

Review

A Review on the Role of Silicon Treatment in Biotic Stress Mitigation and Citrus Production

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Abstract: This paper reviews the threat of citrus pathogens during citrus production, with a focus on two pre-harvest diseases, citrus leaf spot, caused by *Alternaria alternata* (Fr.) Keissl. (1912) and brown rot, caused by *Phytophthora citrophthora* (R.E. Sm. and E.H. Sm.) Leonian, (1906) as well as green and blue mold post-harvest disease, caused by *Penicillium digitatum* (Pers.) Sacc. and *P. italicum* Wehmer, (1894), respectively. Furthermore, it reviews the role of soluble silicon, Si nutrition in biotic stress mitigation and potential mitigation mechanisms. Previous studies on the use of Si fertilizers have focused on high accumulator Si crops. These have demonstrated the potential of Si to reduce the occurrence of biotic stresses, which takes place through both physical and biochemical mechanisms. However, few studies have demonstrated the potential of Si to mitigate biotic stress in citrus, or the mechanisms involved. There is a clear need for studies on the impact of Si on various stress biochemical pathways in plants generally, and specifically for citrus due to the huge loss caused by pre- and post-harvest pathogens. This will assist in deepening our understanding of the pathophysiology which is essential to develop resistant cultivars.

Keywords: *Alternaria*; citrus; *Phytophthora*; silicon



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1. Introduction

Citrus is a major fruit crop in terms of volume produced and extensive cultivation worldwide. Citrus fruits contain many nutritional components beneficial to human health [1–3]. Citrus global production is significantly increasing, and many varieties are grown commercially in more than 100 countries. It is the third-largest horticultural industry after deciduous fruits and vegetables [4]. In 2016, global citrus production was about 131 million tons of fresh fruits [5]. However, citrus is a host of many pests and pathogens that cause disease such as anthracnose which has huge impact on the citrus production around the world, which significantly reduce crop productivity and quality [2]. Citrus post-harvest losses are estimated to reach up to 50% [6], which may be caused by several post-harvest diseases. Green mold, caused by *Penicillium digitatum* (Pers.) Sacc. and blue mold, caused by *P. italicum* Wehmer are the two main sources of citrus fruit decay [7]. *Penicillium digitatum* can account for a yearly loss of up to 90% of the total citrus post-harvest losses [8,9]. Other common post-harvest diseases of citrus fruit include stem-end rot, caused by *Lasiodiplodia theobromae* (Pat.) Griffon and Maubl.), sour rot, caused by *Geotrichum candidum* var. *citri-aurantii* (Ferraris) Cif. and F. Cif. as well as brown rot caused by *Phytophthora citrophthora* (Sm. and Sm.) Leonian [7].

Pre-harvest infections are mainly caused by pathogens such as *Phytophthora* species, and *Alternaria citri* Ellis and Pierce [10–13]. This review, focus on the control of two pre-harvest diseases, leaf spot caused by *A. alternata* and brown rot caused by *P. citrophthora*

as well as two post-harvest diseases, blue and green mold caused by *P. Italicum* and *P. digitatum* respectively. This is because they cause significant loss to citrus production and there is Si related research conducted to address this issue [1,8–13].

Silicon (Si) is the second most abundant element in the earth's crust after oxygen [14,15]. These two elements are combined in silicates and aluminosilicates of rocks, clays, and soil minerals [16]. It is also the only element that does not damage plants when applied in excess [17]. Silicon does not cause any environmental hazard as its large surface area allows binding to cations which results in silicates formation and no leaching into the soil [18]. Despite its abundance in soils, it cannot be utilized directly by plants [19]. Plant-available Si, referred to as soluble silicate, is found in the soil solutions in non-dissociated form of monosilicic acid ($\text{Si}(\text{OH})_4$) in a concentration range of 90–150 mg L⁻¹ in soils with a pH lower than 8 [14,15,20]. The availability of Si in soil solution is reduced significantly by the increase in pH, organic complexes, the presence of aluminum, iron, and phosphate ions, temperature, weathering processes that affects the adsorption/dissolution reaction and soil moisture [14,21–23]. The low levels of plant-available Si under the above-mentioned limiting factors warrant Si fertilizer in crops that benefit from Si uptake to improve their quality and yield under abiotic and biotic stress conditions [1,14,17,24]. There are many Si sources available for agriculture production and stress mitigation. However, very few manufactures provide regulations guidelines and adherence to international standards Table 1 presents more information on the availability, regulations, and costs of Si.

