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Chapter

Silicon Use in the Integrated Disease Management of Wheat: Current Knowledge

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Abstract

Silicon (Si) is a benefic element for higher plants such as wheat (*Triticum aestivum*) in which it is accumulated in the shoot tissues. In this crop, leaf diseases and spike diseases are the cause of yield losses, and therefore several studies had been conducted under field and greenhouse conditions to demonstrate that plants supplied with Si reduced most of the diseases damage due to the amelioration of the plant defenses. However, the benefits of Si depend on its accumulation in the plant's tissue, which is influenced by the availability of the element in the soil as well as the up-take ability of the wheat cultivar. In this chapter we present the current knowledge about the mechanisms of Si absorption and its accumulation in different tissues of the wheat plant, the most studied options for silicate fertilization, and the benefits of Si on grain yield. We also present some insight of the effect of Si-supply in wheat on the reduction of main leaf and ear diseases, bringing evidence and explanation of the defense mechanisms involved. In addition, we provide an overview of the Si effect on the physiology (gas exchange, chlorophyll *a* fluorescence and carbohydrate metabolism) of the wheat plant. Finally, questions have been raised about the Si uses as fertilizer that still needs to be answered. We recognized that some studies have enhanced our understanding of Si providing evidence of the Si use as disease management strategy, but further research is needed to make the Si uses a simple task for wheat growers under field condition.

Keywords: disease control, diseases management, silicate fertilization, sustainable management, wheat diseases, wheat yield

1. Introduction

Wheat (*Triticum aestivum* L.) is the most cultivated crop on Earth [1, 2] being a key cereal for global food security. Wheat provides calories to 85% of the world population (contributing of 5 to 57% of daily consumed calories, depending of the country) and proteins to more than 82% of the world population (contributing of 6 to 60% of daily calories intake, depending of the country) [3]. Historically (1961–2009) the increase in the world production of wheat occurred primarily due to the increase in productivity which supplied the increase in the demand for this cereal [4]. As the global population continues to increase, the world demand for wheat is predicted to continue raising [2, 4], being forecast that in order to feed the world population in 2050 it will be necessary to almost double the current wheat

production [5]. The challenges to achieving this production target include abiotic (drought, heat and salinity) and biotic (insects, pathogens and weeds) stresses that can be enhanced by climate changes [5].

Pathogens are among the main threats to high yield of wheat and a threatening to food security. Wheat is affected by many pathogens, however their occurrence and yield loss, estimated for each disease, vary from country to country and season to season. The main aboveground wheat diseases worldwide are rusts (*Puccinia* spp.), septoria nodorum blotch (*Parastagonospora nodorum*), septoria tritici blotch (*Zymoseptoria tritici*), tan spot (*Pyrenophora tritici-repentis*), fusarium head blight (*Fusarium graminearum* species complex), powdery mildew (*Blumeria graminis* f. sp. *tritici*) and wheat blast (*Magnaporthe oryzae* Pathotype Triticum).

The control of these diseases is carried out preferably through resistant cultivars. However, for some of the diseases, there are no cultivars with sufficient resistance to contain the damage in yield or the resistance is ephemeral, especially when governed by race-specific resistance genes, due to the rapid evolution of the pathogen [6–9]. As a result, the use of fungicides is common in wheat crops, but it raises the cost of production and it does not always give the expected control for some diseases [10, 11]; furthermore there is risk of development of resistance in the fungal to fungicides [12].

In this scenario, silicon (Si) become as an attractive alternative to be included in the management of wheat crop. Silicon is a mineral element considered benefic to plants, however in many soils its concentration available for plants is low [13]. In these soils, fertilization with Si sources has shown positive results. Numerous studies demonstrate the beneficial effect of Si in relieving abiotic stresses and in the control of biotic diseases on Si-accumulator plants (reviewed by [14–17]). This chapter presents the current knowledge on Si up take by the wheat plant, its effects on grain productivity and wheat technological quality, physiological aspects, and biochemical and histological defenses enhanced by the element, on several wheat-pathogen interaction.

2. Silicon wheat absorption

The knowledge of Si absorption has been studied in different plants such as monocotyledonous and dicotyledonous species providing evidence to explain the process [18–21]. Initially was believed that the transpiration was the main factor determining Si uptake in plants. New evidence confirmed that the Si absorption and accumulation could be explained by the active transport mechanisms inherent to the roots and the shoots.

In wheat, the first evidences of active transport mechanisms come with studies showing that approximately 90% of the Si absorbed by the plant was transferred to the shoots, maintaining the roots in a relatively low-Si status [22, 23]. Later, Mayland et al. [24] reported that the amount of Si accumulated by the wheat plant was higher than expected to occur only via transpiration providing data to support the classification of wheat as a Si accumulator (accumulating Si in concentration up to 20 g kg^{-1} of dry weight). Advancing, Rafi and Epstein [25] reported that Si is rapidly absorbed by wheat plants from solution containing Si at 0.5 mM, a concentration near of that of the element in soil solutions, and the uptake rate were similar between plants 'preloaded' with Si and plants grown previously in solutions without Si addition. Further studies demonstrated that Si uptake by wheat is under metabolic control due to the absorption of Si show a concentration dependence obeying Michaelis–Menten kinetics and it is affected by metabolic inhibitors (dinitrophenol and potassium cyanide) [26]. Later, Montpetit et al. [21] cloned and functional characterized the *TaLsi1*, a wheat Si transporter gene, which is an ortholog of *OsLsi1*

from rice. The genes *TaLsi1* and *OsLsi1* belong to Nod26-like intrinsic proteins (NIPs) III subgroup of the aquaporin membrane protein family.

Thus, the Si absorption is facilitated by specific NIPs with a distinct selectivity that facilitate the passive transport of water and/or small uncharged solutes such as monosilicic acid [$Si(OH)_4$] [27]. According to Ma and Yamaji [19] specific NIPs as *Lsi1* (Si influx transporter) facilitates the passive transport of Si across the plasma membrane from the environment (external solution) to the plant cell in the form of [$Si(OH)_4$], and efflux transporters known as *Lsi2* mediate the loading of Si into the xylem to facilitate root-to-shoot translocation, which, in turn, moves Si to the aerial parts where it is deposit as amorphous Si (SiO_2). According to the authors, these Si transporters are localized to the plasma membrane, but, in different plant species, show different expression patterns and tissue or cellular localizations that are associated with different levels of Si accumulation [19]. In this context, the molecular characterization and phylogeny of the Si permeable channel, *TaLsi1*, which is expressed only in the roots and independent from Si concentrations, can explain the Si absorption by wheat plants [14, 21].

The concentration of Si on wheat tissue varies according to the soil and cultivar. For example, a study conducted in two locations (Abed and Sejet, Denmark) showed that Si concentration in the wheat straw ranged from 11.3 g kg^{-1} to 23.4 g kg^{-1} of dry weight. The study performed with 20 genotypes, showed that on average wheat grown in Abed contained 25% more Si than wheat grown in Sejet, which as attributed to variation in edaphic factors such as soil pH or silicate mineral composition which affect the Si availability to plants [28]. In regarding to wheat genotypes, the difference between the lowest and highest Si concentration was 75% at Abed and 44% at Sejet reflecting differences in the ability of roots to take up Si from the soil solution [28]. Carter et al. [29] and Ranjbar et al. [30] also observed difference among wheat cultivars regarding Si concentration in the shoot. Ranjbar et al. [30] also showed that there is a relationship between shoot Si concentration and Si acquisition efficiency. These studies clearly indicated that accumulation of Si in the wheat shoot is variable among cultivars which may influenced by the cultivar ability to absorption and also by the availability of Si in the soil.

After uptake by roots, Si follow the transpiration flow and it is accumulated beneath cuticle forming a double layer Si-cuticle, associated to cell wall and in Si-accumulating cells [31]. Furthermore, it was been previously reported that the highest Si concentration was present in major transpiration parts of the plants followed by the other parts of the plants [32]. In wheat, the highest silicified cells were present in leaf blade followed by the awn, leaf sheath, lemma, rachilla and stem, thus leaf blade contains the highest Si concentration [33]. In agreement, another study showed that the accumulation of Si was highest in vegetative tissue (leaf blades > leaf sheaths > stem) and lowest in grain followed by roots, increasing with increasing stomata density in the tissues [34]. In awns, the number of silicified cells was linearly correlated to Si concentration in dry weight which suggests cellular control over silicification [35]. Using scanning electron microscopic, authors found a continuous silica layer under the cuticle, extended silicification in the epidermis cell wall and in sclerenchyma cells near the vascular bundles, but not in the stomata, suggesting that an active process directs the soluble Si away from the water evaporation stream [35]. On the leaves, X-ray microanalysis revealed that Si was deposited in a linear pattern that corresponded to the silica cells, being greater the amounts of Si in the linear areas of silica cells from plants grown in soil supplied with silicate fertilizer [36, 37]. Another study showed that Si was predominantly deposited in the epidermis cells of the leaves and their cell walls [38].

