreover, soluble Si in the cytosol triggers various metabolic pathways that result in the production of jasmonic acid and herbivore induced plant organic compounds. Combination of these Si-mediated physical and biochemical processes enhances plant defenses against biotic stresses (insects, fungus and bacteria). In addition, soluble Si in the plant system attracts natural predators and parasitoids during pest attack and consequently increases biological control. Although, a large set of data shows that Si provides natural defense against pest attack, application of Si as a pest control agent has not gained much attention from the scientists, policy makers and farming communities. Here, current knowledge regarding Si-mediated plant defense to pest attack is reviewed. Si-application tends to reduce pest infestations and may provide a sustainable environment friendly integrated strategy as an alternative to extensive pesticide use.

1. Introduction

Plant growth depends on various mineral nutrient elements present in the soil. These can be categorized into essential, beneficial and toxic elements (Bienert et al., 2008). Essential elements are critical for all plants in different growth conditions while, toxic elements disrupt various metabolic processes and negatively affect plant growth. Beneficial elements are vital for some specific plant species growing under certain environmental conditions. Although each and every plant contains silicon (Si), its essentiality is not proven yet because concrete evidences are lacking on the biochemical and physiological role of Si in plant biology. Various studies have shown that plants fertilized with Si have higher biomass production compared with non-Si-fertilized plants. The useful effects of Si on different plant species are well documented (Ma and Takahashi, 2002; Datnoff et al., 2001). Conversely, many researchers have also documented the beneficial effects of exogenous Si under various biotic and abiotic conditions on plant growth (Zia et al., 2017; Liang et al., 2007). In plants, a relatively higher quantity of Si is found than many other essential macronutrients such as calcium, magnesium and phosphorus. Grasses even may contain higher levels of Si than any of the other inorganic mineral nutrients. The concentrations of Si in various plants differ depending on genotype and species of a plant owing to differences in the Si uptake mechanism of the plant. Furthermore, Si transportation follows passive as well energy-dependent pathways. Low temperatures and some metabolic processes limit Si transportation (Sahebi et al., 2015). Although plants are able to survive with very low Si availability under greenhouse or some controlled laboratory conditions, Si-deprived plants are often structurally weaker than Si-rich plants. They show some abnormalities in growth, development, and reproduction (Rafi et al., 1997). Plants deficient in Si are more prone to abiotic stresses such as drought, metal toxicities, salinity, and nutrient deficiency (Bakhat et al., 2017; Datnoff et al.,

* Corresponding author.
** Corresponding author. Department of Agriculture, University of Swabi, Khyber Pakhtunkhwa, Pakistan.
E-mail addresses: faiqsiddique@ciitvehari.edu.pk (H.F. Bakhat), shah.fahad@mail.hzau.edu.cn, shah_fahad80@yahoo.com, shahfahad@uoswabi.edu.pk (S. Fahad).

http://dx.doi.org/10.1016/j.cropro.2017.10.008
Received 16 March 2017; Received in revised form 7 October 2017; Accepted 11 October 2017

Table 1
Different sources of silicon fertilizers along with their total Si content and chemical composition (Tubaña and Heckman, 2015).

Source	Chemical composition	Silicon contents (%)	References
Rice hull fresh	SiO_2	7–9.2	Sun and Gong (2001)
Rich hull ash	SiO_2	> 28.0	Kalapathy et al. (2002)
Wollastonite	$CaSiO_3$	24.2	Haynes et al. (2013)
Silicic acid	H_4SiO_4	36.0	Sebastian et al. (2013)
Iron/steel slag	$CaSiO_3$	5.4	Haynes et al. (2013)
Silica gel	Not known	46.7	Sebastian et al. (2013)
Talc ($MgSiO_3$)	$MgSiO_3$	28.5	Sebastian et al. (2013)
Electric furnace slag	$CaSiO_3/MgSiO_3$	21.1	Sebastian et al. (2013)
Fly ash	Not known	29.1	Haynes et al. (2013)
Miscanthus biochar	SiO_2	38.3	Houben et al. (2014)
Quartz sand (finely ground)	SiO_2	46	Meena et al. (2014)
Potassium silicate	K_2SiO_3	18	Meena et al. (2014)
Sodium silicate	Na_2SiO_3	23	Meena et al. (2014)
Calcium silicate	Ca_2SiO_3	24	Meena et al. (2014)

2001). They are also more susceptible to diseases, phytophagous herbivores including phloem feeders (Epstein, 1999). Epstein and Bloom (2005) stated that Si is necessary for plant growth and survival and therefore it should be allocated the status of "quasi-essential".

