Revisão de Literatura

Silicon in plant disease control

Edson Ampélio Pozza[1], *Adélia Aziz Alexandre Pozza*[2] *e Deila Magna dos Santos Botelho*[1]

http://dx.doi.org/10.1590/0034-737X201562030013

ABSTRACT

All essential nutrients can affect the incidence and severity of plant diseases. Although silicon (Si) is not considered as an essential nutrient for plants, it stands out for its potential to decrease disease intensity in many crops. The mechanism of Si action in plant resistance is still unclear. Si deposition in plant cell walls raised the hypothesis of a possible physical barrier to pathogen penetration. However, the increased activity of phenolic compounds, polyphenol oxidases and peroxidases in plants treated with Si demonstrates the involvement of this element in the induction of plant defense responses. The studies examined in this review address the role of Si in disease control and the possible mechanisms involved in the mode of Si action in disease resistance in plants.

Key words: Management, plant diseases, resistance barriers, soil fertility, resistyance inducers.

RESUMO

O Silício no controle de doenças de plantas

Todos os nutrientes essenciais podem influenciar a incidência e a severidade das doenças de plantas. O silício (Si), embora não seja considerado nutriente essencial para plantas, destaca-se por seu potencial para diminuir a intensidade de doenças em várias culturas. O mecanismo de ação do Si na resistência de plantas ainda não está totalmente esclarecido. A forma de deposição do Si na parede celular de plantas gerou a hipótese de uma possível barreira física, dificultando a penetração do patógeno. No entanto, o aumento da atividade de compostos fenólicos, polifenoloxidases e peroxidases em plantas tratadas com Si demonstra o envolvimento deste elemento na indução de reações de defesa da planta. A presente revisão visa abordar o papel do Si no controle de doenças e os possíveis mecanismos envolvidos no modo de ação do Si na resistência de plantas às doenças.

Palavras-chave: Manejo, doenças de plantas, barreiras de resistência, fertilidade do solo, indutores de resistência.

Submitted on 07/20/2014 and aproved on 11/30/2014.

[1] Universidade Federal de Lavras, Departamento de Fitopatologia, Lavras, Minas Gerais, Brasil. edsonpozza@gmail.com; deilamagna@hotmail.com

[2] Universidade Federal de Lavras, Departamento de Ciência do Solo, Lavras, Minas Gerais, Brasil. adelia.pozza@dcs.ufla.br

*Autor para correspondência: edsonpozza@gmail.com

INTRODUCTION

Silicon (Si) is the second most abundant element in the earth's crust, being surpassed only by oxygen. It is present in the soil solution in the form of monomeric or monosilicic acid (H_4SiO_4) and is readily absorbed into the root system. Although it is not considered essential nutrient for plants, Si is classified by many authors as beneficial or useful as it improves tolerance to drought, gives greater resistance to metal toxicity and lower intensity of diseases and pests. Silicon, therefore, can contribute as part of the management of different crops to increase yield, as long as other crop needs such as good soil fertility, pH correction, appropriate soil type, favorable climate, among others have been met.

The beneficial effect of Si was associated with reducing disease intensity, initially in monocots, including grasses or poaceae, in the 60s (Jones & Handreck, 1967), because of its ease of uptake, translocation and accumulation (Marschner, 1995). In rice, it was associated with lower incidence and severity of rice blast, brown spot and sheath blight (Datnoff *et al*., 1997; Zanão Junior *et al*., 2009 a e b; Prabhu *et al*., 2012). It was associated with rust (*Puccinia melanocephala*) in sugarcane (Naidoo *et al*., 2009), control of *Blumeria graminis* f. sp. *tritici* in wheat (Belanger *et al*., 2003) and control of *Erysiphe graminis* in barley (Carver *et al*., 1987). Then, promising results in reducing disease intensity were found in various pathosystems, also in dicots, including Cercospora leaf spot and rust in coffee (Pozza *et al*., 2004; Botelho *et al*., 2005; Amaral *et al*., 2008; Carre-Missio *et al*., 2014), pestalotiopsis leaf spot and powdery mildew in strawberry (Palmer *et al*., 2006; Kanto *et al*., 2006; Kanto *et al*., 2007; Carré-Missio *et al*., 2010), powdery mildew in melon, squash and cucumber (Menzies *et al*., 1991; Samuels *et al*., 1991), rust in soybean (Pereira *et al*., 2009; Lima *et al*., 2010), anthracnose in common-bean and sorghum (Moraes *et al*., 2009; Polanco *et al*., 2012; Resende *et al*., 2013) and root rot in tomato and avocado (Heine *et al*., 2007; Bekker *et al*., 2006).

The effect of silicon on the control of plant diseases, its mode of action and its function in several pathosystems are not yet fully understood. There is the hypothesis of a possible physical barrier formation, which is based on the form of Si accumulation in plants, mainly in the cell wall. In its upward movement, via apoplast, from the roots to the leaves, silicon polymerization occurs in the extracellular spaces, accumulating on the walls of the epidermal cells of leaves and xylem vessels (Samuels *et al*., 1991; Fawe *et al*., 2001; Kim *et al*., 2002). There may also be increased activity of enzymes involved in plant defense such as peroxidase, polyphenoloxidase, phenylalanine ammonia lyase and lipoxygenase (Chérif *et al*., 1994; Fauteux *et al*., 2005; Cai *et al*., 2008; Shetty *et al*., 2011; Polanco *et al*., 2012), which, in this case, is considered as a chemical barrier. Therefore, Si application can contribute in the management of plant diseases, among other practices.

A number of other studies relate the silicon interference with absorption of essential nutrients to plants (Pozza *et al*., 2007; Moraes *et al*., 2009; Botelho *et al*., 2005).

Because the ability to contribute to the formation of disease resistance barriers and studies conducted both in monocotyledonous and dicotyledonous plants, the objective of this review was to add information about the interaction of silicon with plant diseases.

Silicon in disease control in monocotyledons

Studies on silicon-induced disease control initiated with monocotyledons, particularly in rice and some grasses classified as accumulators of Si (Jones & Handreck, 1967).