As wheat is a Si-accumulating species, it may remove considerable amount of Si if straw is removed from the field. In this context, a study considering long-term

cultivated field analyzed the impact of Si accumulating plants on the biogeochemi-cal cycle of Si and indicated that the concentration of amorphous silica is lower in cultivated soils compared to natural ecosystems, due to the amorphous Si pool decreases with time particularly in surface soil, contrary to natural ecosystems [39]. For instance, an estimation of shoot Si uptake by wheat based on 10-year average of harvested area, production level, reported biomass/harvested portion ratio and shoot Si content in United States indicated that the annual shoot Si uptake of wheat is 2.144,278 tons and 108 kg ha^{-1} [40]. In this sense, in crop systems in which the straw is removed from the field, the available Si in soils do not sustain high Si concentrations not only for wheat but also other crops in the long term [39]. Under this condition, it is clear the concern on the Si reduction from field pointing out the necessity of Si sources as fertilizers and eventually the management of the wheat straw to obtain the benefits of Si to wheat plants.

2.1 Silicon fertilization

Orthosilicic is the second most abundant element in the earths crust and plays a number of important roles in the plants. The silicic acid is present in the soil as an uncharged monomeric molecule below pH 9 [19]; their concentration in soil vary-ing between 0.1 to 0.6 mM [41]. In the past 20 years, the scientific documentation on the benefits of Si to crops has helped establish Si fertilization as an agronomic practice in many agricultural lands worldwide [40]. Thus, it is recognized that Si fertilization confers benefits to wheat crop.

In this context, the most common Si fertilizers are wollastonite and slag (calcium silicate). In the case of wollastonite which is a natural calcium silicate [42], that contains higher fractions of easily soluble Si compared to slags [40]. It is considered to be the most efficient Si fertilizer for soil application due to that it can release the largest amount of plant available Si (2.31–3.6%) into soil solution [43, 44]; however, its use is often limited because of its relatively high cost [45]. Calcium silicate slags are by-products of the metallurgical smelting process, contain varying percentages of Si [46], and have been observed positive effects on correcting soil acidity [47], plant growth and alleviation of stresses [48–50]. Other commonly used Si fertilizers are sodium metasilicate and potassium silicate. These Si fertilizers have been found very helpful in improving growth parameters in biotic, drought and salt stress in wheat [38, 51].

In the case of pyrolitic fine silica particles, sodium metasilicate or silica gel is used for agricultural purposes. In soil, wheat plants grown under identical grow-ing conditions, the efficiency of the Si compounds to increase the Si concentration on the plants increased in the order sodium metasilicate > silica gel >pyrolitic fine silica particles and seemed to correlate with the ease of formation of orthosilicic acid from these compounds [38]. For instance, the application of liquid and powder silicate fertilizers in the soil contributed similarly to the concentration of Si to the soil solution and doubled the Si concentration on wheat tissue [52]. Furthermore, Si uptake by wheat plant as well as its growth is significantly affected by the type of Si pool in the soil and factors controlling its solubility [53].

On the other hand, foliar application, mainly as sodium metasilicate and potas-sium silicate, is cause of debate due to the major portion of the Si uptake come from to the roots; however, some effects under biotic and abiotic stress have been observed (see below).

The demand of Si fertilizer due to the necessity in different agricultural environ-ments allow the introduction and application of nano-Si fertilizer with some kind of efficient. The nano-Si is high bioavailability as smaller particle size that can be rapidly and completely form to absorb by plants and form a thick silicated layer on

leaf surface [54]. In this case a study showed that addition of potassium silicate or nano-Si fertilizer in a Calcaric Cambisols increased the concentration of Si in wheat tissue, mainly in the shoot, but there is a significant relationship between the Si level/source and wheat cultivars [30].

3. Silicon and wheat yield

Silicon fertilization in the soil resulted in positive effect on grain yield and its quality, mainly under stress. In China, a four-year field experiment in Calcareous Paddy soils indicated that Si fertilization increased the wheat yield by 4.1 to 9.3% under biotic stress [55], while other studies obtained increased in the grain yield due to silicate slag fertilization ranging from 5 to 12% [55, 56].

In New Jersey, in a three consecutive years of field experiment, calcium silicate (steel slag by-product) was added on a Quakertown Silt Loam soil increasing yield up to 10%, but only under biotic stress imposed by powdery mildew [57]. A two consecutive growing seasons experiment performed in Idaho evaluated the application of Si in the form of amorphous volcanic tuff in the Greenleaf-Owyhee Silt Loam soil indicated that there was no significant effect of Si on plant height, nutrient uptake, grain yield and grain protein content of winter wheat grown in non-stressed conditions [58]. A three site-years experiment was conducted on the Alluvial Floodplain soils in Louisiana to evaluated silicate slag applications on productivity of wheat under sufficient and high nitrogen application rates showed a numerical trends of grain yield increase increasing silicate slag rate, but significant increase was only observed in one site and year [59]. According authors, the inconsistencies observed in responses to Si treatments could be due to varying physicochemical properties of soils and more research is need to better understand the effect of silicate slag use in wheat production in Louisiana.

In Brazil, calcium silicate was used as a source of soluble Si in a three-years field experiment to control shoot diseases. The results showed that wheat plants grown in soil fertilized with calcium silicate that received one application of fungicide at the stem elongation stage showed a reduction on the biotic stress increasing grain yield by 1.0 t ha^{-1} (Pazdiora, P. C. – unpublished data). Grains from these experiments was used to determine the wheat technological quality through physicochemical and rheological analyses. The data indicated that calcium silicate showed little effect on the wheat technological quality under lower disease intensity, but under higher disease intensity, it ameliorated the damage caused, keeping the technological quality near the expected level of each cultivar (Dallagnol, L. J. – unpublished data). Pot experiment evaluating three soils (Rhodic Acrudox, Rhodic Hapludox and Arenic Hapludult) indicated that application of calcium/magnesium silicate in an acid clayey Rhodic Hapludox improves the development and yield of wheat, but the silicate application in soil with pH higher to 5.3 and high Si availability does not affect the agronomic characteristics and grain yield of wheat [60].

In Poland, a two-year field experiment evaluated different methods of application of powder (diatomaceous earth) and liquid (solution of monosilicic acid) forms of Si to soil, leaves and combined methods of application (to soil and leaves) on growth parameters and yielding [61]. Authors observed that the most efficient form of Si was a liquid formulation, while powder was less effective and only in combined application achieved similar effects such as liquid Si, increasing the number of seedling emergence, the height of plants and density of spikes and yield. Furthermore, according authors, soil and foliar Si application is more effective than soil or foliar application [61]. In Germany, an experiment performed in substrate showed that Si applied in the form of an engineered nanomaterial

(amorphous pyrogenic hydrophilic SiO₂) was readily taken up by the wheat plants increasing the aboveground biomass production at low (1 g SiO_2 pot^{-1}) to medium (10 g SiO_2 pot^{-1}) supply levels of Si; and grain yield at medium Si supply, probably due to increased plant phosphorus availability and nutrition [34].

Foliar Si treatment also provided some effect on wheat growth and/or yield. In Canada, foliar application of potassium silicate increased the high of wheat plants, compared to control plants, but only under biotic stress and variable according Si-based product [62]. A study performed in Iran, under greenhouse, showed that wheat plant grown in pots that received foliar application of 6 mM sodium meta-silicate significantly increased biomass and grain yield, being the highest positive effect of treatment observed with the application both at the tillering and anthesis stages, especially under drought stress [63]. Also, field experiment conducted in two seasons in Egypt to evaluate the effect of two nitrogen source combined with foliar spray of Si (diatomite) indicated that organic nitrogen (farm yard manure) combined to diatomite at rate of 0.4% produced the highest values of grain yield, weight of 100 grains and straw yield [64]. In Brazil, foliar application of Si (0.8% of soluble Si, as stabilized orthosilicic acid) increased mass of wheat seed without effect on its germination or vigor [65].

