

## REVIEW ARTICLE

## The role of silicon (Si) in increasing plant resistance against fungal diseases

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**Summary** The use of silicon (Si) in agriculture has attracted a great deal of interest from researchers because of the numerous benefits of this element to plants. The use of silicon has decreased the intensity of several diseases in crops of great economic importance. In this study, the relationship between silicon nutrition and fungal disease development in plants was reviewed. The current review underlines the agricultural importance of silicon in crops, the potential for controlling fungal plant pathogens by silicon treatment, the different mechanisms of silicon-enhanced resistance, and the inhibitory effects of silicon on plant pathogenic fungi *in vitro*. By combining the data presented in this paper, a better comprehension of the relationship between silicon treatments, increasing plant resistance, and decreasing severity of fungal diseases could be achieved.

*Additional keywords:* pathogenic fungi, severity of fungal disease, silicon treatment

### 1. Introduction

Diseases caused by different fungal pathogens are among the major constraints of plant production (Semal, 1989). The use of resistant varieties/rootstocks and fungicides are therefore the simplest and most effective methods to reduce the severity of fungal diseases (Dubin and Rajaram, 1996; Shephard, 1997). However, resistance is overcome by the genetic diversity of fungal pathogens as well as by genotype  $\times$  environmental interactions (Bayles *et al.*, 2000). Repeated fungicide treatments generate important economic losses, emergence of resistant pathogen populations, and potential environmental impacts (Ma and Michailides, 2005). Therefore, alternative environment-friendly methods for the management of fungal plant pathogens remain to be urgently investigated. Soil fertilizers with nutritional elements were shown to have disease suppressing effects on various pathosystems (Datnoff *et al.*, 2007). In fact, the application of silicon (Si)

has been proposed as a viable alternative to conventional control techniques. Silicon can improve environmental stress tolerance and increase crop productivity (Ma and Yamaji, 2006; Datnoff *et al.*, 2007). Moreover, silicon application is a preventive measure against a number of fungal diseases (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013).

In the literature, two hypotheses for silicon-enhanced resistance to fungal diseases have been proposed (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013). The first one is associated with the higher deposit of silicon in the leaf so as to form physical barrier to impede pathogen penetration. The second one is related to its biologically active role in the expression of natural defense mechanisms. However, the first mechanism (physical defense) may partly explain the prophylactic effects of silicon, the second one (biochemical defense) is more accepted for explaining the protective role of silicon against many plant pathogens (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007).

To date, several studies have documented the ability of silicon to control and reduce the incidence and severity of fungal diseases in both monocotyledons and dicotyle-

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dons (Table 1). The exact nature of protective effects of silicon in plants is uncertain and presently a subject of debate (Van Bockhaven *et al.*, 2013). However, functions including physical and/or biochemical protection systems have been proposed (Datnoff *et al.*, 2007). The aims of this review are to underline the agronomic importance of silicon in plant crops, to present the potential for controlling fungal plant pathogens by silicon treatment, to refer to different mech-

anisms of silicon-enhanced resistance, and to explain the inhibitory effects of silicon on phytopathogenic fungi *in vitro*.

## 2. Silicon and plants

Although silicon has not been considered as an essential element for plant nutrition, according to the classical definition of essentiality (Arnon and Stout, 1939), it is regard-

**Table 1.** Pathosystems on which the role of silicon in reducing the fungal disease incidence has been studied.

Host plant	Fungal pathogen	Reference
Barley	<i>Alternaria</i> spp.	Kunoh and Ishiazaki (1975)
Wheat	<i>Septoria nodorum</i> <i>Erysiphe graminis</i> <i>Blumeria graminis</i> f. sp. <i>tritici</i>	Leusch and Buchenauer (1989) Leusch and Buchenauer (1989) Guevel <i>et al.</i> (2007)
Rice	<i>Pyricularia oryzae</i> <i>Bipolaris oryza</i> <i>Magnaporthe grisea</i> <i>Rhizoctonia solani</i>	Domiciano <i>et al.</i> (2015) Dallagnol <i>et al.</i> (2011) Rodrigues <i>et al.</i> (2005) Zhang <i>et al.</i> (2013)
Corn	<i>Pythium aphanidermatum</i> <i>Fusarium graminearum</i> <i>Fusarium moniliforme</i>	Sun <i>et al.</i> (1994) Sun <i>et al.</i> (1994) Sun <i>et al.</i> (1994)
Banana	<i>Mycosphaerella fijiensis</i> <i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	Kablan <i>et al.</i> (2012) Fortunato <i>et al.</i> (2012)
Pearl millet	<i>Sclerospora graminicola</i>	Deepak <i>et al.</i> (2008)
Arabidopsis	<i>Erysiphe cichoracearum</i>	Ghanmi <i>et al.</i> (2004)
Rose	<i>Diplocarpon rosae</i> <i>Podosphaera pannosa</i>	Gillman <i>et al.</i> (2003) Shetty <i>et al.</i> (2012)
Common bean	<i>Colletotrichum lindemuthianum</i>	Polanco <i>et al.</i> (2014)
Soya bean	<i>Phakospora pachyrhizi</i>	Arsenault-Labrecque <i>et al.</i> (2012)
Bean	<i>Pseudocercospora griseola</i>	Rodrigues <i>et al.</i> (2010)
Pea	<i>Mycosphaerella pinodes</i>	Dann and Muir (2002)
Strawberry	<i>Sphaerotheca aplanis</i>	Kanto <i>et al.</i> (2006)
Cherry	<i>Penicillium expansum</i> <i>Monilinia fructicola</i>	Qin and Tian (2005) Qin and Tian (2005)
Potato	<i>Fusarium sulphureum</i>	Li <i>et al.</i> (2009)
Belle pepper	<i>Phytophthora capsici</i>	French-Monar <i>et al.</i> (2010)
Tomato	<i>Pythium aphanidermatum</i> <i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>	Heine <i>et al.</i> (2007) Huang <i>et al.</i> (2011)
Cucumber	<i>Pythium ultimum</i> <i>Pythium aphanidermatum</i> <i>Sphaerotheca fuliginea</i> <i>Podosphaera xanthii</i> <i>Colletotrichum lagenarium</i>	Cherif <i>et al.</i> (1992) Cherif <i>et al.</i> , (1992) Menzies <i>et al.</i> (1991) Fawe <i>et al.</i> (1998) Liang <i>et al.</i> (2005)
Bitter melon	<i>Pythium aphanidermatum</i>	Heine <i>et al.</i> (2007)