In rice, several authors have reported promising results with Si application in disease control (Rodrigues *et al*., 2004; Prahbu *et al*., 2012). Si fertilization (0 and 2 t ha^{-1} of calcium silicate) was compared with the application of the fungicides Benomyl and Propiconazole for the control of rice blast (*Pyricularia grisea*) and brown spot (*Bipolaris oryzae*) and similar effects were observed for both the application of Si and fungicides on the control of these diseases (Datnoff *et al*., 1997). In rice brown spot, the Si application (0.402 g pot^{-1}) in the soil decreased by approximately 55% disease severity compared with the control (Zanão Junior *et al*., 2009). However, according to Rezende *et al*. (2009) and Zanão Junior *et al*. (2009), the management of rice brown spot with Si is effective when it is applied in the soil. The severity of sheath blight, caused by the fungus *Rhizoctonia solani* in rice plants grown in nutrient solution, was also reduced (Schurt *et al*., 2012).

The application of Si in other monocot pathosystems also showed promising results. Resende *et al*. (2013) reported that sorghum grown in nutrient solution added with Si (2 mmol L^{-1}) had severity of anthracnose (*Colletotrichum sublineolum*) around 20%, while the control was 93%, at 10 days after inoculation. There are also reports of reduction of disease severity in sugarcane rust *(Puccinia melanocephala*) (Naidoo *et al*., 2009), control of *Blumeria graminis* f.sp.. sp. *tritici* on wheat (Belanger *et al*., 2003) and *Erysiphe graminis* in barley (Carver *et al*., 1987).

Silicon in disease control in dicotyledons

Studies on Si disease control in dicotyledonous plant pathosystems began with research on powdery mildew and damping-off in cucumber (Adatia & Besford, 1986; Samuels *et al*., 1991; Cherif *et al*., 1994) and vine (Bowen *et al*., 1992), among others.

Several studies confirmed the effective action of Si in controlling powdery mildew (*Sphaerotheca fuliginea*) in cucurbits (Samuels *et al*., 1991; Menzies *et al*., 1992; Belanger *et al*., 2003). Cucumber plants inoculated with *S. fuliginea* and grown in nutrient solution supplemented with sodium silicate showed a reduction in spore germination and the number and area of colonies per leaf compared with the control plants without Si (Menzies *et al*., 1991).

Another important disease influenced by fertilization with Si is the bean anthracnose (*Colletotrichum lindemuthianum*). Plants in nutrient solution supplemented with Si (2 mmol L^{-1}) had higher incubation period compared with plants without Si (Polanco *et al*., 2012). In the same pathosystem, Moraes *et al*., (2009) observed a linear decrease of 7% in the area under the progress curve of bean anthracnose incidence with calcium silicate doses ranging from zero to 1.89 g kg^{-1} SiO_2 applied to the soil (Figure 1). The silicon content in bean shoots increased from 0.86 to 1.14 mg kg^{-1}.

The spodogram, or image from the ashes of bean leaves made after the last anthracnose assessment, showed the greatest accumulation of silica in the ribs (Figure 2B), precisely where the initial infection of *C. lindemuthianum* occurs in treatments with the addition of this element.

In coffee, promising results were reported for Cercospora leaf spot (*Cercospora coffeicola*), rust (*Hemileia vastatrix*) and phoma/ascochyta leaf spot (*Phoma tarda*) (Pozza *et al*., 2004; Reis *et al*., 2008; Botelho *et al*., 2005; Carré-Missio *et al*., 2012 b; Carré-Missio *et al*., 2014).

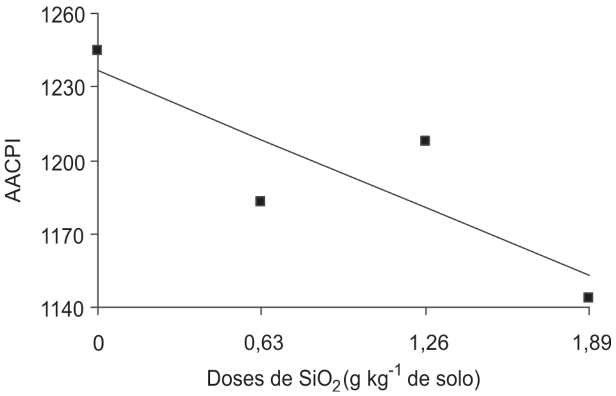

Figure 1: Area under the progress curve of incidence (AACPI) as a function of calcium silicate doses applied to the soil (Moraes *et al*., 2009).

The effect of calcium silicate applied to the substrate in tubes on the intensity of the Cercospora leaf spot in three coffee cultivars (Red Catuaí, Novo Mundo and Icatú) was evaluated by X ray microanalysis. Cultivar Catuaí fertilized with silicate and maintained for at least six months in the substrate showed reduction by 63.2% in the damaged leaves and 43% in total lesions per plant compared with the control. There was uptake and translocation of silicon according to mapping by X-ray microanalysis (MAX) (Figure 3). The leaf silicon content obtained through chemical analysis in Catuaí seedlings varied from 1.5 g kg^{-1} in the control to 4.7 g kg^{-1} in the substrate added with 1 g kg^{-1} $CaSiO_3$ (Pozza *et al*., 2004).

The above mentioned contents were similar to those obtained in the shoots of plants of Catuaí Amarelo by Cunha *et al*. (2012). These authors found contents of 5 g kg^{-1} of Si in plants treated with 2 mmol L^{-1} of SiO_2 in nutrient solution and 1.83 g kg^{-1} in the control at 33 days after the treatments have initiated. However, Carré-Missio *et al*. (2009) found no difference in the silicon application in nutrient solution for translocation to shoots, although the contents ranged from 4.3 to 4.5 g kg^{-1} in the treatments without and with addition of 2 mmol L^{-1} of Si in the form of monosilicic acid, respectively.

Studying the same pathosystem, Botelho *et al*. (2005) observed a linear decrease of 10.8% in the area under the progress curve of the number of diseased plants with increased doses of SiO_2 from 0 to 1.22 g kg^{-1} and a decrease in total damage for 0.85 g kg^{-1} SiO_2 applied to the substrate (Figure 4).

According to Carré-Missio *et al*. (2012), the foliar application of 15 g L^{-1} potassium silicate can reduce the coffee rust severity. However, according to these authors, coffee plants were inefficient to translocate the Si from roots to shoots when grown in nutrient solution, restricting it exclusively to the root system.

