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A Comparative Study of Various Aspects of "Defense Mechanism" Acquired by Silicon with Regard to Different Pathogenic Interactions

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ABSTRACT: Earlier, while considering the requirements of general vascular plants, Silicon was not acknowledged as something vital. But later, it was found that Silicon is greatly responsible to resist fungal as well as bacterial diseases in plants. Also, it influences the growth and development of an extensive range of plant species. Silicon is well-acknowledged for its nature of effective mitigation against numerous climatic stresses. Silicon generally functions as an immune-modulator for influencing the possible measures of plant defense responses in plants. Mainly, it will interact with the major components that are releasing stress signals in plant system. Hence, Silicon will be ultimately responsible for the induced resistance. In this review, we will be considering a comparative analysis of physical, chemical, molecular and cellular defense response produced by Silicon in different crops. Another major summarization from this review will be regarding the role of Silicon in plant-microbe interaction. But as there are no direct instances of silicon being responsible for plant pathogenic functionary it could be questionable that how silicon is hindering the plant pathogenic interactions. This article is attempting to answer such doubts by giving a brief comparison of silicon being assessed in physical, chemical, molecular and cellular manner. The assessment is purely based on how pathogens react to the silicon application on different levels of physiology. Consequently, this evaluation will be helpful in ameliorating the plant resistance by certain modifications in Silica fertilizers input. Although one major drawback can be convincing the farmers to swaping to a new type of fertilizer. This article highlights the future aspect of research concerning the performance of Silicon in agriculture-farming.

Keywords: Silica, Defense response, Plant-pathogen interactivity

INTRODUCTION

Silicon is considered as the second most plentiful element in the universe consisting 70 percent soil abundance (Epstein, 1994; Savant *et al.,* 1997; Ma and Yamaji, 2006). New studies have shown Silicon as a beneficial element, contradicting the previous reports where its essentiality was considered minimum. Major uptake of Silicon is done via root system and hence it affects the accumulation rate of Silicon among different plant species (Takahashi *et al.,* 1990). Numerous studies have found that it is not essential for silicon mediated resistance to always locate in the root system of the plant. By considering an example of Silicon influencing resistance in tomato we can verify the previous statement. In case of silicon influencing resistance in tomato crop against pathogen *Ralstonia solanacearum*, the resistance is detected in the shoot complex. This could be because of certain alterations in the pectic polysaccharide morphology of shoot plasma membrane, hence restricts the bacterial fluctuations towards stem (Diago and Wydra, 2007).

While contemplating the uptake of silicon via the roots, appears as silicic acid that is hydrate of silica (Ma and Yamaji,2006). The movement of this silicic acid occurs through cytomembrane with the help of two carriers namely Lsi1 and Lsi2. These two acts as influx and efflux transporters respectively (Ma *et al.,* 2006, 2008). The captivated silicon is largely sedimented in the plasma membrane and is highly necessitate with stress linked signals (Fauteux *et al.,* 2005).

After all things considered about stress linked signals, one of the most important properties of Silicon can be evaluated here. It improves the mechanically operated and functional features of plants and works well for controlling certain biotic as well as abiotic stress conditions (Epstein, 1994; Richmond and Sussman, 2003; Ma, 2004; Heine *et al.,* 2007; Ma and Yamaji, 2006). Abiotic stress could be any drought situation, lodging, salinity stress, imbalance in nutrients, toxicity due to some metal etc. (Epstein 1994 & 1999; Savant *et al.,* 1997; Liu *et al.,*2014; Ma and Yamaji, 2006; Coskun *et al.,* 2016). Silicon enriches the resistance towards diseases caused by bacteria, fungi as well as pests (Fauteux *et al.,* 2005; Marschner, 2012). Theolder approaches used for pathogenic management are becoming resistant with continuous application. Ultimately, plant protection needs some changes and advancements now. Silicon application can be a great replacement as it is required and applied in minute amount that will reduce the toxic pressure on environment as well as soil.