ed as one of the most beneficial elements that increases plant resistance against abiotic and biotic stresses. However, the mechanisms responsible for alleviating biotic and abiotic stresses remain unclear because they may act in the soil, at the root surface and *in planta* (roots and shoots) (Liang *et al.*, 2007; Van Bockhaven *et al.*, 2013).

### 2.1. Absorption of silicon by plants

Silicon is as important as phosphorus and magnesium (0.03%) in the biota (Exley, 1998). It is the second most abundant element on the earth's crust after oxygen. It comprises up to 70% of the soil mass in the form of minerals and water-soluble monosilicic acid ( $H_4SiO_4$ ) (Lowenstam, 1981). In soil solution, silicon occurs mainly as monosilicic acid in concentrations between 0.1 and 0.6 mM (Savant *et al.*, 1997).

Silicon is taken up by plant roots as non-charged monosilicic acid (Ma and Yamaji, 2006), when pH of the soil solution is below 9 (Ma and Takahashi, 2002). Monosilicic acid uptake is passive and largely determined by transpiration rate (Datnoff *et al.*, 2007). Once it reaches a concentration of around 2 mM, monosilicic acid is polymerized into insoluble silica, known as species-specific solid bodies (phytoliths) (Mitani *et al.*, 2005). It is deposited in cell walls, intercellular spaces and as a subcuticular layer outside the cells of leaves (Datnoff *et al.*, 2007). Moreover, silicon accumulates in higher amounts in mature leaves than in young ones (Ma and Takahashi, 2002). Plants absorb a significant fraction of dissolved silicon that originates from litterfall decomposition i.e phytolith dissolution (Datnoff *et al.*, 2007). The concentration level of absorbed silicon in plants ranges from 0.1 to 10% dry weight, depending on the plant genotype, the concentration of silicon in soil and the environmental conditions (Ma and Yamaji, 2006).

### 2.2. Agronomic importance of silicon in plant crops

Silicon is reported to increase and enhance yield, growth and production of plants. It improves some morphological

and mechanical characteristics (height, stature, root penetration into the soil, exposure of leaves to light, resistance to lodging) in several plant species. Silicon reduces transpiration and enhances plant resistance to drought stress, salinity and metal toxicity, and increases enzyme activity (Datnoff *et al.*, 2007). On the other hand, regarding biotic stresses, the accumulation of silicon in plant plays an important role in plant defense against insect herbivores. Several herbivorous insects suffer adverse effects when feeding on silica-rich plants (Reynolds *et al.*, 2009). Moreover, silicon has been shown to improve resistance in many plants to various fungal, viral and bacterial pathogens (Rodriges and Datnoff, 2005; Silva *et al.*, 2010; Zellner *et al.*, 2011; Van Bockhaven *et al.*, 2013). Most interesting, silicon protects plants against a multitude of stresses without the occurrence of resistance trade-offs and/or growth and yield penalties (Fauteux *et al.*, 2005; Ma and Yamaji, 2006; Epstein, 2009; Van Bockhaven *et al.*, 2013).