Other crops such as strawberry, soybean, tomato and rose also showed promising results in reducing disease with Si application (Kanto *et al*., 2006; Carré-Missio *et al*., 2010; Lima *et al*., 2010; Ghareeb *et al*., 2011; Shetty *et al*., 2011). Conidia of *Sphaerotheca aphanis* var. *aphanis* (causal agent of strawberry powdery mildew) had germination percentage reduced in leaves of strawberry grown with potassium silicate (Kanto *et al*., 2007). Carré-Missio *et al*. (2010) observed 61% reduction in the severity of pestalotiopsis leaf spot (*Pestalotia longisetula*) on strawberry plants sprayed with 30 g L^{-1} potassium silicate compared with the control treatment (plants sprayed with water).

Soybean plants grown in nutrient solution with potassium silicate doses (0, 56, 112, 168, 224 and 280 mg L^{-1}) with decreasing K addition to the treatments, so to obtain the same element concentration in all treatments, were inoculated with *Phakopsora pachyrhizi* and showed a 27.5% reduction in the area under the progress curve of the number of rust lesions (AACNL) with increasing doses of silicon in the nutrient solution (Lima *et al.*, 2010) (Figure 5).

The reduction in disease intensity is not limited to fungal diseases. Studies reported the Si efficacy in controlling bacterial wilt of tomato (*Ralstonia solanacearum*) (Dannon & Wydra, 2004; Ghareeb *et al.*, 2011; Wang *et al.*, 2013).

Modes of silicon action in plant disease control

The mode of silicon action in plant disease control is not yet completely understood. Studies attribute its

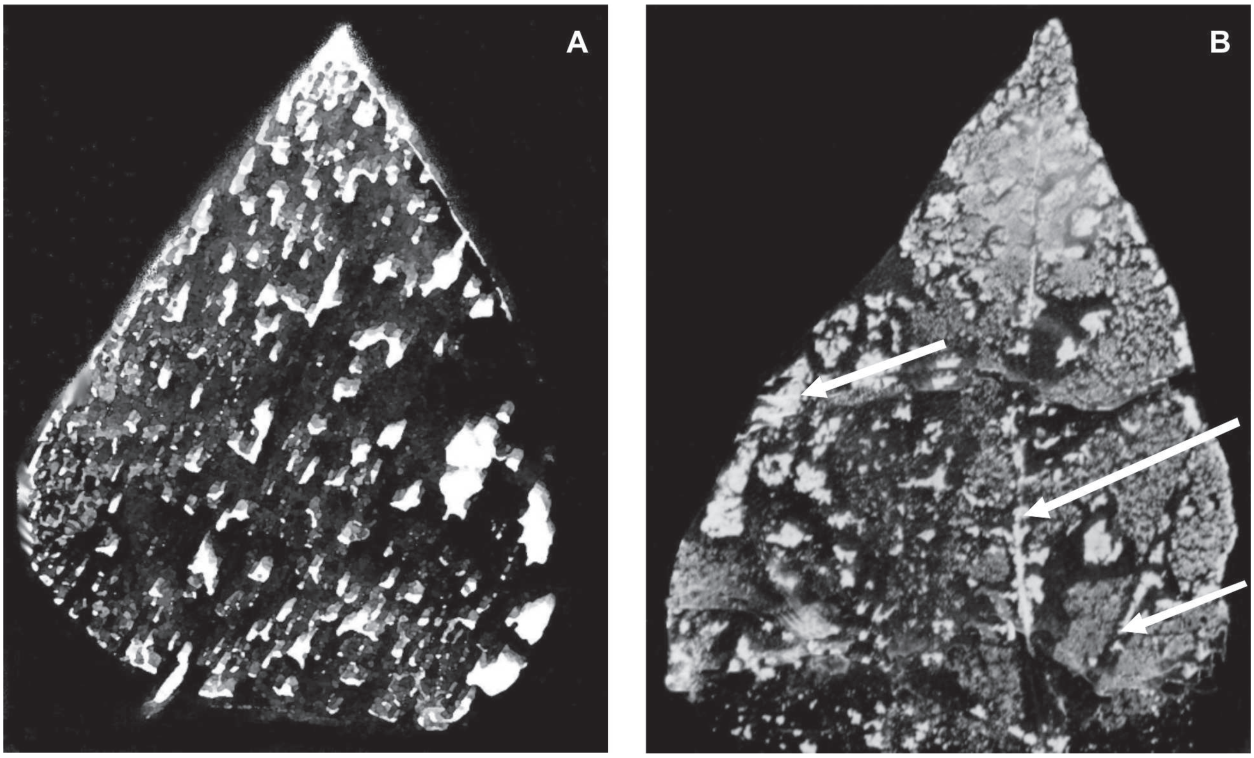

Figure 2 - Spodogram of bean leaves. A. Si non-treated plants; B. Plants treated with 1.89 g kg^{-1} of SiO_2; arrows indicate Si accumulation in the ribs (Moraes *et al*, 2009).