Table 1. Silicon fertilizer products information.

| Product Name | Available Si (%) | Regulations | Manufacturer Website | Cost/ha in Citrus Orchards Monthly Application |
|----------------------------------|---|---|---|--|
| AgSil K 50 | 21% Si | Non-toxic agricultural input with no MRL requirements (Reg. No. B3756, Act 36 of 1947) | Madumbi.co.za (accessed on 20 June 2021) | US\$2 |
| Si granules | 98–99% Si | Products standardized according to FDA guidelines. SAR Agrochemicals and fertilizers Pvt. Ltd, Pune, India. | www.saragro.co.in/silicon-product.html (accessed on 20 June 2021) | US\$1.64 |
| AgSil 21 AgSil 25 AgSil 16 | 26.5% silica liquid 21% silica liquid 53% silica hydrous powder | No regulations issues SO certified (9001; 14001; 18001; 45001; 50001; 22716) low hazard to water | www.pqcorp.com | |

MRL: Minimum Residue level.

According to the widely accepted definition of mineral essentiality by Arnon and Stout [25], Si was not initially defined as an essential element for higher plants (vascular plants). This definition was proposed for revision by Epstein and Bloom [26]. However, the 'essential' nature of Si to plant survival is still in controversy. While there is a lack of evidence for silicon's role in normal growth and development of plants when absent, there are many examples of plant responses when Si is added [14,24,27,28]. Several studies have demonstrated that Si exhibits numerous effects on plant growth and development surpassing any other non-essential plant nutrient, this highlights the fact of Si underappreciation [14,22,29,30]. Therefore, Si was reclassified as an essential element for higher plants [31].

Many studies have shown that Si enhances the yields of many crops, especially when they are grown under abiotic (temperature, water, and salinity stresses) and biotic stress [14,29,30]. Silicon fertilizer has been found to enhance disease resistance in many cases [32–35].

Plant surfaces, below and above the ground, serve as a protective barrier between the plant interior and the environment [36]. The cell wall, with its cuticle, constitutes the first line of defense against attacks from insects, fungi, and bacteria. Bacteria and fungi break through the defense by chemical means, whereas pests, including phytophagous insects, mainly utilize stylet to penetrate plants [14].

Silicon physiological resistance in biotic stressed plants is expressed by (1) The increase in the activity of defense-related enzymes, such as polyphenoloxidase, glucanase, peroxidase, and phenylalanine ammonia-lyase (PAL); (2) increase in the activity of antimicrobial compounds, such as phenolic, flavonoids, phytoalexins and pathogenesis-related (PR) proteins in plants; and (3) The regulation of host resistance by signaling hormones, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) [24,27,28,32,37,38]. Soluble Si applications as a pre- and post-harvest treatment have provided control of fungal pathogens of many crops [1,33,38,39] (Table 2). Studies in monocots (rice and wheat) and dicots (cucumber) have shown that plants supplied with Si produce enhanced levels of phenolics and phytoalexins in response to fungal infections, such as those causing rice blast and powdery mildew [33,40–42]. In rice, disease resistance has been associated with Si, which produces a physical barrier for penetration of the mycelia of the fungus due to increment in the density of silicified cells in the epidermis of leaves [37]. In an experiment on rice infected with *Magnaporthe grisea* (Hebert) Barr (rice blast), disease expression was reduced by increasing the plant's Si content, with a substantial decrease in lesion length, rate of lesion expansion, and infection area [42]. Si fertilizers prime plant resistance mechanisms, resulting in the elevated production of lignin, phenolic compounds, and phytoalexins [14,15,43]. For example, Zhang et al. [43] found that Si fertilizer stimulated the production of phenolic compounds in rice plants affected by sheath blight (*Rhizoctonia solani* Kuhn). In cucumber plants, proteins associated with resistance reactions such as chitinases, peroxidases, and polyphenoloxidases increased in roots infected and colonized by *Pythium* [33,40,44]. These biochemical responses are induced by soluble Si, suggesting that soluble Si may play an active role in improving host resistance to diseases by stimulating or priming defense reaction mechanisms [17,33].