### 2.3. Accumulation of silicon in plant species

In the absence of abiotic and/or biotic stresses, silicon was believed to have a negligible effect on metabolism of healthy plants, which suggests its nonessential role (Epstein, 2009). However, silicon nutrition promoted agronomic yields of unstressed crops such as rice, as demonstrated by Rodrigues and Datnoff (2005). According to Ma and Yamaji's (2006) agricultural point of view, silicon uptake in graminaceous plants, such as wheat, oat, rye, barley, sorghum, maize, and sugarcane, was much higher than its uptake in other plant species. One typical example was rice, which absorbed 150-300 kg Si/ha. High accumulation of silicon in rice has been demonstrated to be necessary for healthy plant growth, and high and stable production (Snyder *et al.*, 2006). Moreover, graminaceous plants absorb silicon at concentration levels equal to or greater than some of the essential nutrients like N and K (Savant *et al.*, 1997). In rice, for example, silicon accumulation was about 108% greater than

nitrogen (Rodrigues and Datnoff, 2005). The majority of dicotyledonous plants, such as cucumbers, melons, strawberries, and soybeans, absorb silicon inertly (Ma and Yamaji, 2006). Nonetheless, some plants, especially dicotyledons, such as tomatoes, beans, and other plant species, are not able to absorb silicon from soil (Ma and Yamaji, 2006). The Si/Ca ratio is another criterion used to determine whether a plant species is classified as a silicon absorber (Datnoff *et al.*, 2007).

### 3. Silicon controls fungal plant pathogens

In plant species, the association between silicon and reduced severity of fungal diseases has been documented in several studies. Another interesting association is the seemingly stronger efficacy of silicon against biotrophic and hemibiotrophic pathogens (e.g. rice blast, powdery mildews) compared to necrotrophs (Belanger *et al.*, 2014).

Adding silicon to plants as a fertilizer makes them more resistant to various pathogenic fungi (Datnoff *et al.*, 2007). There are several silicon fertilizers (solid and liquid sources) that could be used for agronomic purposes (Heckman, 2013; Datnoff and Heckman, 2014). To be beneficial for plants, silicon fertilizers should provide a high percentage of silicon in a soluble form, be cost effective, have physical properties that will facilitate storage ability, ease their application, be uncontaminated with heavy metals, and perhaps have the ability to raise soil pH (Heckman, 2013; Datnoff and Heckman, 2014). Calcium silicate ( $\text{CaSiO}_3$ ) incorporated into soil has been used successfully as a solid source. Liquid sources, which are primarily used as a foliar spray, include potassium silicate ( $\text{K}_2\text{SiO}_3$ ) or sodium silicate ( $\text{Na}_2\text{SiO}_3$ ). Silicon has proved effective in controlling both soil- and air-borne fungal diseases in several plant crops.

#### 3.1. Air- and soil- borne fungi

Numerous studies have shown increased plant resistance to foliar fungal pathogens

as a response to silicon application. For example, soil treatments with silicon-rich materials reduced the incidence of diseases caused by *Erysiphe graminis* (powdery mildew) and *Septoria nodorum* (leaf and glume blotch) on wheat, as reported by Leusch and Buchenauer (1989). Foliar sprays of potassium silicate at concentrations  $\geq 17$  mM effectively reduced the number of powdery mildew (*Sphaerotheca fuliginea* on cucumber and muskmelon; *Erysiphe cichoracearum* on zucchini squash) colonies on leaves (Menzies *et al.*, 1992). Bowen *et al.* (1992) also reported that foliar sprays of potassium silicate at 1.7 mM reduced the number of powdery mildew (*Uncinula necator*) colonies on grape leaves by more than 60%. Soil silicon fertilization at 100 mg/l appeared to increase wheat resistance to *Blumeria graminis* (powdery mildew), *Mycosphaerella graminicola* (septoria leaf blotch), *Phaeosphaeria nodorum* (leaf spot), and *Puccinia recondita* (brown rust) only under high disease pressure (Rodgers-Gray and Shaw, 2004). A 40% reduction in the incidence of neck blast (*Pyricularia oryzae*) on rice plants supplied with silicon was reported by Seebold *et al.* (2004). Foliar application of 1% sodium metasilicate solution to sweet cherry reduced blue mold decay (*Penicillium expansum*) by 63% and brown rot decay (*Monilinia fructicola*) by 87% (Qin and Tian, 2005). The root application of silicon reduced powdery mildew severity on cucumber (Liang *et al.*, 2005). Potassium silicate application to soil reduced strawberry powdery mildew (*Sphaerotheca aphanis*) by 86% in the first year and by 60% in the second year (Kanto *et al.*, 2006). In the *Colletotrichum lindemuthianum*-bean pathosystem, silicon reduced both the area under the anthracnose incidence progress curve and the area under the anthracnose severity progress curve (Moraes *et al.*, 2006). Root applications of 1.7 mM Si reduced the severity of powdery mildew disease (*Blumeria graminis* f. sp. *tritici*) on wheat by as much as 80% (Guevel *et al.*, 2007). Guo *et al.* (2007) reported that sodium silicate reduced significantly the severity of post-harvest pink rot of Chinese cantaloupe caused by *Trichoth-*