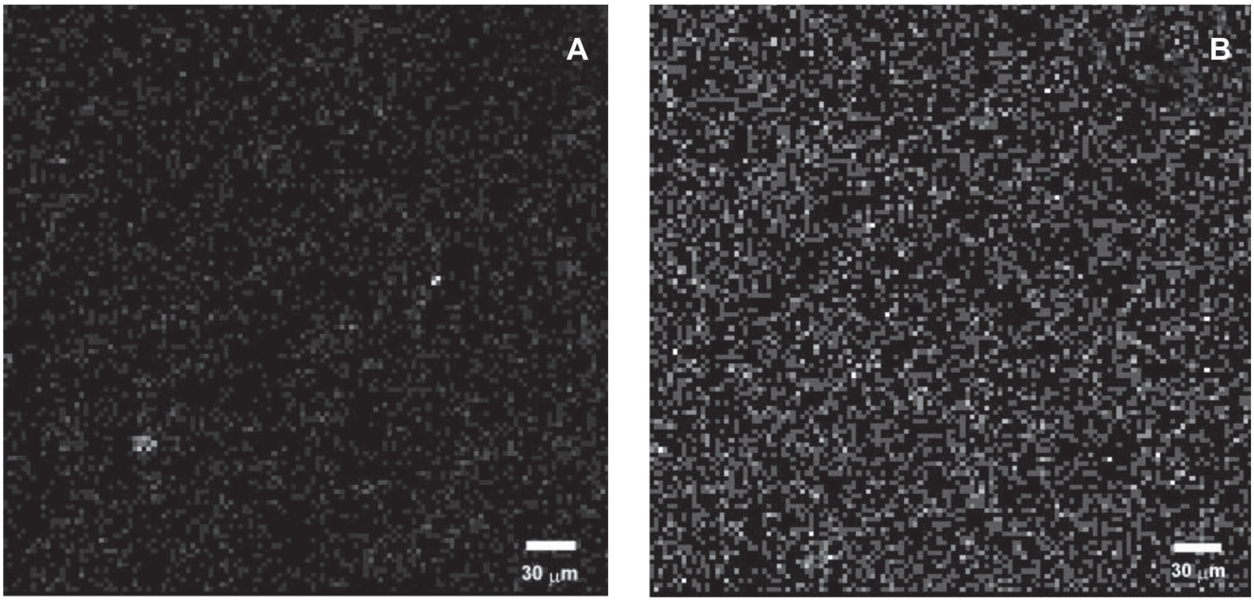

Figure 3 - Si mapping by X-ray microanalysis (MAX), leaf blade area of leaves of cultivar Catuaí. A. Control; B. $CaSiO_3$ fertilized. (Photo: Eduardo Alves)

effect on disease reduction to the formation of both physical barriers, by deposition of Si (Sangster *et al.*, 2001; Kim *et al.*, 2002; Pozza *et al.*, 2004; Carré-Missio *et al.*, 2012b), and chemical barriers such as defense enzymes (Cherif *et al.*, 1994; Fauteux *et al.*, 2005; Cai *et al.*, 2008; Shetty *et al*, 2011; Polanco *et al.*, 2012). The joint action of these barriers in disease control in plants fertilized with Si was observed by Cai *et al.* (2008) and Resende *et al.* (2013). Moreover, silicon is reported to interfere with the absorption of essential nutrients to plants, including horizontal resistance to form barriers as the wax layer and the cell wall, among others (Pozza *et al.*, 2007; Moraes *et al.*, 2009; Botelho *et al.*, 2005).

Physical barrier formation

The hypothesis of a possible physical barrier formation is based on the form of Si accumulation in plants. In its upward movement, via the apoplast, from the roots to the leaves, silicon undergoes polymerization in the extracellular spaces of the walls of leaf epidermal cells and xylem vessels (Fawe *et al.*, 2001). Si is absorbed in roots, in the form of monosilicic acid, and is transported passively through transpiration stream and deposited beneath the cuticle, forming a cuticle-silica double layer (Sangster *et al.*, 2001). According to Kim *et al.* (2002), this double layer delayed penetration of *Pyricularia grisea* in rice leaves.

Vine seedlings sprayed with potassium silicate (17 mmol L^{-1} of Si) showed a significantly reduced penetration of *Uncinula necator*, due to the Si layer formation in the leaf cuticle. In contrast, there was a higher intensity of the disease in non-treated leaf areas (Bowen *et al.*, 1992). Polymerization of potassium silicate on the leaf surface of cucumber, melon and pumpkin was also observed by Menzies *et al.* (1992) who reported that this physical barrier reduced the penetration of the fungus *Sphaerotheca fuliginea*.

Pozza *et al.* (2004) observed the presence of a well-developed wax layer on the abaxial surface of coffee seedlings grown in plastic tube substrate and Lima *et al* (2010), to a lesser extent, on soybean in nutrient solution. The reduction in the intensity of Cercospora leaf spot in coffee was attributed to the formation of a thicker epicuticular wax layer, which hampers the pathogen penetration (Figure 6). The combined effect of calcium was isolated by the addition of calcium oxide at the zero dose of $CaSiO_3$. To produce this wax layer, the seedlings remained in tubes with silicate for 7 months, from the "jaguar ear" stage to the harvest of the experiment.

The presence of Si in the outer epidermal layer was reported by Carver *et al.* (1987). These authors observed the complexation of phenolic compounds with silicon in the wall of epidermal cells so as to reduce and hamper the expansion of lesions and the disease intensity by making the cells more rigid, which was later confirmed by Rodrigues *et al.* (2011).

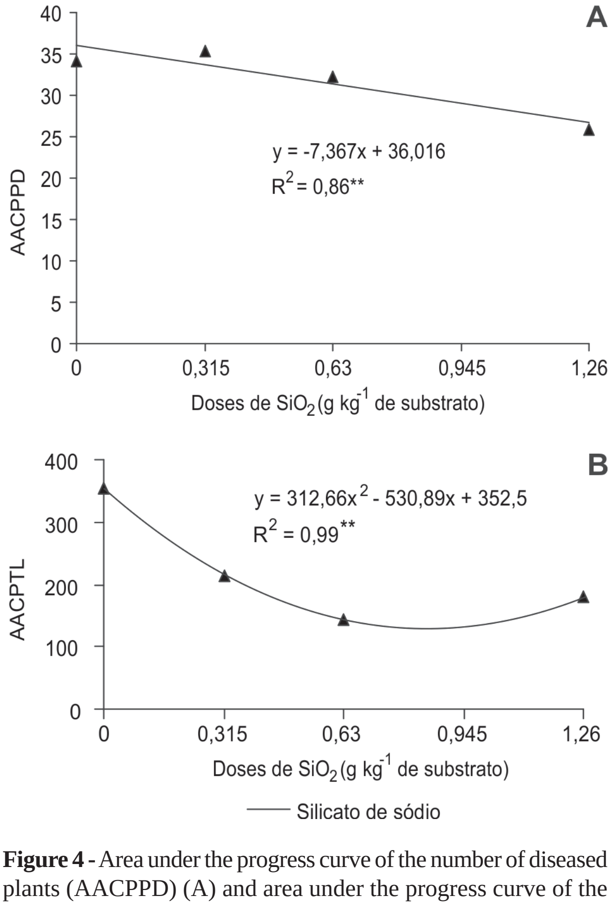

Figure 4 - Area under the progress curve of the number of diseased plants (AACPPD) (A) and area under the progress curve of the total number of lesions (AACPTL) (B), as a function of the silicon dose applied to the substrate.