Table 2. Si uptake in plants and its mechanism in alleviating biotic stress.

| Biotic Stress | Crop | Treatments | Si Effects under Stress | Reference |
|---|--|--|--|--|
| Crown and root rot <i>Pythium ultimum</i> Trow | Cucumber | Potassium silicate (KaSil, 23.6% SiO ₂) | Increase in β -glucosidase activity and fungi-toxic aglycones | Chérif et al. [40] |
| Powdery mildew <i>Podosphaera fulginea</i> Braun and Takam. | Cucumber | Potassium silicate (K ₂ SiO ₃) | Peroxidase, polyphenoloxidase and chitinase levels enhanced | Fawe et al. [33]; Liang et al. [44] |
| Rice blast (<i>P. grisea</i>) | Rice | (0, 50, 100 and 200 mg L ⁻¹ Si) | Fortification of cell wall | Kim et al. [45] |
| Fusarium wilt <i>Fusarium oxysporum</i> f.sp. <i>cubense</i> Snyder and Hansen | Banana | K ₂ SiO ₃ (0, 490 and 7840 mg L ⁻¹ Si) and inoculation of non-pathogenic <i>F. oxysporum</i> strains | Combination of silicon and non-pathogenic <i>F. oxysporum</i> strains reduced the rate of infection, inhibiting hyphal growth | Kidane [46] |
| Dry rot of potato tubers (<i>Fusarium sulphureum</i> Schltdl.) | Potato | Sodium silicate | Fungitoxic effect by the thickening of the hyphal cell walls, cell distortion, and deposition of electron-dense material in hyphal cells. | Li et al. [47] |
| Fusarium wilt <i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i> Snyder and Hansen) | Cotton | Potassium silicate | Increase in phenolic content and lignin formation | Whan et al. [48] |
| <i>Blumeria graminis</i> f. sp. <i>tritici</i> Speer | Wheat | K ₂ SiO ₃ | Disease in resistance correlated with a reduced expression of gene induced by the pathogen. | Chain et al. [49] |
| Brown rust <i>Puccinia melanocephala</i> Syd. and Syd. | Sugarcane (<i>Saccharum</i> spp. hybrids) | K ₂ SiO ₃ | Si deposited in the lower epidermis, the upper epidermis and the mesophyll reduced rust infection. | Naidoo et al. [50] |
| Bacterial wilt (<i>Ralstonia solanacearum</i> (Smith) Yabuuchi) | Tomato | Silicon | Induced changes in gene expression which prime host resistance. | Ghareeb et al. [51] |

Table 2. Cont.

| Biotic Stress | Crop | Treatments | Si Effects under Stress | Reference |
|---|--------------|---|---|--|
| Bacterial wilt (<i>R. solanacearum</i>) | Tomato | Silicon + rhizobacteria | The up-regulated genes were involved in signal transduction, defense, protein synthesis and metabolism, while a large proportion of down regulated genes were involved in photosynthesis, lipid metabolism. | Kurabachew et al. [52] |
| Bacterial wilt (<i>R. solanacearum</i>) | Sweet pepper | Calcium silicate | Increased production of chitinase, superoxide dismutase, ascorbate, peroxidase, β -1,3-glucanase, lignin and total protein. | Alves et al. [53] Dallagnol et al. [54] |
| Tobacco ringspot virus | Tobacco | Potassium silicate Si (0, 0.1 and 1 mmol L ⁻¹) | Enhanced Si levels delayed development of systemic ringspot symptoms, | Zellner et al. [55] |
| Bacterial speck (<i>Pseudomonas syringae</i> van Hall) | Tomato | Supa Silica (SS) (Agrichem; 23.7% K ₂ O + 10% Si, pH 9.42) | Increased activity of peroxidase, polyphenoloxidase and glucanase | Andrade et al. [56] |
| Anthraxnose (<i>Glomerella graminicola</i> Politis) | Sorghum | Calcium silicate | Si plus fungicide reduced anthracnose severity by 90% | Resende et al. [57] |
| Blast (<i>P. oryzae</i>) | Wheat | Silicon | Partly decrease the negative effects of salinity by increasing SOD and CAT activities, chlorophyll content and photochemical efficiency of PSII, but reduced H ₂ O ₂ and MDA | Cruz et al. [58] |
| Bacterial fruit blotch (<i>Acidovorax citrulli</i> Williams et al.) | Melon | Silicon | The significant increase of Ca and Mg in Si treated melon inhibited bacterial blotch. | Ferreira et al. [59] |
| Brown spot (<i>Cochliobolus miyabeanus</i> (Ito and Kurib.) Drechsler ex Dastur) | Rice | Silicon | Si application increased photorespiration rates, and enhanced disease resistance, maintaining photosynthetic activity. | Van Bockhaven et al. [60] |