*ecium roseum*. Potassium silicate solutions (pH 5.5 and 10.5) applied to bean plants reduced the intensity of angular leaf spot (*Pseudocercospora griseola*) by 42 and 30%, respectively (Rodrigues *et al.*, 2010). Supply of silicon to wheat plants reduced the severity of spot blotch caused by *Bipolaris sorokiniana* (Domiciano *et al.*, 2010). Regarding the wheat–*Pyricularia oryzae* interaction, Xavier *et al.* (2011) demonstrated that supply of silicon to plants decreased the area under the blast progress curve and the number of lesions per cm<sup>2</sup> of leaf area. Application of 2mM silicate solution decreased the area under brown spot progress curve and the number of brown epidermal cells caused by *Bipolaris oryzae* on rice plants (Dallagnol *et al.*, 2011). Kablan *et al.* (2012) showed that sodium metasilicate added to banana plants at a concentration of 1.7 mM reduced the severity of the disease caused by *Mycosphaerella fijiensis* (black sigatoka). Soybean plants supplied with soluble silicon exhibited a near absence of symptoms of Asian rust caused by *Phakopsora pachyrhizi* (Arsenault-Labrecque *et al.*, 2012). The efficacy of silicon applied at 0.5 and 1.0 l/ha in controlling apple scab (*Venturia inaequalis*) on leaves and fruit ranged from 67 to 81% and from 78 to 80%, respectively (Meszka and Wilk, 2014). Foliar sprays with 2 mM potassium silicate applied to common bean plants reduced the severity of the disease caused by *Colletotrichum lindemuthianum* (anthracnose) by 34% (Polanco *et al.*, 2014). Regarding the perennial ryegrass–*Magnaporthe oryzae* pathosystem, Rahman *et al.* (2015) found that calcium silicate applied at the rate of 5 metric ton/ha suppressed significantly gray leaf spot in plants achieving a reduction in disease incidence and severity by 39.5 and 47.3%, respectively. Application of 2 mM silicon reduced the severity of blast disease (*Pyricularia oryzae*) in rice plants (Domiciano *et al.*, 2015). Silicon treatment of soybean was highly associated with increased plant resistance to target spot caused by *Corynespora cassiicola* (Fortunato *et al.*, 2015). Root application of silicon was more effective compared to foliar application in reducing

the severity of powdery mildew (*Podosphaera xanthii*) on melon (Dallagnol *et al.*, 2015).

A number of studies have indicated that silicon application can also reduce the severity of soil-borne fungal diseases. For example, potassium silicate at a concentration of 1.7mM amended to nutrient solutions of cucumber plants significantly reduced the incidence of *Pythium ultimum* and *P. aphanidermatum*, the causal agents of root rot (Cherif *et al.*, 1992). The application of potassic and siliceous fertilizers increased resistance of corn to stalk rot caused by *Pythium aphanidermatum*, *Fusarium graminearum* (syn. *Gibberella zeae*) and *F. moniliforme* (syn. *G. fujikuroi*) (Sun *et al.*, 1994). Soil silicon fertilization applied to wheat plants reduced severity of brown foot rot (*Fusarium culmorum*) and eyespot (*Oculimacula yallundae*), under high disease pressure (Rodgers-Gray and Shaw, 2004). Application of 100 and 200 mM sodium silicate solutions decreased the diameter of dry rot (*Fusarium sulphureum*) lesions in potato tubers by 44 and 45%, respectively (Li *et al.*, 2009). Regarding the belle pepper–*Phytophthora capsici* pathosystem, French-Monar *et al.*, (2010) reported that supply of silicon to plant roots can potentially reduce the severity of Phytophthora blight while enhancing plant growth. Huang *et al.* (2011) showed that foliar application of silicon at the dose of 100 mg Si/l to tomato plants significantly reduced the severity of Fusarium crown and root rot (*Fusarium oxysporum* f.sp. *radicis-lycopersici*); data suggested that the decrease in disease severity was probably due to a delay in the onset of the initial infection of roots and the movement of the pathogen from roots to stems (Huang *et al.*, 2011). Silicon amended to soil at a rate of 0.39 g/kg soil reduced the symptoms of Fusarium wilt caused by *Fusarium oxysporum* f. sp. *cubense* on banana plants (Fortunato *et al.*, 2012). Zhang *et al.* (2013) demonstrated that application of 1.5 mM silicon improved resistance of rice to sheath blight (*Rhizoctonia solani*). Moreover, silicon solution at a concentration of 2 mM decreased the area under relative lesion expansion progress curve of sheath blight (R.

*solani*) by 34.2% in rice plants (Schurt *et al.*, 2014).

For air- and soil-borne fungi, the mode of silicon action in a number of components of host plant resistance could be summarized as follows (Datnoff *et al.*, 2007; Datnoff and Heckman, 2014): silicon delays the incubation and latent periods, decreases conidial production, and reduces some features of the lesions produced by the fungal pathogens (expansion rate, size and number). Subsequently, disease development and/or definitive disease incidence is dramatically decreased, and the resistance of susceptible cultivars is, in some cases, raised to nearly the same level as that of cultivars with complete or partial resistance. Moreover, for susceptible and partially resistant rice cultivars, the observed disease resistance is greatest when silicon is applied to the soil and is root-absorbed as oppose to when it is applied to the foliage (Rezende *et al.*, 2009). This is mainly due to the silicon transporters which are not expressed in the leaves. Regarding foliar sprays, the disease suppressive effects observed are probably due to silicon being deposited on the leaf surface and thus, having an osmotic or pH effect. However, the underlying mechanisms that govern disease protection when silicon is root-absorbed remain largely unclear (Datnoff *et al.*, 2007; Datnoff and Heckman, 2014).