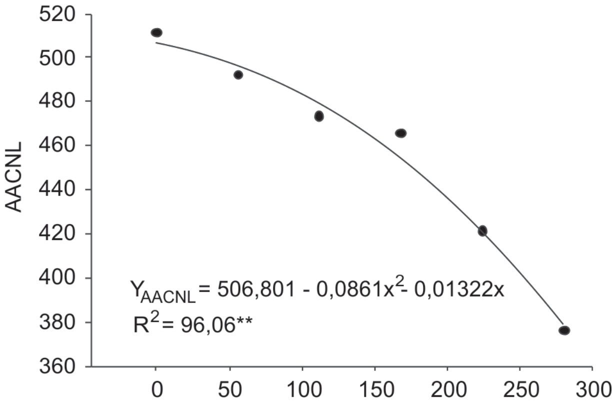

Figure 5 - Area under the progress curve of the number of rust lesions (*Phakopsora pachyrhizi*)/cm^2 of leaf area (AACNL) of soybean (*Glycine max*) as a function of increasing concentration of silicon in nutrient solution.

Biochemical mechanisms

Biochemical and physiological mechanisms of resistance associated with Si include the increased production of phenolic compounds, phytoalexins and lignin, the activity of enzymes related to defense such as chitinases and β-1, 3 - glucanases, as weel as increased expression of genes associated with plant resistance to pests and diseases (Cherif *et al*., 1994; Dann & Muir, 2002; Liang *et al*., 2005; Lima *et al*., 2010).

The application of 3.6 mmol L^{-1} Si on rose (*Rosa hybrida*) increased the concentration of antimicrobial flavonoids and phenolic compounds in response to inoculation with *Podosphaera pannosa* (causal agent of downy mildew of rose). Simultaneously, there was the expression of genes that encode key enzymes in the pathway of phenylpropanoids (phenylalanine ammonia lyase, cinnamyl alcohol dehydrogenase and chalcone synthase). The authors discussed that the mode of Si action in controlling rose diseases is by production of antifungal phenolic compounds (Shetty *et al*., 2011). Studies on cucumber leaves treated with Si showed that the resistance to infection may be involved in the expression of the gene encoding proline-rich protein (PRP1) (Kauss *et al*., 2003).

Joint action of physical barrier and biochemical mechanisms

Some studies have described the joint action of physical barrier and activation of enzymes related to plant defense. Cai *et al*. (2008) discussed that the reduction in severity of rice diseases such as rice blast, by Si, is a complex process which is not limited to the formation of passive mechanical barriers - deposition and polymerization of Si below the cuticle – or the induction of biochemical reactions (production of phenolic compounds), but results from the combined action of these two mechanisms. Sorghum leaves inoculated with *Colletotrichum sublineolum* and supplemented with Si showed high Si deposition on infection sites and fewer and smaller acervuli compared with the non-treated leaves. In addition, there was a higher concentration of plant defense enzymes, peroxidases and polyphenol, and anthocyanin in Si-treated leaves (Resende *et al*., 2013). The authors also reported the joint action of physical and biochemical barriers promoted by Si action, reducing *C. sublineolum* infection.

Silicon influence on the absorption of essential nutrients to plants

Silicon is usually provided as calcium silicate dissociated into silicate and calcium. It influences the absorption of both the silicate anion and the Ca^{2+} cation. Following the application, it acts on the soil as a competitive anion for adsorption sites. Adsorption reactions occur mainly in the clay fraction and soil organic matter, and aluminum, iron and manganese oxides, among others, are the most representative reactive inorganic surfaces in soils of variable charge in Brazil. The silicon adsorption on mineral reactive surfaces, prior to the application of phosphate, increases the availability of phosphate, sulfate and nitrate in soils with high capacity of retaining these anions, because H_4SiO_4 is a molecule that competes with these ions for soil adsorption sites (Pozza *et al*., 2009). Such competition

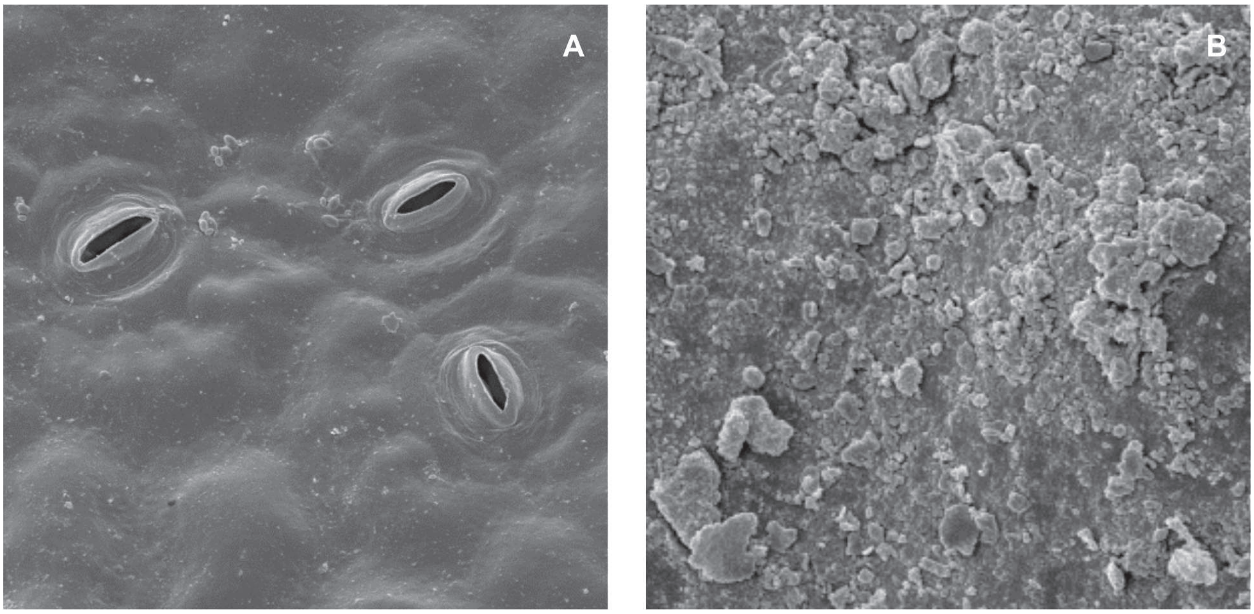

Figure 6 - Absence of wax layer (A) on control plant leaves and wax deposits on leaves of coffee seedlings treated with calcium silicate in the soil (B). (Photo: Eduardo Alves)

may cause the silicic acid to promote the phosphate desorption, for example, and vice versa (Camargo *et al*., 2005). Phosphorus desorbed from the reactive surfaces of the soil becomes available in the soil solution and can be absorbed by plants and, thus, enter into metabolic pathways to increase the resistance of plants to diseases.