The fertilization results with Si sources on the yield and quality of wheat indicate that there is a trend of significant gains, especially under some kind of stress. However, the results among different studies are variable due to the differences in Si sources, the genetic variations of the wheat cultivars used and the stress levels imposed on the plant.

4. Wheat diseases affected by silicon

The positive effect of Si fertilization on the control of diseases has been reported for pathosystems, mainly involving fungi as pathogens, around the world (**Figure 1**).

For blast (*Magnaporthe oryzae* pathotype Triticum), greenhouse experiments showed reduction of leaf blast severity up to 70% and up to 78% on the area under diseases progress curve (AUDPC) on plants grown in media containing 2 mM of Si compared to plants grown in media without addition of Si source [66, 67]. This effect of Si was associated to the increase in the incubation period by 28% and reduction up to 45% for the number of lesions per cm^2 of leaf [37]. The reduction on blast severity by Si was also associated to the restriction on the host cell colonization by the pathogen [68]. According to authors, in Si-supplied plants the fungal hyphae was restrict to the first-invaded epidermal cell compared to plants not amended with Si in which the fungal hyphae grew successfully and formed an extensive branched mycelium in the first-invaded epidermal cell and several neighboring cells. Leaf application of potassium silicate reduced blast severity, but the positive effect was variable among cultivars [51]. Another study evaluating leaf application of potassium silicate indicated blast severity reduction on the same proportion of fungicide treatment, but no additive or synergistic effect was observed mixing fungicide and potassium silicate [69]. Two-years field experiment showed that Si, applied in the soil as calcium and magnesium silicate in the furrow, and as potassium silicate applied on the leaves, reduced the incidence and severity of blast in the spike, but it effect was variable both with years and cultivars [70].

Powdery mildew (*Blumeria graminis* f. sp. *tritici*) was the first wheat disease reported to be affected by Si [71]. In a three-years experiment evaluating the straw incorporated in the soil conferred the reduction of several wheat disease including

Disease		Si Supply	Environ. (Country)	Variable/Reduction	Ref.
Blast	*M. oryzae* Pathotype Triticum	Root	Field (Brazil)	Inc./ 0 to 40% Sev./ 30 to 40%	70
		Foliar	Field (Brazil)	Inc./ 0 to 40% Sev./ 30 to 40%	70
		Root	Greenhouse (Brazil)	AUDPC/ ~31 to 78% Sev./ ~67 to 70%	37, 66, 67, 98
		Foliar	Greenhouse (Brazil)	AUDPC/ ~56	69
Powdery mildew	*B. graminis* f.sp. *tritici*	Root	Greenhouse (Brazil, Canada, UK)	Sev./ ~45 to 90%	62, 73-75
			Field (USA)	Sev./ ~29 to 44%	57
		Foliar	Greenhouse (Canada)	Sev./ ~40%	62
Tan spot	*P. tritici-repentis*	Root	Greenhouse (Brazil)	AUDPC/ ~73 to 88% Sev./ ~34 to 88%	82 80, 82
			Field (Brazil)	Sev./ ~20 to 50%	unpublished
FBH	*F. graminearum*	Root	Greenhouse (Brazil)	Sev./ 20 to 32% AUDPC/ 12 to 21%	83
			Field (Brazil)	Inc./ 0 to 25% Sev./ 0 to 40%	83

Figure 1.
Examples of the effect of silicon (Si) on wheat diseases through root or foliar application (Si supply) in experiments conducted under greenhouse or field environments (Environ.) in different regions (Country) through evaluating disease incidence (Inc.), disease severity (Sev.) or area under disease progress curve (AUDPC) and the percentage of control obtained by silicon treatment. Credits of blast photos to Amanda Baseggio.

powdery mildew [72]. Authors attributed this effect to the increase in the Si availability in the soil conferred by the straw incorporated, being this effect of Si increased in the soil confirmed under greenhouse experiment [72, 73]. Bélanger et al. [74] reported that on wheat plants not supplied with Si the first signs of *B. graminis* f. sp. *tritici* infection were observed at five days after inoculation developing rapidly thereafter reaching to disease severity of up to 40% after five weeks, while plants supplied with Si, colonies of *B. graminis* f. sp. *tritici* were reduced even after five weeks with severity lesser than 5%, indicating very limited fungal colonization on leaf tissue. Later, another study reported reduction on powdery mildew severity up to 80% when Si was supplied via the roots, but leaf spray was less effective reducing the disease severity up to 40% [62]. Field experiment during three consecutive years indicated that calcium silicate (steel slag by-product) reduced powdery mildew severity, in all season that disease occurred, up to 44% [57]. Wheat plants grown in

nutrient solution containing different doses of soluble sodium metasilicate showed that the increase of Si concentration in plant showed inverse proportionality to pathogen index indicating an effective action of Si against *B. graminis* f. sp. *tritici* infection in the foliar surface [75].

For spot blotch (*Bipolaris sorokiniana*) the AUDPC was reduced by 59% due soil fertilization with calcium silicate (wollastonite) [76]. The effect of Si on the AUDPC of spot blotch was associated to an increase in the incubation period and decrease in the number of lesions per cm^2 of leaf area and disease severity [77, 78]. This effect of Si on the infectious process of *B. sorokiniana* indicated a limited fungal growth in tissue of Si-supplied plants because authors detected only a sparse network of hypha colonizing the cells as well as a reduced number of epidermal cells showing browning [79].

For tan spot (*Pyrenophora tritici-repentis*), greenhouse experiment using calcium and magnesium silicate (steel slag by-product) incorporated in the soil increased leaf Si concentration which was correlated to longer incubation period and reduced infection efficiency, final number of lesions per cm^2, rate of lesion expansion, lesion size, disease severity and AUDPC [80–82].

For fusarium head blight (*Fusarium graminearum* specie complex), greenhouse experiment indicated that calcium and magnesium silicate incorporated in the soil increased the incubation period in 15% and reduced up to 32% de disease severity and up to 53% de concentration of deoxynivaleonol (a harmful mycotoxin produced by *Fusarium* species) [83]. As the chemical control of fusarium head blight is closely linked to the timing of fungicide application at spike and not all tillers start anthesis at the same time, Si showed a potential to increase the time of fungicide application and still providing a good control of the disease due a longer incubation period and lower rate of colonization (Pazdiora, P. C. Unpublished data).

Field experiment during three years indicated that calcium and magnesium silicate fertilization increased the Si concentration in the soil and wheat leaf and spike tissues, which was associated to the reduction in the severity of both tan spot and fusarium head blight. The reduction of disease severity conferred by Si was greater for tan spot than to fusarium head blight. The greatest control of tan spot and fusarium head blight was obtained with the moderately resistant cultivar treated with two fungicide sprayings. On the other hand, wheat plants grown in soil fertilized with calcium and magnesium silicate that received one application of fungicide at the stem elongation stage showed a reduction up to 50% on tan spot severity and an increase of grain yield by 1 t ha^{-1} compared to the same fungicide treatment on plants grown on soil that received limestone (Pazdiora, P. C. – unpublished data).

Another wheat disease that was affected by Si are leaf blotch (*Parastagnospora nodorum*) under both field and greenhouse trials [72, 73], septoria leaf blotch (*Zymoseptoria tritici*) and eyespot (*Oculimacula yallundae*). However, the efficiency of Si in reducing these diseases was variable and attributed to the type of growing substrate used in the experiments [73]. Furthermore, for bacterial leaf streak (*Xanthomonas translucens* pv. *undulosa*), the Si treatment in the soil not affected the incubation period, latent period, necrotic leaf area, and severity, but reduced up to 50% the chlorotic leaf area [84].

5. Defense responses of wheat activated against pathogens in the presence of Silicon

Several researches have demonstrated the potential of Si in increasing the resistance of wheat against a range of pathogens. Several diseases were reduced on wheat plants supplied with Si through roots or foliar and the mechanism of defense

studied. The role of Si on wheat-pathogen interactions is related to its action to increase the plant's defense against to the stressor agent [85].