Some studies have been attentive about the role of silicon in the interaction of microbes with plant system. This not only enhances host resistance but also stimulates the defense responses (Cai *et al.,* 2008; Ghareeb *et al.,* 2011; Ye *et al.,* 2013). Certain experiments showed that Silicon shows more resistance in particular crops e.g. rice and cucumber (Ma *et al.,* 2006). As we know that plant diseases are the ultimate result of plant pathogen interaction and hereby considering its the primary role of silicon, we will see what type of resistance this silicon will show with several plant diseases in different crops (Table 1).

Table 1: Silicon showing resistance mechanism with respect to different aspects (crop species and pathogen invading).

Crop	**Disease**	**Pathogen**	**Resistance Mechanism**	**Reference**
Arabidopsis	Powdery mildew	*Erysiphe cichoracearum, Agrobacterium tumefaciens*	Physical, Biochemical, Molecular	Ghanmi *et al.,* 2004; Fauteux *et al.,* 2006; Vivancos *et al.,* 2015)
Banana	Black sigatoka	*Mycosphaerella fijiensis*	Physical, Biochemical	Kablan *et al.,* 2012
Barley	Powdery mildew	*Blumeria graminis*	Physical	Wiese *et al.,* 2005
Bean	Angular leaf spot	*Pseudocercospora griseola*	Physical	Rodrigues *et al.,* 2010

Silicon initiates resistance by preventing the penetration by various means-

1. Structural implementation (Epstein,1999, 2001; Rodrigues *et al.,* 2015).
2. Stimulation of systemically acquired resistance.
3. By producing anti-microbial compound (Fauteux *et al.,* 2005; Datnoff *et al.,* 2007; Fortunato *et al.,* 2012; Van *et al.,* 2013).
4. By activating numerous signaling pathways (Chen *et al.,* 2009, 2014; Vivancos *et al.,* 2015).

A. Silicon-mediated resistance

1. Physical resistance: Every plant pathogen requires to penetrate through wax layers, cuticles and cell walls to cause infection successfully in any host plant (Schmelzer,2002; Nawrath, 2006; Lazniewska *et al.,* 2012). Silica improves this protective layer by improving its mechanical strength (Epstein, 1999 &2001; Sun *et al.,* 2010). Mainly Silicon acts as physical barrier that inhibits the penetration of the pathogen in host plant and make it less vulnerable to degradation done by enzymes that are secreted by pathogen annexation (Innaga *et al.,*1995; Fauteux *et al.,* 2005; Datnoff *et al.,* 2007; Van *et al.,* 2013). Silicon gets sedimented under the cuticle layer form a cuticle-silicon double layer which prevents plant from pathogen penetration and hence automatically reduces the disease incidence (Ma and Yamaji, 2006 & 2008).

Silicon gets interconnected with hemicellulose present in cell membrane and this linkage highly improves the mechanical possessions and regeneration (He *et al.,* 2015; Guerriro *et al.,* 2016). Various studies also found some proofs regarding a noticeable increase in cell wall turgidity due to silicon (Marschner, 2012). In context to previous statement it was found that in earliest cell walls if silicon applied, it interacts with cell wall components like pectins or polyphenols, this leads to increase in turgidity of cell wall in growing period (Emadian and Newton, 1989). Supplement of silicon delays the invasion of pathogen into epidermal cells and hence less colonization of pathogen will be there. Some popular examples to physical resistance are-

a. In case of rice infected with *Pyricularia oryzae,* Silicon prevents the hyphal entry and for other several leaf cells where silicon could not reach, a noticeable amount of invasion was there (Sousa *et al.,* 2013). No. of appressorial sites was also reduced where silicon was supplied (Hayasaka *et al.,* 2008).

b. For rice infected with *Pyricularia grisea* and *Rhizoctonia solani*, less no. of leaf blade lesions was found when silicon was applied. (Rodrigues *et al.,* 2001; Seebold *et al.,* 2004).