Fawe et al. [61] reported that the application of Si on cucumber stimulated an auto-defense mechanism via gene expressions that enhanced the expression of proteins responsible for the transformation of soluble Si to insoluble SiO₂ at the site of the attempted penetration of fungi into epidermal cells. Silicon is known to be involved in cell-wall reinforcement, and to enhance plant resistance to insect pests by providing a mechanical barrier against probing and chewing insects [17,62]. However, the exact nature of the interaction between the soluble Si and the biochemical pathways of the plant that leads to disease resistance remains unknown, although several possible mechanisms have been proposed [1,14,24,27,33,35,38,43,46,57,63–65].

Few recent papers have reviewed Si role in biotic stress tolerance [27,28,65,66]. These reviews have highlighted two mechanisms of Si protection against pathogens. Primarily, Si fosters mechanical protection against several pathogens via three mechanisms. Firstly, the deposition around the cell wall which prevents pathogen penetration. Secondly, the strengthening of the cell wall by the silica deposited beneath the cuticle and forming double silica layer. In addition, Si forms complexes with organic compounds in epidermal cell walls which strengthens the plants mechanically [63,67]. Thirdly, a reduction in enzymatic degradation by pathogens confers rigidity to the plant structure [65]. These mechanisms were also found in cucumber [68]; rice [37,45,69,70]; tomato [51]; sweet pepper [71]; sugarcane [72].

Biochemical plant defenses can be induced by Si through activation of defense-related enzymes, such as polyphenoloxidase, peroxidase, glucanase in infested roots, and salicylic acid production [53,54,65,73].

To understand the interaction between silicon application and fungal resistance in citrus, this review aims to (1) Underline the agricultural importance of silicon in plant diseases; (2) Present several mechanisms of Si in reducing the effect of biotic stresses; (3) Present pre-harvest diseases such as those caused by *Phytophthora* Spp. and *A. alternata* in citrus; (4) Present post-harvest diseases such as those caused by *Penicillium* Spp.; and

(5) Highlight Si involvement in citrus *Phytophthora* Spp., *Alternaria* Spp. and *Penicillium* Spp. diseases mitigation and identify future research direction.

2. Phytophthora Diseases of Citrus

Phytophthora Spp. are important causes of soil and water-borne diseases in citrus [74,75]. *Phytophthora* Spp. are distributed worldwide and cause significant losses of citrus fruit in the high rainfall subtropics, including the first- and second-largest global citrus production areas in the states of São Paulo, Brazil, and Florida, USA [39]. The most prevalent *Phytophthora* Spp. in citrus are *P. nicotianae* and *P. citrophthora* [76–78]. *Phytophthora citrophthora* R.E (Sm. and E.H. Sm.) Leonian is a genus of microorganisms in the Kingdom; Stramenopile order: Class Oocmycetes, which includes water molds, diatoms, and brown algae. *Phytophthora* species resemble true fungi because they grow by means of fine filaments, called hyphae, and produce spores [7].

Phytophthora nicotianae Breda de Haan is the main cause of root rot and foot rot of citrus trees in and tropical areas of the world [10,73,79]. It has been identified as the most dangerous species infecting citrus plants as it causes both root/foot rot and may be spread over the citrus tree canopy via water splash [76]. It is also the main *Phytophthora* species infecting citrus in Brazil, Egypt, South Africa, and Tunisia [80].

Phytophthora citrophthora R.E. (Sm and E.H. Sm) Leonian causes both winter and summer root rot characterized mostly by brown lesions on the fruit which later turn into rot and causes gummosis symptoms in Mediterranean climate [75]. *Phytophthora citrophthora* is a major *Phytophthora* pathogen reported on citrus production in South Africa [78]. However, it is mostly restricted to the Western Cape province of South Africa, an important commercial citrus producing region of the country [78]. *Phytophthora citrophthora* is more virulent in Mediterranean climatic areas [81,82]. Its damage is mostly significant especially when the roots of the affected citrus plant have a low resistance to fungal infections [82].