For blast, in which the pathogen infection leads to increase in the production of reactive oxygen species (ROS) and damage to cell membranes [86], in Si-supplied plants occurred lower concentrations of hydrogen peroxide(H_2O_2) and malondialdehyde indicating, therefore, that the ROS generation and cellular damage were greatly limited [87]. According to authors, the activities of enzymes superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX) and glutathione-S-transferase (GST) were higher in the leaves of the plants not supplied with Si, while in leaves from Si-supplied plants the glutathione metabolism seemed to play a role in such defense because glutathione reductase activity was increased. In line with this hypothesis, the higher expression levels of the defense-related genes pathogenesis-related 1, chitinase (CHI), POX and phenylalanine ammonia-lyase (PAL), as well as the higher activities of CHI and POX at intermediate and advanced stages of *M. oryzae* infection, respectively, associated to an increase on the concentration of ligninthioglycolic acid derivatives was reported contributing to defense against blast in Si-supplied plants [37, 88]. Cytological and histochemical analysis revealed that in Si-supplied plants the pathogen hyphae were restricted to in the invaded cells, delaying the colonization of the neighboring cells and consequently reducing the progress of the disease [68]. In another study, *M. oryzae* colonization was constrained in the cells on the leaves of Si-supplied plants in association with intense deposition of phenolic-like compounds (flavonoids) [36]. Phenolic-like material was also detected in the parenchyma cells of spikes, and scanning electron micrographs showed that fungal hyphae were scarcely observed in the epidermis, parenchyma and collenchyma cells indicating that these tissues were less colonized by fungal in comparison to the plants not supplied with Si [88].

In the wheat–*B. graminis* f. sp. *tritici* pathosystem, Si increased the resistance to fungus infection by specific defense reactions including papilla formation, production of callose, fungitoxic phenolic compounds and Si deposition at the site of infection [74]. The release of glycosilated phenolics along the cell wall and in association with the compromised haustoria was associated to the degradation of *B. graminis* haustoria [74, 89]. These defense responses potentiated by Si resulted in growth restriction to 10% of epidermal cells and poorly development of haustoria contrasting to leaves of wheat plants not treated with Si that had abundant hyphae of *B. graminis* on epidermal surface and typical haustoria formation in 90% of epidermal cells [74]. The study performed by Rémus-Borel et al. [89] verified that necrotic zones were not detected on *B. graminis* infected tissue, indicating that the response to infection potentiated by Si was not associated with a hypersensitive response, but the newly produced compounds of phenolic-like material that were associated with degraded *B. graminis* haustoria and collapsed conidial chains which interfered with pathogen development. In addition, biochemical defense response *to B. graminis* infection was reported to be associated to production of phytoalexins linked to metabolism of aconitate, which limited the diseases development [90]. A transcriptomic analysis revealed that wheat plants reacted to inoculation with *B. graminis* by an upregulation of many genes linked to stress and metabolic processes and a downregulation of genes linked to photosynthesis, but in Si-supplied plants the disease development is reduced fact that is translated into a nearly perfect reversal of genes regulated by the effect of *B. graminis* [91]. Another study revealed that *B. graminis* development established a close relationship with the antioxidant response of wheat plants [75]. According authors, the activity of SOD, CAT and APX decreases as Si doses increases indicating a relationship between the applied doses of Si and decrease in *B. graminis* infection due to the reduction of basal antioxidant enzyme

activity and ROS. Thus, the decrease of antioxidant enzymes influenced by Si could generate ROS status for more efficient responses of defense to *B. graminis* [75].

On the spot blotch, Si-supply to wheat plants caused a reduction in the rate of infection of *B. sorokiniana* in wheat epidermal cells, due to the physical barrier formed by the cuticle-Si double layer [79]. According to authors, this physical barrier may have reduced the diffusion of lytic enzymes and selective non-host toxins released by the pathogen on the leaf surface, as shown by the reduction of the wax layer degradation. However, even evident the potential of Si accumulated in the plant tissue (cell wall, beneath the cuticle and cell cumulating Si) in inhibiting or delaying the pathogen infection process, this deposition is not homogeneous in the epidermal tissue, which allows the formation of successful infection sites. At this infection sites, others defense potentiated by Si played an important role. Indeed, the increase in the activity of the enzyme POX and increase on the concentration of ligninthioglycolic acid derivatives were related as defense mechanisms, triggered by Si, in the wheat - *B. sorokiana* pathosystem [76].

For tan spot, Si-supply to wheat plants increased biochemical defense mechanisms and histo-cytological defense responses [80, 81]. The most prominent responses from Si-supplied plants were: the accumulation of H_2O_2 in the epidermal cells that occurred early, more intensely and in more epidermal cells, mainly at the beginning of pathogenesis; the alteration of enzyme activities such as SOD, CAT, POX, CHI and PAL; and the accumulation of phenylpropanoid derivatives at the infection site [80, 81]. Together, these defense responses restricted the spread of the pathogen and the damage caused in the plant tissues resulting in a reduction in cell death at *P. tritici-repentis* infection sites [80]. In regarding to the fast and greater accumulation of H_2O_2 in the epidermal cells of the Si-supplied plants is important highlight that the accumulation of H_2O_2 is known to be a mechanism of pathogen attack inducing cell death through *P. tritici-repentis* toxins [92]. However, the early (<12 hours after inoculation) accumulation of H_2O_2 in the epidermal cell of the Si-supplied plants of moderately resistant cultivar, compared to late accumulation (>24 after inoculation) in the mesophyll and epidermal cells of the non supplied plants, indicated that H_2O_2 was a defense mechanism. This inference is because accumulation of H_2O_2 occurred before pathogen penetration into the leaf tissue and was related to lower infection efficiency (the ratio between the number of conidia on the leaf surface and the number of lesions formed). Furthermore, on the Si-supplied plants, early fluorescence in epidermal cells, in neighboring cells and in the cell in which *P. tritici-repentis* attempted to penetrate, indicated that phenylpropanoid derivative accumulation were also contributing to disease resistance [81].

6. Physiological effects of silicon in wheat under pathogen stress

The photosynthesis is the major physiological process in plants; therefore, if plants are infected by pathogens some process in their physiology can be negatively affected. The pathogen infection can be responsible to decrease photosynthesis at different levels [93], modification or damage of the photosynthetic apparatus [94] and interfering with normal source-sink relationships in plants [95, 96].

In this sense exist a general consensus that Si improves the plant resistance to various biotic and abiotic stresses. Thus, the effect of Si on plant physiology it has been observed mainly when plant is under some kind of stress. For example, under biotic stress imposed by *B. graminis* f. sp. *tritici*, an analysis of around 55,000 transcripts indicated that around 3000 genes were differentially expressed on

pathogen-inoculated plants, but a nearly perfect reversal in the transcript profile of downregulated stress-related genes occurred when Si was supplied [91]. This result indicated that Si rather than being involved directly in the regulation of gene expression, prevented or attenuated the effects on transcription imposed by pathogen [91]. Furthermore, several studies revealed that wheat plants supplied with Si when challenged by pathogens showed lower affectation and/or ameliorative on photosynthetic process as assessed via measurements of the leaf gas exchange and the chlorophyll *a* (Ch*a*) fluorescence kinetics.

In this regard, some studies showed that concentration of photosynthetic pigments and structural and functional damage of chloroplasts produce alterations on photochemical machinery with losses in the amount of chlorophylls and carotenoids, as a result it has been observed decreased values for the net photosynthesis rate [93]. In a study on wheat-*Magnaporthe oryzae* interaction, in Si-supplied plants occurred a maintaining the concentration of photosynthetic pigments such as total chlorophyll, violanxanthin + antheraxanthin + zeaxanthin, β-carotene and α-carotene which helped to maintain the structural and functional viability of the photosynthetic machinery minimizing, therefore, lipid peroxidation and the production of ROS to ensure the integrity of the leaf cells [97]. In the same pathosystem, photosynthetic performance was studied in Si-supplied plants which showed higher values for net photosynthesis rate coupled with improved photochemistry associated to Ch*a* fluorescence parameters, and also increased concentrations of total chlorophylls [66, 98]. Also, Si-supplied plant showed less functional damage to the photosystem II (PSII) without reductions in the values of maximum quantum quenching, photochemical yield of PSII and electron transport rate, but higher values for quenching non-photochemical [97].

Likewise, the impairment caused by blast on the photosynthetic process, primarily related to the F_v/F_m parameter, on wheat leaves, was in lesser extent on the plants sprayed with potassium silicate [69]. Furthermore, authors did not detect any significant alteration on the gas exchange and Ch*a* fluorescence parameter for plants sprayed three times (every 96 h interval) as the potassium silicate rates increased from 2.5 to 12.5 g L^{-1} indicating that potassium silicate do not cause perturbation to the photosynthetic machinery of wheat plants.