Formation of papillae: Under physical resistance one more important aspect is formation of papillae. This process is enhanced by Silicon during pathogen interaction. Accumulation of silicon occurs in haustorial neck of fungus and also in the papillae. This accumulation helps in preventing the invasion of the pathogen (Zeyen *et al.,* 1993; Samuels *et al.,* 1994). Certain reports showed that in case of barley, the papillae formation will be there. Here, epidermal cells with induce the production of this papillae when *Blumeria graminis* f.sp. *hordei*cause the infectionduring silicon application. Another example is of rose plant where silicon application increases the papillae formation in the cells of leaves that restricts *Podosphaera pannosa* (Shetty *et al.,* 2012). Similarly, in case of rice and wheat papillae formation will restrict rice blast (Cai *et al.,* 2008) and powdery mildew (Belanger *et al.,* 2003) respectively.

In 2007, Heine *et al.,* gave the reports declaring that the potential of silicon to inhibit disease spread inthe root area depends on the uptake of silicon done by root cell protoplasts. The accumulation that occurs on later stage may not be responsible for the physical barrier as noted in *Pythium aphanidermatum* in tomato. Cucumber also showed systemic resistance when supplied with silicon (Liang *et al.,* 2005). Physical resistance is much simpler than biochemical and molecular resistance.

2. Biochemical resistance: Silicon induced biochemical resistance is linked with certain features-

a. Increases the potential of defense enzymes e.g. glucanose, peroxidase, phenylalanine ammonia-lyase etc.

b. Induction of anti-microbial compounds production e.g. phenolic, flavonoids, PR proteins and phytoalexins.

c. Regulates certain systemic signals e.g. Jasmonic acid, ethylene, salicylic acid (Datnoff *et al.,* 2007; Fortunato *et al.,* 2012; Van *et al.,* 2013).

Defensive enzymes and anti-microbial compounds

Whenever plant pathogen interaction occurs Silicon has been reported to stimulate Defense-related enzymes and also certain anti-microbial compounds (Fauteux *et al.,* 2005; Datnoff *et al.,* 2007; Van *et al.,* 2013). Silicon mainly activates the important defense related enzymes e.g. polyphenol oxidases, catalase, peroxidases, chitinase, glucanase etc. Major enzymes such as phenylalanine ammonia- lyase are responsible for producing secondary anti- microbial compounds. These compounds are really important for resistance towards plant diseases (Waewthongrak *et al.,* 2015).

After the application of silicon if amount of phenylalanine ammonia-lyase increases, it will lead to accumulation of derivatives of totally resolvable phenic and lignine- thioglycolic acid in the banana leaves and also in coffee plant. This accumulation will reduce the disease prevalence (Silva *et al.,* 2010; Fortunato *et al.,* 2012). Furthermore, the other component PPO (polyphenol oxidase) is also an important enzyme for phenolic substance oxidation. It is found free in cytoplasm or sometimes bound with particular organelle (Quarta *et al.,* 2013). PPO is responsible for lignin synthesis, increases the anti-bacterial potential of host plants and hence correlated with plant disease resistance (Piperno, 2006; Song *et al.,* 2016). Another important activity which is affected by silicon could be peroxidase and chitinase activities which are the crucial components for host-disease resistance (Brisson *et al.,* 1994).

Certain defensive enzymes are regulated by SI in accordance to different plant pathogen network (Table 2). Here defense related enzymes are secreted when silicon is applied. Examples are taken of beans, cucumber, melon and pea. For diseases like anthracnose, crown and root rot, pink rot and leaf spot. For all these diseases pathogen interaction will be different hence releasing different defense related enzymes. Higher the activity of these enzymes higher will be the accumulation of antimicrobial compounds which will give a substantial response as induced defense system (Fawe *et al.,* 1998; Rodrigues *et al.,* 2004; Remus-Borel *et al.,* 2005). Antimicrobial compounds like phenols, phytoalexins, flavonoids etc. helps the host plant to fight back the infection (Fauteux *et al.,* 2005; Van *et al.,* 2013).

Systemic signals

Host plant develops numerous layers of constitutive and inducible mechanism of defense that ultimately gets regulation with the help of signal transduction pathway (Grant *et al.,* 2013). Salicylic acid, Jasmonic acid and ethylene functions great for immunity networks (Clarke *et al.,* 2000; Devadas *et al.,* 2002). The reactivity for three of them are different as salicylic acid works against biotrophs and hemi biotrophs whereas Jasmonic acid and ethylene works against necrotrophs (Pieterse *et al.,* 2012). These signaling pathways and some modulating plant hormone homeostasis together are also regulated by silicon (Fauteux *et al.,* 2006; Iwai *et al.,* 2006; De-Vleesschauwer *et al.,* 2008; Ghareeb *et al.,* 2011; Reynolds *et al.,* 2016).