Herbivore plant interaction can be explained in three ways; 1) Plant traits or characteristics that results in insect mortality and/or reduced growth when the insect uses host-plant for food is termed as "Antibiosis" 2) Plant traits that change the behavior of insect pests towards the plants so that the insect prefers to avoid the plant as its host is called "Antixenosis or non-preference" while 3) the plant ability to regrow and repair the losses due to insect injury are referred to as "Tolerance". The term tolerance is more or less independent of the behavior of the insect towards the host (Kogan and Ortman, 1978). This study deals with antibiosis and antixenosis (non-preference) mechanisms of plant against arthropods caused by the presence of Si.

A wide range of heterotrophic organisms use plants as the sole source of nutrients and cause diseases in their hosts. Physical barriers in the form of rigid cell walls and waxy cuticular layers may act as deterrents and provide some protection against phytopathogens. Similarly, Si deposition in plants may increase the plants adaptability to biotic stresses through physical and chemical defenses. Silica deposition in plant leaves increases the roughness, and number of spines and hairs on above-ground plant parts, which limit the damage by the pests (Massey and Hartley, 2009; Massey et al., 2007). For example, the Si layer on the leaf sheath is thought to be a more important physical defense than chemical defenses in deterring herbivory in grasses (Garbuzov et al., 2011). Integration of Si in the cell walls of leaves increases the mechanical barrier which inhibits insect damage (Kvedaras and Keeping, 2007; Massey et al., 2006). Moreover, Si presence in the leaf tissues changes the feeding preference of herbivores. Kvedaras et al. (2007) observed that insects fed on Si-rich diet results in reduced digestive efficiency and growth. Scientists proposed two mechanisms by which Si reduces herbivore damage. First, leaf abrasiveness could increase the wear and tear of insects/pest mandibles (Lucas et al., 2000; Vicari and Bazely, 1993). Second, Si could decrease the digestibility of foods (Calandra et al., 2016; Massey et al., 2006). Reasons that contribute to the reduced feeding efficiency on Si-rich diet may include; i) the silica layer acts as a physical barrier and prevents access to nitrogen and other metabolites within leaves (Vicari and Bazely, 1993); ii) mastication of leaf material is reduced, therefore, much nitrogen is not released from plant tissues; iii) or the physical damage to the digestive tracts of herbivores due to silica, thus reducing digestive efficiency. A recent study proved that *Tuta absoluta* (Meyrick) reared on tomato plants show decreased larval and pupal survival when they are fed with Si-treated plants because the plants badly affect the midgut and mandibles of the insect. The morphology of the insect midgut such as the basal membrane from digestive epithelium was detached which may be responsible for the decrease in the digestive efficiency in *T. absoluta* (Meyrick) (dos Santos et al., 2015). Silicon treatments were found to increase tolerance against spittlebug in sugarcane plants (Korndörfer et al., 2011). Several studies showed that Si inhibit the damage caused by insects pests such as green leaf hopper, stem borers, brown plant hoppers, and spider mites (non-insect pests) (Vicari and Bazely, 1993; Ma and Takahashi, 2002; Ferreira and Moraes, 2011).

Pests and diseases are major limiting factors in crop production and yield. The important agricultural pests include insect (sucking and chewing/mastication), and fungal and bacterial diseases. In addition small mammals e.g. voles, may induce plant herbivory while phytoliths could represent a powerful mechanical defense against vole populations (Calandra et al., 2016). They can cause a wide range of destruction by inhibiting various metabolic processes, sucking plant juices, rolling the leaves and chewing the stems and fruits. In order to avoid crop damage to meet the growing demand of food, crops are heavily sprayed with pesticides causing a threat to the environment (Lechenet et al., 2017). One possible remedy to reduce the intensive use of pesticides is using some environment-friendly alternatives such as natural elements/compounds like Si that pose no threat to the human health and environment (Laing et al., 2006).

2. History and sources of silicon fertilization

Almost 160 years ago, Julius Sachs (1862) raised questions about the role of Si in plant biology as "whether silicic acid is an indispensable substance for those plants that contain silica, whether it takes part in the nutritional processes, and what is the relationship that exists between the uptake of silicic acid and the life of the plant?" (Lewin and Reimann, 1969). Many experiments were conducted on Si in the 20th century to prove its benefits in agriculture. Due to its non-toxic behavior and abundance in nature, Si has received great attention. Si can be used for carbon exchange in all major classes of insecticides and in most cases, the Si analogue has insecticidal activity (Guntzer et al., 2012; Sieburth et al., 1990). In Japan, Si has been applied to paddy soils since 1955 (Takahashi et al., 1990) and it has increased rice production (Aetiba, 2015; Ahmad et al., 2013). Numerous Si fertilizers are now commonly applied in various countries, including the USA, Korea, and China (Table 1). Silicon fertilizers mostly have a neutral or slightly alkaline pH and these may be a good contributor in neutralizing the effects of soil acidity (Savant et al., 1999).

3. Silicon in the soil-plant system

3.1. Silicon in soils

Silicon has been regarded as the second most abundant element in the lithosphere making up about 27% of the earth crust. Generic term