Sulfate retention in soil is lower than the phosphate in a wide pH range, which helps explain the higher sulfate movement in the soil after P fertilization and, consequently, the silicate fertilization. Nitrate adsorption in variable charge soils tends to increase in depth and this phenomenon is associated with an increased number of positive electric charges in this direction (Dynia *et al*., 2006). This phenomenon tends to hamper this oxyanion leaching (Araújo *et al*., 2004), implying less eutrophication of water bodies.

Assays with competitive adsorption and desorption of anions on natural soil gibbsite have demonstrated the increasing adsorption sequence: sulfate<nitrate<<<silicate<phosphate, hence, the proximity of the adsorption strength of phosphate and silicate anions, assays were set with the displacement of phosphate adsorbed by the previous silicate application. The silicon adsorption on mineral reactive surfaces, prior to phosphate application, can increase the phosphate availability in soils with high capacity of anion retention, such as oxidic anions. The silicate anions are considered as competitors with phosphate for the same soil adsorption sites, so that silicon can move (desorb) phosphate or being moved by it, from the solid to the liquid phase. The same can occur with nitrate and sulfate, thus providing these essential nutrients to the soil solution and hence to plants (Pozza *et al*., 2007). These anions released into the soil solution will be absorbed by plants which will be able to build resistance barriers with these nutrients.

Another mode of silicon action in plant disease resistance is the effect on plant mineral nutrition. Mineral nutrients, in general, influence plant resistance to diseases. According to Marschner (1995) and Pozza & Pozza (2006), both macro and micronutrients in non-balanced doses influence vigor and defense reactions of plants and can contribute to changes in host susceptibility to disease. They can act directly on secondary metabolic pathways, where fungistatic phenolic compounds are produced and also increase cell wall resistance, either by thickening or increasing the resistance of the middle lamella forming physical and chemical barriers, as in the case, for example, of calcium. The application of calcium silicate also supplies Ca^{2+} ions, which are also responsible for resistance barriers. However, if not applied in balance with other cations in the soil, it can compete with Mg^{2+}, K^{+} and NH^{4+} for the same absorption sites, render the plants deficient in these minerals and unbalance plant nutrition. Studies in this line were carried out in coffee (Garcia Junior *et al*., 2003), soybean (Pinheiro *et al*., 2011) and corn (Carvalho *et al*., 2013).

Final considerations

Undoubtedly, silicon can contribute to reduce the intensity of diseases in the field. Silicon is absorbed and translocated and can be found at the infection sites, especially in monocotyledons, forming both physical and biochemical resistance barriers. Several studies have also reported the effect of Si on reducing disease in dicotyledons. Knowing its effects, it can be included in disease management plans, not as the only method able to solve all pest problems, but as an important component of the integrated pest management, that is, it can contribute. The balanced plant nutrition, with Ca, Mg and K and the supply of Si, is not able in most cases to reduce drastically the disease, when compared with a fungicide, which should always be added to the experiment as a positive control. Another important fact is the source of Si and other elements present in the trade product, which is usually calcium silicate, and both silicon and Ca are responsible for forming resistance barriers. There are silicates with other cations in the market, in this case, when the product is tested or used in experimentation, one should take care to isolate or separate the effects of each product component. Moreover, the particle size of the product to be purchased must be taken into account. In general, coarse grained products take longer to react in the soil. Products based on slag must always be chemically analyzed to determine the presence and amount of metals. In conclusion, silicon can contribute to the management of plant diseases, but always knowing its real effects and its source.

REFERENCES

Adatia MH & Besford RT (1986) The effects of silicicon on cucumber plants grow in recirculating nutrient solution. Annual Botany, 58:343-351.

Amaral DR, Resende MLV, Ribeiro Júnior, PM, Borel JC, Mac Leod REO & Pádua M A (2008). Silicato de potássio na proteção do cafeeiro contra *Cercospora coffeicola*. Tropical. Plant Pathology, 33:425-431.

Araújo AR, Carvalho JLN, Guilherme LRG Curi N & Marques JJ (2004) Movimentação de nitrato e amônio em colunas de solo. Ciência e Agrotecnologia, 28:541-545.

Bekker TF, Kaiser C & Labuschagne N (2006) Efficacy of water soluble silicon against *Phytophthora cinnamomi* root rot of avocado: A progress report. South African Avocado growers. Association Yearbook, 29:59-62.

Bélanger RR, Benhamou N & Menzies JG (2003) Cytological Evidence of an Active Role of Silicon in Wheat Resistance to Powdery Mildew (Blumeria graminis f. sp. tritici). Phytopathology, 93:402-412.

Botelho DMS, Pozza EA, Pozza AAA, Carvalho JG, Botelho CE & Souza PE (2005) Intensidade da Cercosporiose em mudas de cafeeiro em função de fontes e doses de silício. Fitopatologia Brasileira, 30:582-588.

Bowen P, Menzies J & Ehret D (1992) Soluble silicon sprays inhibit powdery mildew development on grape leaves. Journal of the American Society for Horticultural Science, 117:906–912.

Camargo MS, Korndorfer GH, Corrêa GF, Pereira HS, Barbosa DS & Resende RH (2005) Extratores de silício solúvel em solos: influência do calcário e fósforo. Bioscience Journal, 21:9-19.

Cai K, Gao D, Luo S, Zeng R, Yang J & Zhub X (2008) Physiological and cytological mechanisms of silicon-induced resistance in rice against blast disease Physiologia Plantarum, 134:324–333.

Carre-Missio V, Rodrigues FA, Schur, DA , Resende RS, Souza NFA, Rezende DC, Moreira WR & Zambolim L (2014) Effect of foliar-applied potassium silicate on coffee leaf infection by *Hemileia vastatrix*. Annals of Applied Biology, 164:396-403.