Table 2: DR-Enzymes induced by silicon in disease infection.

Host	Disease	Pathogen	Defense related enzymes	Reference
Bean	Anthracnose	*Colletotrichum lindemuthianum*	Superoxide dismutase, ascorbate peroxidase, glutathione reductase	Polanco *et al.,* 2014
Cucumber	Crown and root rot	*Pythium* spp.	Chitinase, peroxidase, polyphenol oxidases	Cherif *et al.,* 1994
Melon	Rot	*Trichothecium roseum*	Peroxidase	Bi *et al.,* 2006
Pea	Leaf spot	*Mycosphaerella pinodes*	Chitinase, beta-1,3- glucanase	Dann and Muir, 2002

In case of silicon supplied *Arabidopsis* plants that are having powdery mildew infection (*Erysiphe cichoracearum),* production of salicylic acid, jasmonic acid and ethylene were seen in the leaves of plants that leads to increased resistance (Fauteux *et al.,* 2006). In this similar case Silicon also increased the gene expression that is encoded with enzymes that participates in salicylic pathway. Phenotypes that were resistant showed significant lower level for salicylic acid as compared to the susceptible ones (Vivancos *et al.,* 2015).

Majorly three types of active mechanism of defense are available in biochemical resistance that are induced by Silicon. First mechanism includes initial response by cells when infection starts, second mechanism includes the secondary response initiated by elicitors and it remains restricted to the area of initial infection and third mechanism includes the tertiary systemically acquired response which gets transferred throughout the infected plant (Hutcheson, 1998).

3. Molecular mechanism

Silicon plays an important role in the metabolic activities of Phyto-pathological interaction. It leads to activation of defense genes in host plants by initiating functional and biochemical reactions. Signal transduction also occurs here which induces resistance and defense mechanism in plants (Vivancos *et al.,* 2015). Some transcriptomic experiments have been performed to illustrate the role of silicon in inducing defense responses in different plant systems (Chain *et al.,* 2009; Majeed Zargar *et al.,* 2010; Ghareeb *et al.,* 2011; Nwugo and Huerta *et al.,* 2011). In case of tomato plant, Silicon induces resistance against *Ralstonia solanacearum* by regulating the gene expressions with regard to stress and defensive responses, e.g. DRR proteins, trehalose phosphatase, WRKYI transcription (Ghareeb *et al.,* 2011).

Signaling pathways that are regulated by silicon have already been discussed in the portion of “Systemic signals”.

In cucumber, systemic acquired resistance is induced by silicon by expressing gene encoded with a new strain of proline rich protein when fungal infection occurred (Kauss *et al.*, 2003). In tomato also, *CHI-II, GLU, PGIP* and *POD*when expressed, were found restricting *R. solanacearum* (Ghareeb *et al.*, 2011).

4. Cellular mechanism: For explaining the cellular mechanism, an illustration was done. Let's review this experiment further.

a. Plant material: Cotton seeds (*Gossypium hirsutum)* of cultivar Sicot was obtained for this experiment. 5 plants were grown in pot of 10cm with requirements as given- 16h light, 23-degree Celsius Day temperature, 8h night with 18-degree Celsius and light fraction440πmol m^{-2} s^{-1} (Bunt,1998).

b. Treatments: Silicon source was potassium silicate soil drench. Potassium silicate (1.5 mL L^{-1} water, equivalent to 0.56 g SiO_2. Make it a soil drench and apply 150 mL per pot. Potassium silicate reduced the disease incidence as well as promoted the plant growth (Whan, 2010). With regular addition of liquid silicate, it was found that silicon uptake was more in such plants as compared to the plants that are not regularly supplied with silicon.

c. Inoculation: 3 weeks seedlings were infected with pathogen *F. oxysporum* f.sp. *vasinfectum* by root dip method.