In addition, the pathogen infection usually leads to the development of symptoms that result in a decrease on the photoassimilates production [99], resulting in low performance of photochemical reactions associated to PSII, that mainly influence the reduction in CO_2 assimilation [93] producing alteration in some parameters of leaf gas exchange. In this way, alterations with diffusional limitations and significant losses both in the electron transport rate and biochemical capacity for carboxylation associated with losses in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity have been measured on the leaves of wheat plants infected with *M. oryzae* [87]. In this pathosystem, Aucique Perez [66] observed that these dysfunctions could largely be avoided in the presence of Si, which might directly be associated with lower blast symptoms on Si-supplied plants; in those plants net CO_2 assimilation rate, stomatal conductance to water vapor, and transpiration rate were significantly higher, showing that Si improving gas exchange performance. Furthermore, Araujo et al. [95] measured several parameters of Ch*a* fluorescence, sugars (glucose, fructose and sucrose) and starch concentration, the activities of enzymes acid invertase and sucrose phosphate synthase in leaves and spike of wheat challenged by *M. oryzae* showing evidences of the beneficial effects of Si in improving the source-sink relationship on infected leaves and spikes by preserving the alteration in assimilates production and partitioning during the grains filling process.

Overall, in all the experiments the authors agreed that the effect of Si on photo-synthesis process is major in plants challenged by the pathogen. Indeed, transcrip-tomic studies performed on several plant species submitted to different types of biotic stress showed a reduction in transcript levels of genes related to photochemistry, Calvin cycle and the synthesis of chlorophylls [100]. Observations in non-inoculated plants, in general, does no showed significant difference between the non-supplied and Si-supplied plants for the values of leaf gas exchanges, photochemical parameters associated with Chl*a* fluorescence, soluble sugars and some enzymes of sucrose metabolism [95]. These findings are in line with previous study in which was not found any differences on the photosynthetic activity of rice plants with and without Si supply [46]. In this context, Coskun et al. [14] pointing out to the question of Si's role in the absence of stress having little or no effect, however remains a contentious issue. Probably Si is indirectly involved in the nutrition of the plant and it is undeni-able that Si prevents or mitigates the strains imposed by stress, and this, ultimately, is reflected in improvements in plant growth, function and metabolic activity.

7. Conclusion and perspectives

The importance of Si and Si fertilization for improving plant health are recognized. Several studies clearly demonstrate that silicate fertilization for wheat plants increases grain yield and its quality, especially under both biotic and abiotic stress. In the case of biotic stress, the Si effect reduces the intensity of the diseases due to the enhancement of the defense mechanisms that are earlier expressed and better coordinated. In addition to the effect on defenses against the pathogen, plants supplied with Si also show less physiological damage, in fact this is associated with increased on the yield. These effects are clearly evident and largely accepted, indicating that Si fertilization could be incorporated in the wheat management.

Nevertheless, for silicate fertilization to become widely used by wheat growers, several issues still need to be clarified. Initially, an important point is that most of the studies demonstrating the effect of Si on disease control and the reduction of physiological damage was carried out in a controlled environment with only a single stress imposed on the plant, and few studies were carried out in field conditions with multiple stresses simultaneously. Therefore, more studies need to be carried out under field conditions to obtain a greater amount of data of the silicate fertiliza-tion effect and with all these data should be analyzed through meta-analyzes to provide a holistic view of the effect.

Taking into account that we can mostly use two forms of Si application: leaf or root, there are still many unanswered questions. For example, in soil fertilization we can consider the following questions.

1. What is the best form of application? In this sense, we can consider situations in which the farmer plows the soil and the silicate fertilizer can be incorporated during this procedure. However, for wheat growers who use no-till, incorpora-tion is not possible. In this case, the application of the Si source can be carried out on the soil surface or in the sowing line. For application to the surface without incorporation, we still do not know clearly how long it takes for Si to be available in the soil solution in sufficient quantity to meet the demand of the wheat plant. With respect to the application in the sowing line, there is still not enough data to indicate which is the best source or dose of Si to supply to the plant without interfering in the initial stages of seedling development, and also is still unknown which is the amount to applied without compromising the lo-gistic yield of the sowing procedure to obtain the Si benefits as well as possible.

2. How often should silicate fertilization be carried out? Evidently, this information can be obtained by analyzing the amount of Si available in the soil. However, for the wheat growers to adopt silicate fertilization it will be necessary to know the cost benefit of the application and the frequency of application. In the case of fertilization in the sowing line, the financial impact for the producer is easier to be determined. However, in surface or incorporated applications, where specific activities are required for this procedure, more information is needed. For example, how many crop cycles/years should the reapplication be carried out? What dose should be applied and/or reapplied? What is the best product for reapplication: soluble or powder? Can we make a basic application to increase the Si pool in the soil and the reapplications be carried out via the seeding line? Does crop rotation or succession affect the frequency and/or rate that we should be used when reapplying silicate fertilization? These are questions that remain unanswered to wheat growers.

3. Considering the great variation in the ability of Si absorption among different wheat cultivars, it is important that this factor to be considered in breeding programs, aiming to obtain cultivars that present a higher efficiency Si absorption for different soils and climates it will be expected. This is important to maximize the use of silicate fertilization and consequently maximize the economic return to the producer. Furthermore, according to Ranjbar et al. [30] the selection and modification of silicon-efficient wheat cultivars can be a successful and promising strategy to maintain production in low-input and environmentally friendly agricultural systems.

4. With regard to foliar application, we agree with the consideration pointed out by Puppe and Sommer [101] that, there is little knowledge on Si foliar application and Si fertilizers for different purposes (biotic and abiotic stress). The foliar application needs further detailed studies, especially on the knowledge on concentrations of foliar Si fertilizers application, type of fertilizers, frequency of application and the timing of spraying.

Further research should be done to answer these questions, even though we will be closer to being able to clearly demonstrate to wheat growers the real benefit, in economic terms, and the routinely adopt silicate fertilization for wheat crop.

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Conflict of interest

The authors declare no conflict of interest.

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References

[1] FAO- Food and Agriculture Organization. FAOSTAT - Crops. [Internet]. 2020. Available from: http://www.fao.org/faostat/en/#data/QC/ [Accessed: 2020-19-13]

[2] Tadesse W, Halila H, Jamal M, El-Hanafi S, Assefa S, Oweis T, Baum M. Mint: Role of sustainable wheat production to ensure food security in the CWANA region. Journal of Experimental Biology and Agricultural Sciences. 2017;5:S15-S32. DOI: 10.18006/2017.5(Spl-1-SAFSAW).S15.S32

[3] Chaves MS, Martinelli JÁ, Wesp-Guterres C, Graichen FAZ, Brammer SP, Scagliusi SM, Consoli L. The importance for food security of maintaining rust resistance in wheat. Food Security. 2013;5:157-176. DOI: 10.1007/s12571-013-0248-x

[4] Shiferaw B, Smale M, Braun H-J, Duveiller E, Reynolds M, Muricho G. Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Security. 2013;5:291-317. DOI: 10.1007/s12571-013-0263-y

[5] Acevedo M, Zurn JD, Molero G, Singh P, He X, Aoun M, Juliana P, Bochleman H, Bonman M, El-Sohl M, Amri A, Coffman R, McCandless L. The role of wheat in global food security. In: Nagothu US, editor. Agricultural Development and Sustainable Intensification: Technology and Policy Challenges in the Face of Climate Change. 1st ed. New York: Routledge; 2018. p. 81-110. DOI: 10.4324/9780203733301-4

[6] Bai G, Su Z, Cai J. Wheat resistance to Fusarium head blight. Canadian Journal of Plant Pathology. 2018;40:336-346. DOI: 10.1080/07060661.2018.1476411

[7] Faris JD, Liu Z, Xu SS. Genetics of tan spot resistance in wheat. Theoretical and Applied Genetics. 2013;126:2197-2217. DOI: 10.1007/s00122-013-2157-y

[8] Goddard R, Steed A, Chinoy C, Ferreira JR, Scheeren PL, Maciel JLN, Caierão E, Torres GAM, Consoli L, Santana FM Fernandes JMC, Simmonds J, Uauy C, Cockram J, Nicholson P. Dissecting the genetic basis of wheat blast resistance in the Brazilian wheat cultivar BR 18-Terena. BMC Plant Biology. 2020;20:1-15. DOI: 10.1186/s12870-020-02592-0

[9] Periyannan S, Milne RJ, Figueroa M, Lagudah ES, Dodds PN. An overview of genetic rust resistance: From broad to specific mechanisms. PLoS Pathogens. 2017;13: e1006380. DOI: 10.1371/journal.ppat.1006380

[10] Santana FM, Lau D, Sbalcheiro CC, Goussain RCS, Venancio WS, Custódio AAP, Moreira LSO, Sussel AAB, editors. Eficiência de fungicidas para controle de brusone de trigo: resultados dos ensaios cooperativos, safra 2018.53nd ed. Embrapa Trigo. Circular Técnica Online. Passo Fundo, RS: 2020. 18 p.