#### 4. Mechanisms of silicon-enhanced resistance

In spite of the many scientific reports about silicon effects on fungal pathogens, the properties, spectrum of efficacy and mode of action of silicon remain largely speculative (Ghanmi *et al.*, 2004; Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013). Under controlled hydroponic conditions, silicon does not affect plant growth or development (Ma and Yamaji, 2006). However, where plants are exposed to multiple stresses, silicon plays an important role in plant health (Epstein, 2009). Generally, the effect of silicon on resistance of plants to

diseases is considered to be due to either an accumulation of absorbed silicon in the epidermal tissue, or an expression of metabolic or pathogenesis-mediated host defense responses (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013).

##### 4.1. Physical defense

For the first hypothesis of silicon physical enhanced resistance, silicon deposited on the tissue surface acts as a physical barrier that protects plants from fungal infection. In this model, the increase of resistance has been associated with several factors, such as (1) the density of the long and short silicified cells present in the epidermis of the leaves, (2) the thick silica layer below the cuticle, (3) the double cuticular layer, (4) the thickened silicon-cellulose membrane, and (5) the papilla formation (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013).

Silicon prevents physical penetration by pathogenic fungi, strengthens plants mechanically, and / or makes the plant cell less susceptible to enzymatic degradation by fungal pathogens. Yoshida *et al.* (1962) reported that a thick layer of silica is formed beneath the cuticle of rice leaves and sheaths after polymerization of monosilicic acid. This silicon layer beneath the cuticle might be partially responsible for impeding pathogen penetration. Furthermore, silicon might also form complexes with organic compounds in the wall of the epidermal cells, thus increasing their resistance to degradation by enzymes released by plant pathogenic fungi (Volk *et al.*, 1958). It was also suggested that silicon may be associated with lignin-carbohydrate complexes present in the cell wall of epidermal cells (Inanaga *et al.*, 1995).

Regarding cytological and pathogenic features associated with physical resistance, silicon deposited on the tissue surface decreases the number of lesions on leaf blades, or increases the incubation period, as reported for the *Pyricularia grisea*– and *Rhizoctonia solani*–rice pathosystems (Rodrigues *et al.*, 2001; Seebold *et al.*, 2004). Moreover, Kim *et al.* (2002) reported that silicified epidermal cell walls were closely as-

sociated with the reduced severity of the blast disease (*Magnaporthe grisea*) in susceptible and partially resistant rice cultivars, although the thickness of the epidermal cell wall was not significantly affected by the presence of silicon. For the cucumber–*Podospheera xanthii* pathosystem, the foliar applied silicon produced only physical barrier and osmotic effect. However, the root applied silicon led to systemic acquired resistance when plants were infected by the powdery mildew pathogen (Liang *et al.*, 2005). Moreover, Hayasaka *et al.* (2008) confirmed that silicon in the rice leaf epidermis may confer resistance against *M. grisea* (blast) appressorial penetration. However, the prophylactic effect against powdery mildew was lost when silicon feeding to cucumber plants was interrupted (Samuels *et al.*, 1991). Heine *et al.* (2007) reported that the accumulation of silicon in root cell walls did not represent a physical barrier to the spread of *Pythium aphanidermatum* in the roots of bitter melon and tomato. Although these authors concluded that silicified epidermal cell walls in leaves could be the main factor for the reduction in severity of plant diseases caused by fungal pathogens, they did not report that this was sufficient evidence to explain the impediment of fungal penetration in the leaves. Based on these results, it was suggested that resistance to fungal pathogens in plants treated with silicon was much more complex than a physical resistance, which was strongly contested and doubted in recent years (Van Bockhaven *et al.*, 2013).

#### 4.2. Biochemical defense

Regarding the second hypothesis of silicon biochemical enhanced resistance, the soluble silicon in plant tissue may be associated with an increase in resistance to fungal diseases. In this model, the enhancement of resistance is due to (1) increased activity of defense-related enzymes in leaves, such as polyphenoloxidase, peroxidase, phenylalanine ammonia-lyase, and glucanase, (2) increased production of antifungal compounds, such as phenolic metabolism prod-

ucts (lignin), flavonoids, phytoalexins and pathogenesis-related proteins in plants, and (3) activation of some plant defense-related genes (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013). When infected with necrotizing pathogens, many plants developed an enhanced resistance against further pathogen attack, which is referred to as systemic acquired resistance (SAR) (Conrath, 2006). The two mechanisms involved in increasing the activity of enzymes and antifungal compounds due to silicon application on plants could induce defense response similar to SAR (Cai *et al.*, 2009). Moreover, there might be other biochemical and physiological mechanisms involved in the silicon-mediated resistance of plants to diseases. For example, higher levels of salicylic acid, jasmonic acid, and ethylene have been reported to be induced by silicon supplements in some host-pathogen interactions: powdery mildew of *Arabidopsis* caused by *Golovinomyces cichoracearum* (Vivancos *et al.*, 2015) and rice-brown spot caused by *Cochliobolus miyabeanus* (Van Bockhaven *et al.*, 2015).