Carre-Missio V, Rodrigues FA, Schurt DA, Moreira WR, Rezende DC, Korndorfer GH & Zambolim L (2012a) Proteção local, não sistêmica, do silicato de potássio reduz os sintomas da ferrugem do cafeeiro. Tropical Plant Pathology, 37:275-280.

Carre-Missio V, Rodrigues FA, Schurt DA, Rezende DC, Moreira WR, Korndorfer GH & Zambolim L (2012b) Componentes epidemiológicos da ferrugem do cafeeiro afetados pela aplicação foliar de silicato de potássio. Tropical Plant Pathology, 37:50-56.

Carré-Missio V, Rodrigues, FA, Schurt DA, Rezende DC, Ribeiro NB & Zambolim L (2010) Aplicação foliar de silicato de potássio, acibenzolar-S-metil e fungicidas na redução da mancha de Pestalotia em morango. Tropical Plant Pathology, 35:182-185.

Carré-Missio V, Rodrigues FA, Schurt DA, Pereira, SC, Oliveira MG & Zambolim L (2009) Ineficiência do silício no controle da ferrugem do cafeeiro em solução nutritiva. Tropical Plant Pathology, 34:416-421.

Carvalho DO, Pozza EA, Casela CR, Costa RV, Pozza AAA & Carvalho CO (2013) Adubação nitrogenada e potássica na severidade da antracnose em dois cultivares de milho. Ceres, 60:380-387.

Carver TLW, Zeyen RJ & Ahlstrand GG (1987) The relationship between insoluble silicon and success or failure of attempted primary penetration by powdery mildew (*Erysiphe graminis*) germiling on barley. Physiological and Molecular Plant Pathology, 31:133-148.

Chérif M, Asselin A & Bélanger R R. (1994) Defense responses induced by soluble silicon in cucumber roots infected by *Pythium* spp. Phytopathology, 84:236-242.

Cunha ACMM, Oliveira ML, Caballero EC, Martinez HEP, Fontes PCR & Pereira PRG **(**2012) Growth and nutrient uptake of coffee seedlings cultivated in nutrient solution with and without silicon addition. Ceres, 59:392-398.

Dann EK & Muir SB (2002) Peas grown in media with elevated plant-available silicon levels have higher activities of chitinase and â-1,3-glucanase, are less susceptible to a fungal leaf spot pathogen and accumulate more foliar silicon. Australasian Plant Pathology, 31:9-13.

Dannon E & Wydra K (2004) Interaction between silicon amendment, bacterial wilt development and phenotype of *Ralstonia solanacearum* in tomato genotypes. Physiological and Molecular Plant Pathology, 64:233-243.

Datnoff LE, Deren CW & Snyder GH (1997) Silicon fertilization for disease management of rice in Florida. Crop Protection, 16:525-531.

Dynia JF, Souza MD & Boeira RC (2006) Lixiviação de nitrato em Latossolo cultivado com milho após aplicações sucessivas de lodo de esgoto. Pesquisa Agropecuária Brasileira, 41:855-862.

Fauteux F, Remus-Borel W, Menzies JG & Belanger RR (2005) Silicon and plant disease resistance against pathogenic fungi. FEMS Microbiology Letters, 249:1–6.

Heine G, Tikum G & Horst WJ (2007) The effect of silicon on the infection by and spread of *Pythium aphanidermatum* in single roots of tomato and bitter gourd. Journal of Experimental Botany, 58:569–577.

Fawe A, Menzies JG, Cherif M & Bélanger RR (2001) Silicon and disease resistance in dycotiledons. In: Datnoff LE, Snyder GH & Kordorfer GH (Eds) Silicon in Agriculture. London, Elsevier Science. p.159-169.

Jones L & Handreck K (1967) Silica in soils, plants, and animals. Advances in Agronomy, 19:107-149.

Garcia Júnior D, Pozza EA, Pozza AAA, Souza PE, Carvalho JG & Balieiro AC (2003) Incidência e severidade da cercosporiose do cafeeiro em função do suprimento de potássio e cálcio em solução nutritiva. Fitopatologia Brasileira, 28:286-291.

Ghareeb H, Bozsó Z, Ott PG & Wydraa K (2011) Silicon and *Ralstonia solanacearum* modulate expression stability of housekeeping genes in tomato. Physiological and Molecular Plant Pathology, 75:176-179.

Kanto T, Maekawa K & Aino M (2007) Suppression of conidial germination and appressorial formation by silicate treatment in powdery mildew of strawberry. Journal General Plant Pathology, 73:1-7.

Kanto T, Miyoshi A, Ogawa T, Maekawa K & Aino M (2006) Suppressive effect of liquid potassium silicate on powdery mildew of strawberry in soil. Journal General Plant Pathology, 72:137–142.

Kauss H, Seehaus K, Franke R, Gilbert S, Dietrich RA & Kroger N (2003) Silica deposition by a strongly cationic proline-rich protein from systemically resistant cucumber plants. Plant Journal, 33:87-95.

Kim SG, Kim KW, Park EW & Choi D (2002) Silicon-induced cell wall fortification of rice leaves: a possible cellular mechanism of enhanced host resistance to blast. Phytopathology, 92:1095-1103.

Liang YC, Sun WC, Si J & Romheld V (2005) Effects of foliar and root applied silicon on the enhancement of induced resistance to powdery mildew in *Cucumis sativus*. Plant Pathology, 54:678–685.

Lima LM, Pozza EA, Pozza AAA, Fonseca TAPS & Carvalho JG (2010) Quantificação da ferrugem asiática e aspectos nutricionais de soja suprida com silício em solução nutritiva. Summa Phytopathologica, 36:51-56.

Marschner H (1995) Mineral nutrition of higher plants 2Ed. New York, Academic. 889p.

Menzies J, Bowen P, Ehret DL & Glass ADM (1992) Foliar applications of potassium silicate reduce severity of powdery mildew on cucumber, muskmelon, and zucchini squash. Journal of the American Society for Horticultural Science, 117:902–905.