[11] Santana FM, Lau D, Sbalcheiro CC, Schipanski CA, Venancio WS, Dallagnol LJ, Guterres CW, Kuhnem Junior PR, Chagas DF, editors. Eficiência de fungicidas para controle de giberela do trigo: resultados dos Ensaios Cooperativos - Safra 2018. 52nd ed. Embrapa Trigo. Circular Técnica Online. Passo Fundo, RS: 2020. 20 p.

[12] Frac-Fungicide Resistance Action Committee. Pathogen risk list [Internet]. 2019. Available from: https://www.frac.info/docs/default-source/publications/pathogen-risk/frac-pathogen-list-2019.pdf. [Accessed: 2020-19-13]

[13] Haynes RJ. A contemporary overview of silicon availability in agricultural soils. Journal of Plant Nutrition and Soil Science. 2014;177:831-844. DOI: 10.1002/jpln.201400202

[14] Coskun D, Deshmukh R, Sonah H, Menzies JG, Reynolds O, Ma JF, Kronzucker HJ, Bélanger RR. The controversies of silicon's role in plant biology. New Phytologist. 2019;221:67-85. DOI: 10.1111/nph.15343

[15] Debona D, Rodrigues FA, Datnoff LE. Silicon's role in abiotic and biotic plant stresses. Annual Review of Phytopathology 2017;55:85-107. DOI: 10.1146/annurev-phyto-080516-035312

[16] Luyckx M, Hausman JF, Lutts S, Guerriero G. Impact of silicon in plant biomass production: Focus on bast fibres, hypotheses, and perspectives. Plants. 2017;6:37. DOI: 10.3390/plants6030037

[17] Rodrigues FA, Dallagnol LJ, Datnoff LE. Silicon control of foliar diseases in monocots and dicots. In Rodrigues FA, Datnoff LE, editors. Silicon and Plant Diseases. 1 ed. Berlin: Springer; 2015. p. 67-108. https://doi.org/10.1007/978-3-319-22930-0_4

[18] Chiba Y, Mitani N, Yamaji N, Ma JF. HvLsi1 is a silicon influx transporter in barley. The Plant Journal. 2009;57:810-818. DOI:10.1111/j.1365-313X.2008.03728.x

[19] Ma JF, Yamaji N. A cooperative system of silicon transport in plants. Trends in Plant Science. 2015; 20:435-442. DOI: 10.1016/j.tplants.2015.04.007.

[20] Mitani N, Yamaji N, Ago Y, Iwasaki K, Ma JF. Isolation and functional characterization of an influx silicon transporter in two pumpkin cultivars contrasting in silicon accumulation. Plant Journal. 2011;66:231-40. DOI: 10.1111/j.1365-313X.2011.04483.x

[21] Montpetit J, Vivancos J, Mitani-Ueno N, Yamaji N, Rémus-Borel W, Belzile F, Ma JF, Bélanger RR. Cloning, functional characterization and heterologous expression of TaLsi1, a wheat silicon transporter gene. Plant Molecular Biology. 2012;79:35-46. DOI: 10.1007/s11103-012-9892-3

[22] Jarvis SC. The uptake and transport of silicon by perennial ryegrass and wheat. Plant and Soil 1987;97:429-437. DOI: 10.1007/BF02383233

[23] Sangster AG, Hodson MJ. Silica deposition in subterranean organs. In: Rapp Jr G, Mulholland SC, editors. Phytolith Systematics: Emerging Issues. Advances in Archaeological and Museum Science. 1 ed. Springer US; 1992. p. 239-251. DOI: 10.1007/978-1-4899-1155-1

[24] Mayland HF, Wright JL, Sojka, RE. Silicon accumulation and water uptake by wheat. Plant and Soil 1991; 137:191-199. DOI: 1007/BF00011197

[25] Rafi MM, Epstein E. Silicon absorption by wheat (*Triticum aestivum* L). Plant and Soil1999;211:223-230. DOI: 10.1023/A:1004600611582

[26] Rains DW, Epstein E, Zasoski RJ, Aslam M. Active Silicon Uptake by Wheat. Plant and Soil 2006; 280: 223-228. DOI:1007/s11104-005-3082-x

[27] Gomes D, Agasse A, Thiebaud P, Delrot S, Geros H, Chaumont F. Aquaporins are multifunctional water and solute transporters highly divergent in living organisms. Biochimica et Biophysica Acta (BBA)-Biomembranes. 2009;1788:1213-1228. DOI: 10.1016/j.bbamem.2009.03.009

[28] Murozuka E,Bang TC, Frydenvang J, Lindedam J, Laursen KH, Bruun S, Magid J, Schjoerring JK. Concentration of mineral elements in wheat (*Triticum aestivum* L.) straw: genotypic differences and consequences for enzymatic saccharification. Biomass and Bioenergy 2015;75:134-141. DOI: 10.1016/j.biombioe.2015.02.017

[29] Carter AH, Rath BB, Gorzkowski EP, Qadri SB. Evaluation of silica content in winter wheat chaff. Agricultural &

Environmental Letters. 2020;5:e20025. DOI:10.1002/ael2.20025

[30] Ranjbar SS, Motesharezadeh B, Moshiri F, Mirseyed Hosseini H, Alikhani, HA. Silicon utilization efficiency of different wheat cultivars in a calcareous soil. SILICON 2019;11:2159-2168. DOI: 10.1007/s12633-018-0038-3

[31] Mandlik R, Thakral V, Rature G, Shinde S, Nikolic M, Tripathi DK, Sonah H, Deshmukh R. Significance of silicon uptake, transport, and deposition in plants. Journal of Experimental Botany. 2020, DOI:10.1093/jxb/eraa301

[32] Raven JA. Cycling silicon–the role of accumulation in plants. New Phytologist. 2003;158:419-421. DOI: 10.1046/j.1469-8137.2003.00778.x

[33] Tripathi, D.K., Kumar, R., Pathak, A.K, Chauhan DK, Rai AK. Laser-Induced Breakdown Spectroscopy and Phytolith Analysis: An Approach to Study the Deposition and Distribution Pattern of Silicon in Different Parts of Wheat (*Triticum aestivum* L.) Plants & Agriculture Research. 2012;1:352-361. DOI: 10.1007/s40003-012-0042-6

[34] Neu S, Schaller J, Dudel EG. Silicon availability modifies nutrient use efficiency and content, C:N:P stoichiometry, and productivity of winter wheat (*Triticum aestivum* L.). Scientific Reports 2017;7:40829. DOI:10.1038/srep40829

[35] Peleg Z, Saranga Y, Fahima T, Aharoni A, Elbaum R. Genetic control over silica deposition in wheat awns. Physiologia Plantarum 2010;140:10-20. DOI:10.1111/j.1399-3054.2010.01376.x

[36] Silva WL, Cruz MFA, Fortunato AA, Rodrigues FÁ. Histochemical aspects of wheat resistance to leaf blast mediated by silicon. Scientia Agricola 2015;72:322-327. DOI:10.1590/0103-9016-2014-0221

[37] Xavier Filha MS, Rodrigues FA, Domiciano GP, Oliveira HV, Silveira PR, Moreira WR. Wheat resistance to leaf blast mediated by silicon. Australasian Plant Pathology. 2011;40:28-38. DOI:10.1007/s13313-010-0010-1

[38] Mecfel J, Hinke S, Goedel WA, Marx G, Fehlhaber R, Bäucker E, Wienhaus O. Effect of silicon fertilizers on silicon accumulation in wheat. Journal of Plant Nutrition and Soil Science. 2007;170:769-772. DOI:10.1002/jpln.200625038

[39] Guntzer F, Keller C, Poulton PR, McGrath SP, Meunier JD. Long-term removal of wheat straw decreases soil amorphous silica at Broadbalk, Rothamsted. Plant and Soil 2012;352:173-184. DOI: 10.1007/s11104-011-0987-4

[40] Tubana BS, Babu T, Datnoff LE. A Review of silicon in soils and plants and its role in US agriculture: History and future perspectives. Soil Science. 2016;181:393-411. DOI: 10.1097/SS.0000000000000179

[41] Epstein S. Integration of the cognitive and the psychodynamic unconscious. American Psychologist. 1994;49:709-724. DOI: 10.1037//0003-066X.49.8.709