##### 4.2.1. Defense-related enzymes

Defense-related enzymes are important in relation to disease resistance. Several studies indicated that lower disease intensity in the silicon-treated plants was related to higher activity of protective enzymes. Silicon has been demonstrated to stimulate accumulation of defense-related enzymes in plant leaves after fungal infection (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013).

Activities of chitinase, peroxidases and polyphenoloxidases in cucumber plants infected by *Pythium* spp. were enhanced as a result of silicon root application (Cherif *et al.*, 1994; Liang *et al.*, 2005). Increased activity of chitinase and  $\beta$ -1,3-glucanase in pea seeds supplied with potassium silicate reduced incidence of *Mycosphaerella pinodes* (Dann and Muir, 2002). Enhanced peroxidase activity in wheat leaves, due to silicon treatment, decreased the severity of powdery mildew caused by *Blumeria graminis*

*f.sp.tritici* (Yang *et al.*, 2003). Regarding the rice–*M. oryzae* interaction, increased resistance against the blast pathogen is characterized by higher accumulation of glucanase, peroxidase, polyphenol oxidase and phenylalanine ammonia-lyase (Rodrigues *et al.*, 2003, 2004, 2005; Cai *et al.*, 2008). Liang *et al.* (2005) found that enhanced peroxidases, polyphenoloxidases and chitinases activities due to silicon root application were effective in reducing powdery mildew severity in cucumber. Regarding *Cryptococcus laurentii*-sweet cherry interaction, increased polyphenol oxidase activity reduced disease severity in fruit treated with 1% silicon (Qin and Tian, 2005). Enhanced peroxidase activity in melon plants treated with sodium silicate decreased incidence of pink rot caused by *Trichothecium roseum* (Bi *et al.*, 2006). Increased rice resistance due to silicon treatment against the brown spot pathogen (*Bipolaris oryzae*) seems to be the result of higher levels of chitinase and peroxidase (Dallagnol *et al.*, 2011). Enhanced peroxidase and phenylalanine ammonia lyase activities in sodium silicate-treated Chinese cantaloupe decreased the severity of pink rot (*Trichothecium roseum*) (Guo *et al.*, 2007). Xavier *et al.* (2011) reported that higher activities of chitinases and peroxidases contributed to the increase in wheat resistance to blast (*Pyricularia oryzae*). Increased activities of superoxide dismutase, ascorbate peroxidase and glutathione reductase in common bean plants reduced severity of *Colletotrichum lindemuthianum* (Polanco *et al.*, 2014). Schurt *et al.* (2014) found that the increased activities of phenylalanine ammonia-lyases, peroxidases, polyphenoloxidases and chitinases in the leaf sheaths of rice plants supplied with silicon led to the reduction in the progress of sheath blight lesions (*R. solani*). Increased activation of chitinase, superoxide dismutase, peroxidase and  $\beta$ -1,3-glucanase reduced the severity of powdery mildew (*Podosphaera xanthii*) in melon plants (Dallagnol *et al.*, 2015). Perennial ryegrass grown in silicon-amended soil exhibited greater activities of peroxidase and polyphenol oxidase following infection by *Magnaporthe*

*oryzae* (Rahman *et al.*, 2015). High activities of superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase and lipoxygenase contributed to the increase in rice resistance to *Pyricularia oryzae* (Domiciano *et al.*, 2015). In leaves of soybean plants supplied with silicon, higher activities of chitinases,  $\beta$ -1-3-glucanases, phenylalanine ammonia-lyases, peroxidases, and polyphenol oxidases reduced the incidence of target spot (*Corynespora cassiicola*) (Fortunato *et al.*, 2015).

#### 4.2.2. Antifungal compounds

Antifungal compounds play important role in plant fungal resistance (Fauteux *et al.* 2005; Datnoff *et al.* 2007; Van Bockhaven *et al.* 2013). Defense-related enzymes have an important role in regulating the production and accumulation of lignin, flavonoids, and phytoalexins (Cai *et al.*, 2009). Rodrigues *et al.* (2005) reported the strong induction of pathogenesis-related protein transcripts following infection by *Magnaporthe grisea*, which corresponded to an increase in the concentration of lignin in rice plants. Moreover, Xavier *et al.* (2011) showed that the high peroxidase activity following leaf blast infection of wheat leaves supplied with silicon was associated with an increase in the concentration of lignin. However, the biochemical pathways by which the phenolic metabolism might mediate silicon-enhanced plant resistance to fungi remains unclear (Fauteux *et al.*, 2005; Datnoff *et al.*, 2007; Van Bockhaven *et al.*, 2013). Silicon application induces the production of antifungal compounds after pathogen penetration of the epidermal cells (Cai *et al.*, 2009).