Phytophthora root rot affects all parts of the tree at different stages of development and is especially harmful on young trees when citrus scion material is grafted on susceptible rootstocks of Cleopatra mandarins and sweet orange [74,83,84]. Foot rot occurs when the scion area of a grafted citrus tree near the ground is infected with *P. nicotianae*. This results in lesions extending upward from the bud union on rootstocks, or up the trunk into main branches [38,74,79,83,84]. Foot and root rot cause a severe decline in yield by slowing down the production of new fibrous roots, stopping trees from maintaining adequate water and mineral uptake. This results in the reduction of fruit size and yield, leaf chlorosis, loss of leaves, and twig dieback [84,85].

Control measurements for *Phytophthora* Spp. root rot disease in citrus are fungicide treatments such as Ridomil, Aliette and phosphite salts and the use of resistant citrus rootstocks derived from breeding programs [85–87]. Both control techniques are expensive and provide temporary resistance which will be reduced overtime due to susceptibility. The fact that Si fertilizer can reduce root rot in avocado (*Phytophthora cinnamomi* Rands) suggests that it might also have a similar role in controlling *P. nicotianae* infection in citrus [10,38,86].

Si has been effective in controlling cucumber root rot caused by *P. melonis* through the increase in antioxidant activities [88,89].

3. Alternaria Disease

Alternaria Spp. are fungi in the Kingdom: Fungi, class: Dothideomycetes which have been recorded to cause brown leaf spot and other diseases on several species [90]. *Alternaria alternata* ((Fr.) Keissl.) is the causal agent of brown spot, a fungal disease is common in most humid and semi-arid growing citrus regions [13]. The disease may affect tree growth, causes considerable crop loss, and renders fruit unacceptable to consumers due to blemishes. Control of the disease is largely based on the spraying of large volumes of fungicides regularly onto orchards to ensure good leaf coverage. However, high volume sprays can result in excessive runoff from foliage and fruits, which is an economic loss and presents risks for environmental pollution [91]. In *Alternaria alternata* fungicide spray

program is difficult to implement as it is difficult to predict when the disease occurs due to the short incubation period that varies from 24 h to 120 h [11]. This limits the effectiveness of the fungicide as a preventative measure and periodic application can only reduce the infection rate for a short period of time [91].

The leaves of mandarin (*Citrus reticulata* Blanco) trees subjected to Si nutrition for a period of three months demonstrated a significant reduction in the severity of *A. alternata* infections under controlled conditions in comparison with the control plants [92]. Mvondo-She and Marais [93] reported that a double layer of Si was deposited in the epidermal cell of citrus leaves using electron microscopy (Figure 1). This may explain the enhanced resistance of the citrus plants exposed to Si treatments and show the potential role of Si in providing protection to diseases [21,29]. The evidence of the role of Si in reducing fungal infection rate suggests that it has the potential to reduce levels of *A. alternata* in the pre-harvest situation [17,33,92]. This agrees with earlier studies in citrus that showed an increased Si content in citrus leaves, localised in leaf epidermal cells, resulting in reduced levels of insect damage and plant disease due to improved tree vigor [94,95]. In the post-harvest situation, Tian et al. [96] demonstrated that a combination of sodium silicate as a post-harvest and a yeast antagonist (*Cryptococcus laurentii* Kufferath C.E. Skinner. and *Rhodotorula glutinis* Harrison.) as a pre-harvest treatment could control the diseases caused by *A. alternata* in sweet cherry, peach, and jujube fruit, as it increased the population density of the antagonistic yeast on the surface of treated fruit.