[42] Maxim LD, Niebo R, Larosa S, Johnston B, Allison K, McConnell EE. Product stewardship inwollastonite production. Inhalation Toxicology. 2008; 20:1199-1214. DOI: 10.1080/08958370802136749

[43] Buck GB, Korndorfer GH, Datnoff LE. Extractors for estimating plant available silicon from potential silicon fertilizer sources. Journal of Plant Nutrition. 2010; 34:272-282. DOI: 10.1080/01904167.2011.533327

[44] Sebastian D, Rodrigues H, Kinsey C, Korndörfer G, Pereira H, Buck G, Datnoff L, Miranda S, Provance-Bowley M. A 5-day method for determination of soluble silicon concentrations in nonliquid fertilizer

materials using a sodium carbonate-ammonium nitrate extractant followed by visible spectroscopy with heteropoly blue analysis: Single-laboratory validation. Journal of AOAC INTERNATIONAL. 2013;96:251-258. DOI: 10.5740/jaoacint.12-243

[45] Wang M, Jim JW, Xudong W. Effect of KOH-enhanced biochar on increasing soil plant-available silicon. Geoderma 2018; 321: 22-31. DOI: 10.1016/j.geoderma.2018.02.001

[46] Ma JF, Takahashi E, editors. Soil, fertilizer, and plant silicon research in Japan. 1 ed. Elsevier: Amsterdam, Netherlands; 2002. 294 p. DOI: 10.1016/B978-0-444-51166-9.X5000-3

[47] Nolla A, Korndorfer GH, Da Silva CAT, Da Silva TRB, Zucarelli V, Da Silva MAG. Correcting soil acidity with the use of slags. African Journal of Agricultural Research. 2013;8:5174-5180. DOI: 10.5897/AJAR2013.6940

[48] Alvarez J, Snyder GH, Anderson DL, Jones DB. Economics of calcium silicate slag in a rice-sugarcane rotation in the everglades. Agricultural Systems 1988; 28:179-188. DOI: 10.1016/0308-521X(88)90050-9

[49] Ning DF, Song A, Fan FL, Li ZJ, Liang YC. Effects of slag-based silicon fertilizer on rice growth and brown-spot resistance. PLoSOne. 2014;9:e102681. DOI: 10.1371/journal.pone.0102681

[50] Raid RN, Anderson DL, Ulloa MF. Influence of cultivar and amendment of soil with calcium silicate slag on foliar disease development and yield of sugar-cane. Crop Protection. 1992;11: 84-88. DOI: 10.1016/0261-2194(92)90085-J

[51] Cruz MFA, Diniz APC, Rodrigues FA, Barros EG. Aplicação foliar de produtos na redução da severidade da brusone do trigo. Tropical Plant Pathology. 2011;36:424-428. DOI: 10.1590/S1982-56762011000600014

[52] Frayssinet C, Osterrieth LM, Borrelli LN, Honaine MF, Ciarlo E, Heiland P. Effect of silicate fertilizers on wheat and soil properties in Southeastern Buenos Aires province, Argentina. A preliminary study. Soil and Tillage Research. 2019;195:104412. DOI: 10.1016/j.still.2019.104412

[53] Gocke M, Liang W, Sommer M, Kuzyakov Y. Silicon uptake by wheat: effects of Si pools and pH. Journal of Soil Science and Plant Nutrition. 2013;176:551-560. DOI: 10.1002/jpln.201200098

[54] Mousavi SR, Rezaie M. Nanotechnology in agriculture and food production. Journal of Applied Environmental and Biological Sciences. 2011;10:414-419.

[55] Liang YC, Ma TS, Li FJ, Feng YJ. Silicon availability and response of rice and wheat to silicon in calcareous soils. Communications in Soil Science and Plant Analysis. 1994;25:2285-2297. DOI: 10.1080/00103629409369189

[56] Wang HL, Li CH, Liang YC. Agricultural utilization of silicon in China. In: Datnoff LE, Snyder GH, Korndörfer GH, editors. In: Silicon in agriculture. Studies in plant science, 8 ed. Amsterdam: Elsevier; 2001. p. 343-352. DOI: 10.1016/S0928-3420(01)80001-X

[57] Provance-Bowley MC, Heckman JR, Durner EF. Calcium silicate suppresses powdery mildew and increases yield of field grown wheat. Soil Science Society of America Journal. 2010;74:1652-1661. DOI:10.2136/sssaj2010.0134

[58] Walsh OS, Shafian S, McClintick-Chess JR, Belmont KM, Blanscet SM. Potential of silicon amendment for improved wheat production. Plants. 2018;28:26. DOI: 10.3390/plants7020026

[59] White B, Tubana BS, Babu T, Mascagni H, Agostinho F, Datnoff LE, Harrison S. Effect of silicate slag application on wheat grown under two

nitrogen rates. Plants. 2017;11:47. DOI: 10.3390/plants6040047

[60] Sarto MVM, Lana MC, Rampim L, Rosset JSR, Wobeto JR. Effects of silicate application on soil fertility and wheat yield. Semina: Ciências Agrárias. 2015; 36:4071-4082. DOI: 10.5433/1679-0359. 2015v36n6Supl2p4071

[61] Kowalska J, Tyburski J, Jakubowska M, Krzymińska J. Effect of different forms of silicon on growth of spring wheat cultivated in organic farming system. SILICON 2020. DOI: 10.1007/s12633-020-00414-4

[62] Guével M, Menzies JG, Bélanger RR. Effect of root and foliar applications of soluble silicon on powdery mildew control and growth of wheat plants. European Journal of Plant Pathology. 2007;119:429-436. DOI: 10.1007/ s10658-007-9181-1

[63] Maghsoudi K, Emam Y, Ashraf M. Foliar application of silicon at different growth stages alters growth and yield of selected wheat cultivars. Journal of Plant Nutrition. 2016;39:1194-1203. DOI: 10.1080/01904167.2015.1115876

[64] Hellal FA, Zeweny RM, Yassen AA. Evaluation of nitrogen and silicon application for enhancing yield production and nutrient uptake by wheat in clay soil. Journal of Applied Sciences Research. 2012;8:686-692.

[65] Toledo MZ, Castro GSA, CruSciol CAC, Soratto RP, Cavariani C, Ishizuka MS, Picoli LB. Silicon leaf application and physiological quality of white oat and wheat seeds. Semina: Ciências Agrárias. 2012;33:1693-1702. DOI: 10.5433/1679-0359.2012v33n5p1693

[66] Aucique Perez CE, Rodrigues FA, Moreira WR, DaMatta FM. 2014. Leaf gas exchange and chlorophyll a fluorescence in wheat plants supplied with silicon and infected with *Pyricularia oryzae*. Phytopathology 2014;104:143-149. DOI: 10.1094/PHYTO-06-13-0163-r

[67] Debona D, Rodrigues FA, Rios JA, Nascimento KJT, Silva LC. The effect of silicon on antioxidant metabolism of wheat leaves infected by *Pyricularia oryzae*. Plant Pathology. 2014;63:581-589. DOI: 10.1111/ppa.12119

[68] Sousa RS, Rodrigues FA, Schurt DA, Souza NFA, Cruz MFA. Cytological aspects of the infection process of *Pyricularia oryzae* on leaves of wheat plants supplied with silicon. Tropical Plant Pathology. 2013;38:472-477. DOI: 10.1590/S1982-56762013000600002

[69] Oliveira, TB, Aucique-Pérez, CE, Rodrigues, FÁ. Foliar application of silicon decreases wheat blast symptoms without impairing photosynthesis. Bragantia 2019;78:423-431. DOI: 10.1590/1678-4499.20180379

[70] Pagani APS, Dianese AC, Café-Filho AC. Management of wheat blast with synthetic fungicides, partial resistance and silicate and phosphite minerals. Phytoparasitica 2014;42:609-617. DOI:10.1007/s12600-014-0401-x

[71] Germar B. Über einige Wirkungen der Kieselsäure in Getreidepflanzen, insbesondere auf deren Resistenz gegenüber Mehltau. Z. Pflanzenernaehr. Dueng. Bodenk. 1934;35:102-115. DOI: 10.1002/jpln.19340350111

[72] Rodgers-Gray BS, Shaw MW. Substantial reductions in winter wheat diseases caused by addition of straw but not manure to soil. Plant Pathology. 2000;49: 590-599. DOI:10.1046/j.1365-3059.2000.00497.x

[73] Rodgers-Gray BS, Shaw MW. Effects of straw and silicon soil amendments on some foliar and stem-base diseases in pot-grown winter wheat. Plant Pathology. 2004;53:733-740. DOI:10.1111/j.1365-3059.2004.01102.x