Enhanced accumulation of phenolic substances impeded the penetration of *Pythium ultimum* hyphae into the vascular system of cucumber plants (Cherif *et al.*, 1992). Phenolics extracted from silicon-treated cucumber plants displayed a strong fungistatic activity against *Pythium* spp. (Cherif *et al.*, 1994). Increased flavonoid phytoalexin aglycone rhamnetin in cucumber plants due to silicon treatment decreased severity of powdery mildew caused by *Podosphaera xanthii*



(Fawe *et al.*, 1998). Enhanced glycosylated phenolics and lignin activities in epidermal cells of silicon-treated wheat reduced severity of *Blumeria graminis* f.sp. *tritici* (Belanger *et al.*, 2003; Yang *et al.*, 2003). Increased silicon-induced resistance of rice to blast (*M. grisea*) was related to higher production of phytoalexin (Rodrigues *et al.*, 2004; 2005). Higher accumulation of fungitoxic phenolic compounds due to silicon treatment protected *Arabidopsis* from powdery mildew caused by *Erysiphe cichoracearum* (Ghanmi *et al.*, 2004; Fauteux *et al.*, 2005). Increased activity of antimicrobial glycosylated phenolics, diterpenoid phytoalexins, and lignin decreased severity of blast disease in silicon-treated rice plants (Cai *et al.*, 2008). Dallagnol *et al.* (2011) found that decreased level of rice brown spot (*Bipolaris oryzae*) was due to enhanced accumulation of lignin and soluble phenolics. High concentrations of lignin-thioglycolic acid derivatives increased wheat resistance to blast caused by *Pyricularia oryzae* (Xavier *et al.*, 2011). Regarding the rice–*Rhizoctonia solani* pathosystem, silicon-induced enhancement of phenolic metabolism contributed to the improved resistance to sheath blight of a susceptible rice cultivar (Zhang *et al.*, 2013). Enhanced production of flavonoids in wheat leaves reduced incidence of blast caused by *Pyricularia oryzae* (Rodrigues *et al.*, 2014). Fortunato *et al.* (2015) found that higher activity of total soluble phenolics and lignin-thioglycolic acid derivatives in leaves of soybean plants supplied with silicon led to reduced incidence of target spot (*Corynespora cassiicola*). Regarding the perennial ryegrass–*Magnaporthe oryzae* interaction, Rahman *et al.* (2015) found that several phenolic acids, including chlorogenic acid and flavonoids, and relative levels of genes encoding phenylalanine ammonia lyase and lipoxygenase were significantly increased in silicon-amended plants compared with non-amended control plants. Increased lignin concentration reduced the incidence of *Podospaera xanthii* (powdery mildew) in melon plants (Dallagnol *et al.*, 2015)

#### 4.2.3. Molecular mechanism

Silicon acts as a modulator of host resistance to pathogens (Fauteux *et al.*, 2005; Van Bockhaven *et al.*, 2013). However, the biochemical and physiological mechanisms that are potentiated by silicon are complex phenomena (Rodrigues *et al.*, 2005). Under optimum conditions, gene expression had no significant difference between silicon-treated and non-treated plants (Watanabe *et al.*, 2004). A study by Kauss *et al.* (2003) conducted on cucumber leaves and investigating the process of plant infection showed that resistance to infection can be acquired by the expression of a protein rich in proline together with the presence of silica at the site of pathogen penetration. Fauteux *et al.* (2006) stated that only two genes were up-regulated when silicon alone was applied to *Arabidopsis* plants. Brunings *et al.* (2009) studied the gene expression of silicon-treated rice using a microarray and found differential regulation of 221 genes compared to untreated control, including some transcription factors. Chain *et al.* (2009) demonstrated a comparable differential response with 47 genes of varying function in silicon-treated wheat. It has been suggested that silicon could act as a potentiator of defense responses or as an activator of protein-mediated cell signaling (Fauteux *et al.*, 2005; Van Bockhaven *et al.*, 2013).

It has been proposed that in a cell, silicon controls the signaling events that guide the synthesis of antimicrobial compounds, and could also control the generation of systemic signals. In this way, silicic acid, without being a second messenger, might play a role in resistance, both local and systemic (Fauteux *et al.*, 2005; Bockhaven *et al.*, 2013). By using Agilent 44K oligo DNA arrays, it has been shown that silicon increased significantly the level of photorespiration in rice leaves infected by *Cochliobolus miyabeanus* (Van Bockhaven *et al.*, 2014). Genome-wide studies on tomato, rice, *Arabidopsis* and wheat grown in soil amended with silicon and compared to non-amended control plants have shown a differential and unique expression of a large number of genes involved in host

plant defense mechanisms or metabolism (Watanabe *et al.*, 2004; Fauteux *et al.*, 2006; Chain *et al.*, 2009; Brunings *et al.*, 2009; Gha-reeb *et al.*, 2011).