d. Transmission electron microscopy and light microscopy

For this experiment, 50 samples were taken each being representative of different treatments applied. Duration were kept 2,3,7,14 and 28 days after inoculation. Small cuttings of roots were taken and then 3% glutaraldehyde with 0.1 M phosphate buffer was applied. Pelco Biowave Microwave system was used for the processing (Wendt *et al.*, 2004). Uranyl acetate was not applied in this process. Infiltration of samples were done with 100% Epon resin on a rotating machine. An ultramicrotome was used to do the sectioning process. Section with a thick diameter were taken for cellular analysis, they were chopped with the glass knife in the initial stage and Toluidine blue was applied. After that we can illustrate it under light microscope. For a second instance think diameter sections were taken and glass knife was used for chopping. These thin cuttings then placed onto Formvar-coated copper grids. After taking the pieces out of the grid, staining with uranyl acetate and lead citrate was done (Samuels *et al.*, 1994). Then checked under transmission electron microscope. As a result, micrographs of cotton plants treated with silicon showed defense reaction against *F. oxysporum* f.sp. *vasinfectum.*

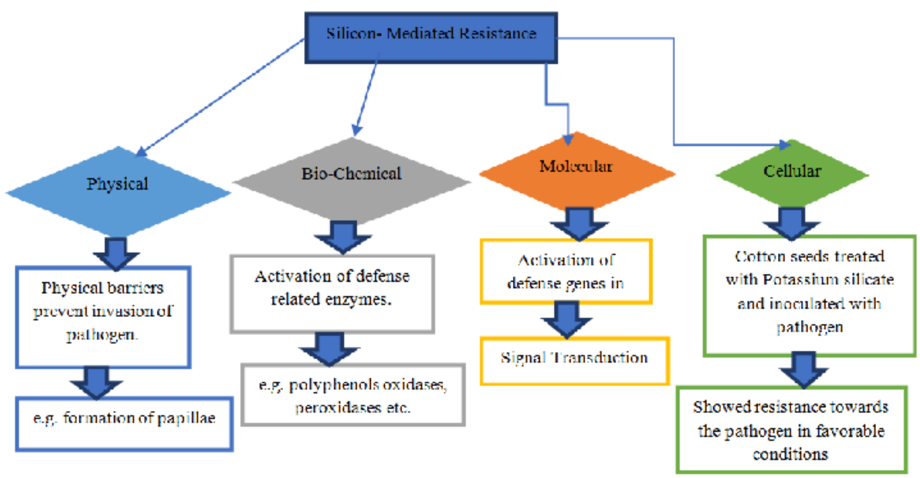

Fig. 1. Silicon-mediated defense at different levels.

As the agriculture nowadays is showing a great incline towards the chemical and synthetic products for a better outcome and disease resistant plants, the environment is suffering badly. Silicon here could be an alternative that can be extracted from natural products and still can resist diseases at a greater peak. Precipitated silica that can be extracted from rice husk ash is a vital source that is absolutely non-toxic to the environment. In areas like Punjab where rice husk and straw are a great headache to remove and degrade, it would be a great alternative providing them the best for their fields.

CONCLUSION

The whole article revolves around the silicon providing the defense mechanism to plants against stress conditions that could be initiated by pathogens. For the following verification different levels or aspects were taken, be it physical, biochemical, molecular or cellular. Experiments were discussed for more clarification. Moreover, how silicon could be non-toxically utilized in the fields, from which particular crop it could be extracted and the other important data is also summarized here. It was found that silicon can bless the plant with a good defense mechanism. And can resist fungal as well as bacterial diseases to an extent. By combining available information on the interaction of plant–microbes mediated by Si, the physical, biochemical, and molecular mechanisms that can be attributed to Si-mediated plant defense responses have been summarized in this review.Although numerous studies have elucidated the possible mechanism of Si-mediated resistance at the physical, biochemical, and molecular levels, detailed mechanisms of Si regulated plant–microbe interactions, such as plant signaling transduction and transcriptome regulation of defense-related pathways, are needed for further study.

Conflict of Interest Statement. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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