Menzies J, Bowen P, Ehret DL, Glass A.D.M, Hemer T, Koch C & Seywerd F (1991) Effects of soluble silicon on the parasitic fitness of *Sphaerotheca fuliginea* on *Cucumis sativus*. Phytopatology, 81:84-88.

Moraes SRG, Pozza EA, Pozza AAA, Carvalho JG & Souza PE (2009) Nutrição do feijoeiro e intensidade da antracnose em função da aplicação de silício e cobre. Acta Scientiarum Agronomy, 31:238-291.

Naidoo PV, McFarlane S, Keeping MG & Caldwell PM (2009) Deposition of silicon in leaves of sugarcane (*Saccharum* spp. hybridus) and its effect on the severity of brown rust caused by *Puccinia melanocephala*. Proceedings of South Africa Sugar Technology, 82:542–546.

Palmer S, Scott E, Stangoulis J & Able A (2006) The effects of foliar-applied Ca and Si on the severity of powdery mildew in two strawberry cultivars. Acta Horticulturae, 708:135-139.

Pereira SC, Rodrigues FA, Carré-Missio V, Oliveira MGA & Zambolim L (2009) Aplicação foliar de silício na resistência da soja à ferrugem e na atividade de enzimas de defesa. Tropical Plant Pathology, 34:164-170.

Pinheiro JB, Pozza EA, Pozza AAA, Moreira AS & Carvalho MC (2011) Severidade da ferrugem da soja em função do suprimento de potássio e cálcio em solução nutritiva. Ceres, 58:43-50.

Polanco LR, Rodrigues FA, Nascimento KJT, Shulman P, Silva LC, Neves FW & Vale FXR (2012). Biochemical aspects of bean resistance to anthracnose mediated by silicon. Annals of Applied Biology, 161:140–150.

Pozza AAA, Alves E, Pozza EA, Carvalho JG, Montanari M, Guimarães PTG & Santos DM (2004) Efeito do silício no controle da cercosporiose em três variedades de cafeeiro. Fitopatologia Brasileira, 29:185-188.

Pozza AAA, Curi N, Costa ETS, Guilherme LRG, Marques, JJGSM & Motta PEF (2007) Retenção e dessorção competitivas de ânions inorgânicos em gibbsita natural de solo. Pesquisa Agropecuária Brasileira, 42:1627-1633.

Pozza AAA, Curi N, Guilherme LRG, Marques, JJGSM, Costa ETS & Zuliani DQ (2009) Adsorção e dessorção aniônicas individuais por gibbsita pedogenética. Quimica Nova, 32:99-105.

Pozza EA & Pozza AAA (2006) A nutrição mineral no controle de doenças de plantas. In: Venzon M, Paula Júnior TJ & Pallini A (Eds.) Tecnologias alternativas para o controle de pragas e doenças. Viçosa, EPAMIG. p.49-80.

Prabhu AS, Barbosa Filho MP, Datnoff LE, Snyder GH, Berni RF, Rodrigues FA & Dallagnol LJ (2012) Silicon reduces brown spot severity and grain discoloration on several rice genotypes. Tropical Plant Pathology, 37:409-414.

Reis THP, Figueiredo, FC, Guimaraes PTG, Botrel PP & Rodrigues CR (2008) Efeito da associação silício líquido solúvel com fungicida no controle fitossanitário do cafeeiro. Coffee Science, 3:76-80.

Resende RS, Rodrigues FA, Gomes RJ & Nascimento KJT (2013) Microscopic and biochemical aspects of sorghum resistance to anthracnose mediated by silicon. Annals of Applied Biology, 163:114–123.

Rezende DC, Rezende, Rodrigues FA, Carré-Missio V, D. A. Schurt DA, Kawamura IK & Korndörfer GH (2009**)** Effect of root and foliar applications of silicon on brown spot development in Rice**.** Australasian Plant Pathology, 38:67–73.

Rodrigues FA, Carré-Missio V, Jham GN, Berhow M & Schurt DA (2011) Chlorogenic acid levels in leaves of coffee plants supplied with silicon and infected by Hemileia vastatrix. Tropical Plant Pathology, 36:404-408.

Rodrigues FA, McNally DJ, Datnoff LE, Jones JB, Labbé C, Benhamou N, Menzies J G & Bélanger RR (2004) Silicon enhances the accumulation of diterpenoid phytoalexins in rice: A potential mechanism for blast resistance. Phytopathology, 94:177-183.

Romero A, Munévar F & Cayón C (2011) Silicon and plant diseases. A review. Agronomía Colombiana, 29:473-480.

Samuels, AL, Glass ADM, Ehret DL & Menzies, JG (1991) Mobility and deposition of silicon in cucumber plants. Plant cell and Environment, 14:485:492.

Sangster AG, Hodson MJ & Tubb HJ (2001) Silicon deposition in higher plants. In: Datnoff LE, Snyder GH, Korndörfer GH (Eds) Silicon in Agriculture. Amsterdam, Elsevier. p.85–113.

Schurt DA, Rodrigues FA, Reis RD, Moreira WR, Souza NFA & Silva WA (2012) Resistência física de bainhas de plantas de arroz supridas com silício e infectadas por *Rhizoctonia solan*i. Tropical Plant Pathology, 37:281-285.

Shetty R, Frette´ X, Jensen B, Shetty NP,Jensen JD, Jørgensen HJL, Newman MA & Christensen LP (2011) Silicon-Induced Changes in Antifungal Phenolic Acids, Flavonoids, and Key Phenylpropanoid Pathway Genes during the Interaction between Miniature Roses and the Biotrophic Pathogen *Podosphaera pannosa*. Plant Physiology, 157:2194-2295.

Wang L, Cai K & Chen Y (2013) Silicon-Mediated Tomato Resistance Against *Ralstonia solanacearum* is Associated with Modification of Soil Microbial Community Structure and Activity. Biological Trace Element Research, 152: 275-283.

Zanão Júnior LA, Fontes RLF & Ávila VT (2009a) Aplicação do silício para aumentar a resistência do arroz à mancha-parda. Pesquisa Agropecuária Brasileira, 44:203-206.

Zanão Júnior LA, Rodrigues FA, Fontes RLF, Korndörfer GH & Neves JCL (2009b) Rice resistance to brow spot mediated by silicon and its interaction whit manganese. Journal of Phytopathology, 157:73-78.