### 5. *In vitro* inhibition of fungal pathogens by soluble silicon

Some studies have been carried out to determine whether silicon has fungicidal activity *in vitro*. Hyphal growth of *Magnoportha grisea* on silicic acid-amended water agar was 62% less compared to growth on non-amended water agar (Maekawa *et al.*, 2003). Bekker *et al.* (2006) reported that mycelial growth of 11 phytopathogenic fungi (*Phytophthora cinnamomi*, *Sclerotinia sclerotiorum*, *Pythium* F-group, *Mucor pusillus*, *Drechslera* spp., *Fusarium oxysporum*, *F. solani*, *Alternaria solani*, *Colletotrichum coccoodes*, *Verticillium theobromae*, *Curvularia lunata* and *Stemphylium herbarum*) was inhibited on potassium silicate (20.7% SiO<sub>2</sub>)-amended PDA, at concentrations  $\geq$  20 ml Si/l agar. The level of mycelial inhibition was dependant on dose indicating different tolerance of the tested fungi to potassium silicate. Bi *et al.* (2006) reported that 100 mM sodium silicate completely inhibited mycelial growth of *Alternaria alternata*, *F. semitectum*, and *Trichothecium roseum*. Sodium silicate inhibited spore germination and mycelial growth of *Penicillium digitatum* (Liu *et al.*, 2010). Nevertheless, Shen *et al.* (2010) indicated that the inhibition of *Rhizoctonia solani*, *F. oxysporum*, *F. oxysporum* f. sp. *fragariae* and *Pestalotiopsis clavispora* colony growth on PDA plates amended with low concentrations of potassium silicate (1.67, 3.33, 5 or 6.67 mM) was due to a pH effect. The range of potassium silicate concentrations tested is suitable for field application (Shen *et al.*, 2010). Also, the potassium silicate concentrations used by Bekker *et al.* (2006) were 50 to 60 times higher than those in Shen's *et al.* (2010) study. Moreover, these concentrations (Bekker *et al.*, 2006; Bi *et al.*, 2006) are unrealistic for field use because the high pH of the resulting potassi-

um silicate solutions could cause phytotoxicity. Shen *et al.* (2010) concluded that the reduction in fungal diseases following treatment of field plants with silicon is probably not due to the fungistatic effects of silicon, but to other biochemical and physical mechanisms mentioned previously.

### 6. Conclusions

Silicon application could be one of the most promising approaches for sustainable, environmentally sound and broad-spectrum control of fungal diseases in plants in various agricultural contexts. That is why in the last few decades, extensive studies have been carried out to investigate its protective role in numerous pathosystems. However, its effect on enhancing plant resistance against fungal pathogens is not limited to high silicon-accumulators as it has also been described in low silicon-accumulators. The role of silicon as a modulator of plant defense-related gene expression in combination with biotic stress is dominant over its function as a mechanical barrier. Silicon does not seem to directly affect phytopathogenic fungi, as fungicides, and therefore exerts no selective pressure. The in-depth understanding of silicon in plants will be helpful to effectively use silicon to increase crop yield and enhance resistance to fungal pathogens.

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## ΑΡΘΡΟ ΑΝΑΣΚΟΠΗΣΗΣ

# Ο ρόλος του πυριτίου (Si) στην αύξηση της αντοχής των φυτών σε μυκητολογικές ασθένειες

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**Περίληψη** Η χρήση του πυριτίου (Si) στη γεωργία έχει προσελκύσει το ενδιαφέρον πολλών ερευνητών εξ' αιτίας των πολλών οφελειών που έχει το στοιχείο αυτό στα φυτά. Η εφαρμογή του πυριτίου έχει μειώσει την ένταση πολλών ασθενειών σε καλλιέργειες μεγάλης οικονομικής σημασίας. Στην παρούσα μελέτη γίνεται ανασκόπηση της βιβλιογραφίας όσον αφορά στη σχέση μεταξύ της θρέψης των φυτών με πυρίτιο και της εμφάνισης και εξέλιξης των μυκητολογικών ασθενειών στα φυτά. Η παρούσα ανασκόπηση υπογραμμίζει τη γεωργική σημασία του πυριτίου στις καλλιέργειες, τη δυνατότητα αντιμετώπισης φυτοπαθολογικών μυκήτων με την εφαρμογή πυριτίου, τους διάφορους μηχανισμούς μέσω των οποίων το πυρίτιο επάγει την αντοχή των φυτών στα παθογόνα, και την *in vitro* ανασταλτική επίδραση

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του πυριτίου στην ανάπτυξη φυτοπαθογόνων μυκήτων. Ο συνδυασμός των δεδομένων που παρουσιάζονται στο παρόν άρθρο θα μπορούσε να συμβάλει στην καλύτερη κατανόηση της σχέσης μεταξύ της εφαρμογής πυριτίου, της αύξησης της αντοχής των φυτών στις μυκητολογικές ασθένειες και της μείωσης της έντασης των ασθενειών αυτών.

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