[74] Bélanger RR, Benhamou N, Menzies JG. Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f.

sp. tritici). Phytopathology 2003;93:402-412. DOI: 10.1094/PHYTO.2003.93.4.402

[75] Moldes CA, Lima Filho OF, Merini LJ, Tsai SM, Camiña JM. Occurrence of powdery mildew disease in wheat fertilized with increasing silicon doses: a chemometric analysis of antioxidant response. Acta Physiologiae Plantarum. 2016;8:206-238. DOI: 10.1007/s11738-016-2217-4

[76] Domiciano GP, Rodrigues FA, Moreira WR, Oliveira HV, Vale FXR, Xavier Filha MS. Silício no progresso da mancha marrom na folha bandeira do trigo. Tropical Plant Pathology. 2010;35:186-189. DOI:10.1590/S1982-56762010000300009

[77] Domiciano GP, Rodrigues FA, Vale FXR, Xavier Filha MS, Moreira WR, Andrade CCL, Pereira SC. Wheat resistance to spot blotch potentiated by silicon. Journal of Phytopathology 2010;158:334-343. DOI: 10.1111/j.1439-0434.2009.01623.x

[78] Zanão Júnior LA, Fontes RLF, Coelho PHM, Korndörfer GH, Zambolim L. Silício aplicado no solo reduz a severidade da mancha-marrom do trigo em solos com baixos teores desse elemento. Revista Brasileira de Ciência do Solo. 2010;34:401-408. DOI: 10.1590/S0100-06832010000200013

[79] Domiciano GP, Rodrigues FA, Guerra AMN, Vale FXR. Infection process of *Bipolaris sorokiniana* on wheat leaves is affected by silicon. Tropical Plant Pathology.2013;38:258-263. DOI:10.1590/S1982-56762013005000006

[80] Dorneles KR, Dallagnol LJ, Pazdiora PC, Rodrigues FA, Deuner S. Silicon potentiates biochemical defense responses of wheat against tan spot. Physiological and Molecular Plant Pathology. 2017;97:69-78. DOI: 10.1016/j.pmpp.2017.01.001

[81] Dorneles KR, Pazdiora PC, Hoffmann JF, Chaves FC, Monte LG,

Rodrigues FA, Dallagnol LJ. Wheat leaf resistance to *Pyrenophora tritici-repentis* induced by silicon activation of phenylpropanoid metabolism. Plant Pathology. 2018;67:1713-1724. DOI: 10.1111/ppa.12876

[82] Pazdiora PC, Dorneles KR, Forcelini CA, Del Ponte EM, Dallagnol LJ. Silicon suppresses tan spot development on wheat infected by *Pyrenophora tritici-repentis*. European Journal of Plant Pathology. 2018;150:49-56. DOI: 10.1007/s10658-017-1251-4

[83] Pazdiora, P.C. Silício, resistência parcial e fungicida no manejo da giberela do trigo (Thesis). Pelotas: Federal University of Pelotas; 2019.

[84] Silva IT, Rodrigues F, Oliveira JR, Pereira SC, Andrade CCL, Silveira PR, Conceição MM. Wheat resistance to bacterial leaf streak mediated by silicon. Journal of Phytopathology 2010; 158: 253-262. DOI: 10.1111/j.1439-0434.2009.01610.x

[85] Islam W, Tayyab M, Khalil F, Hua Z, Huang Z, Chen HTH. Silicon-mediated plant defense against pathogens and insect pests. Pesticide Biochemistry and Physiology. 2020;168:104641. DOI:10.1016/j.pestbp.2020.104641

[86] Debona D, Rodrigues FA, Rios JA, Nascimento KJT. Biochemical changes in the leaves of wheat plants infected by *Pyricularia oryzae*. Phytopathology 2012; 102:1121-1129. DOI: 10.1094/PHYTO-06-12-0125-r

[87] Debona D, Rodrigues FÁ, Rios JA, Martins SC, Pereira LF, DaMatta FM. Limitations to photosynthesis in leaves of wheat plants infected by *Pyricularia oryzae*. Phytopathology 2014;104:34-39. DOI: 10.1094/PHYTO-01-13-0024-r

[88] Cruz MFA, Debona D, Rios JA, Barros EG, Rodrigues FA. Potentiation of defense-related gene expression by silicon increases wheat resistance to leaf blast. Tropical

Plant Pathology.2015;40:394-400. DOI:10.1007/s40858-015-0051-7

[89] Rémus-BoreL W, Menzies JG, Belanger RR. Silicon induces antifungal compounds in powdery mildew-infected wheat. Physiological and Molecular Plant Pathology.2005;66:108-115. DOI: 10.1016/j.pmpp.2005.05.006

[90] Rémus-Borel W, Menzies JG, Belanger RR. Aconitate and methyl aconitate are modulated by silicon in powdery mildew-infected wheat plants. Journal of Plant Physiology 2009;166:1413-1422. DOI: 10.1016/j.jplph.2009.02.011

[91] Chain F, Côté-Beaulieu C, Belzile F, Menzies JG, Bélanger RR. A comprehensive transcriptomic analysis of the effect of silicon on wheat plants under control and pathogen stress conditions. Molecular Plant-Microbe Interactions. 2009; 22:1323-1330. DOI: 10.1094/MPMI-22-11-1323

[92] Ciuffetti LM, Manning VA, Pandelova I, Betts MF, Martinez JP. Host-selective toxins, PtrToxA and PtrToxB, as necrotrophic effectors in the *Pyrenophora tritici-repentis*–wheat interaction. New Phytologist. 2010;187:911-919. DOI:10.1111/j.1469-8137.2010.03362.x

[93] Berger S, Benediktyova Z, Matous K, Bonfig KB, Mueller MJ, Nedbal L, Roitsch T. Visualization of dynamics of plant–pathogen interaction by novel combination of chlorophyll fluorescence imaging and statistical analysis: differential effects of virulent and avirulent strains of *Pseudomonas syringae* and of oxylipins on *Arabidopsis thaliana*. Journal of Experimental Botany. 2007;58:797-806. DOI: 10.1093/jxb/erl208

[94] Lichtenthaler HK, Miehé JA. Fluorescence imaging as a diagnostic tool for plant stress. Trends in Plant Science. 19972:316-320. DOI: 10.1016/S1360-1385(97)89954-2

[95] Araújo MUP, Rios JA, Silva ET, Rodrigues FÁ. Silicon alleviates changes in the source-sink relationship of wheat plants infected by *Pyricularia oryzae*. Phytopathology 2019;109:1129-1140. DOI: 10.1094/PHYTO-11-18-0428-r

[96] Biemelt S, Sonnewald U. Plant-microbe interactions to probe regulation of plant carbon metabolism. Journal of Plant Physiology 2006;163:307-318. DOI: 10.1016/j.jplph.2005.10.011

[97] Aucique-Pérez CE, Menezes Silva PE, Moreira WR, DaMatta FM, Rodrigues FÁ. Photosynthesis impairments and excitation energy dissipation on wheat plants supplied with silicon and infected with *Pyricularia oryzae*. Plant Physiology and Biochemistry. 2017;121: 196-205. DOI: 10.1016/j.plaphy.2017.10.023

[98] Rios J, Rodrigues F, Debona D, Silva L. Photosynthetic gas exchange in leaves of wheat plants supplied with silicon and infected with *Pyricularia oryzae*. Acta Physiologia Plantarum. 2014;36:371-379. DOI: 10.1007/s11738-013-1418-3

[99] Schreiber U.Pulse-Amplitude-Modulation (PAM) fluorometry and saturation pulse method: An overview .In: Papageorgiou GC, Govindjee, editors. Chlorophyll Fluorescence: A Signature of Photosynthesis. 1nd ed. Springer Verlag: Dordrecht; 2004. p. 279-319. DOI: 10.1007/978-1-4020-3218-9

[100] Bilgin DD, Zavala JA, Zhu JI, Clough SJ, Ort DR, DeLucia EH. Biotic stress globally downregulates photosynthesis genes. Plant, Cell and Environment. 2010;33:1597-1613. DOI: 10.1111/j.1365-3040.2010.02167.x

[101] Puppe D, Sommer M. Experiments, Uptake Mechanisms, and Functioning of Silicon Foliar Fertilization—A Review Focusing on Maize, Rice, and Wheat. In Sparks DL Editor. Advances in Agronomy, v. 152; Academic Press, 2018. p. 1-49. https://doi.org/10.1016/bs.agron.2018.07.003.