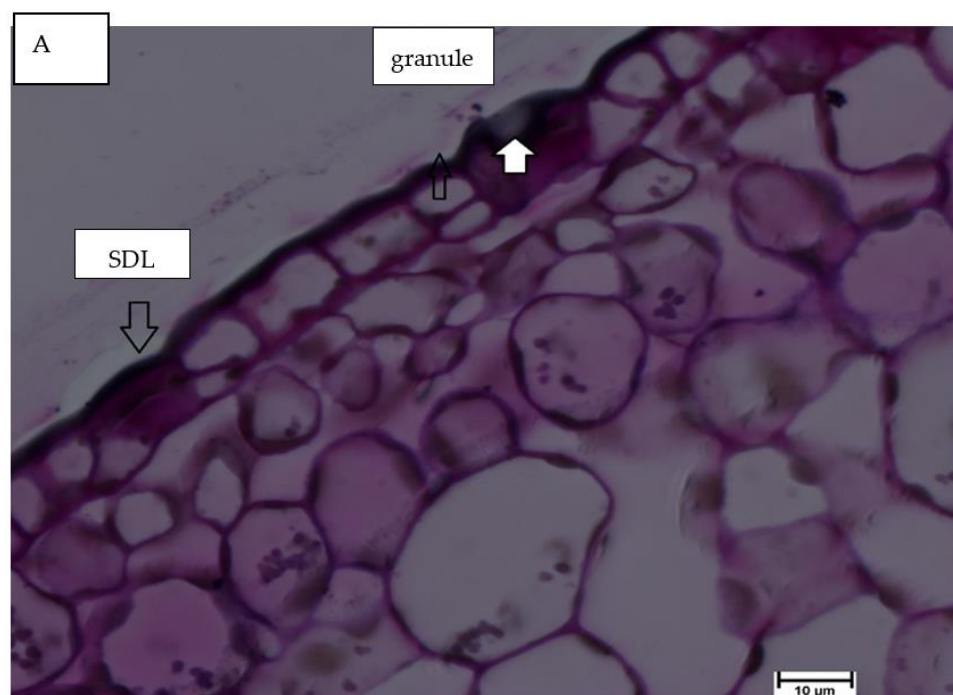


Figure 1. Upper epidermal surface of Si treated citrus leaves examined under light microscopy, 100× magnification: arrows in diagram mark silica granules in the epidermal surface; Si deposits in the outer cell regions constitute the cuticle- silica double layer (SDL) (Mvondo-She and Marais [93]).

4. Green and Blue Mold

During post-harvest storage, citrus is subjected to biotic stress, making it susceptible to green and blue mold which is caused by *Penicillium digitatum* (and *P. italicum* respectively). Blue and green mold are known to be the pathogens that cause the most post-harvest diseases [97,98].

These pathogens reside on healthy citrus fruits and penetrate the fruits through injury caused by rough handling during harvest, transportation, and storage [99]. The economic loss is enormous worldwide [64,97]. These pathogens are treated using systemic fungicides

belonging to the groups of imazalil, benomyl, benzimidazole, and thiabendazole [7,100]. However, repeated use of these chemicals could reduce food safety and can encourage fungicide-resistant strains through genetic mutations [1,99].

Research studies on green mold infection in citrus have shown that a combination of potassium silicate pre-harvest treatment and the post-harvest control using yeast isolate B13 or hot water were significantly reduced, or in some cases equal to control provided by Imazalil in reducing green mold infection [1]. Abraham [1] showed that pre-harvest Si applications improved the control of *P. digitatum* more effectively in Valencia than in Navel orange. This demonstrated that the plant response to Si varies with crop genotype, as reported by Rodrigues [101]. This disease control relied upon the regular drenching of potassium silicate in the field [1]. Therefore, it can be inferred that Si protection is not related to the total Si concentration in the root tissue but rather to the availability of mobile silicic acid at the time of infection [93]. A similar study showed that pre-harvest applications of K_2SiO_3 had the potential to protect citrus fruits ('Delta' Valencia, 'Washington' navel, and 'Eureka' lemon) from the post-harvest disease *P. digitatum*, although further research is required to study the biochemical changes induced by silicon application [64,102].

5. Conclusions

There is growing evidence that Si can play an important role in enhancing the resistance of many crops to pests and diseases, and tolerance of abiotic stresses. However, the exact mechanism(s) by which it contributes to the physiological responses need further investigation. Regarding Si in citrus disease mitigation, this review has highlighted studies that have demonstrated the role of Si in enhancing host resistance via resistance priming effects and by physical strengthening of the epidermal cells. Future studies will need to investigate the biochemical responses to Si treatment in plants infected with citrus pathogens. This will pave the way to understanding the impact of Si fertilizer on gene expression and confirm the role of Si in the management of metabolic processes in stressed plants.

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