

Foliar application of silicon decreases wheat blast symptoms without impairing photosynthesis

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ABSTRACT: Considering the importance of blast, caused by *Pyricularia oryzae*, to impact wheat yield, this study investigated whether the foliar spray of potassium silicate (PS) could affect the photosynthesis of wheat plants and its potential to reduce disease symptoms. The Exp. 1 aimed to determine the effect of the foliar spray of PS on the photosynthetic performance of plants and was arranged in a completely randomized design with six treatments (plants sprayed with PS rates of 2.5, 5.0, 7.5, 10.0, and 12.5 g·L⁻¹ at 35 days after emergence) and six replications. The leaf gas exchange (net CO₂ assimilation rate (A), internal CO₂ concentration (C_i), stomatal conductance to water vapor (g_s), and transpiration rate (E)) as well as fluorescence of chlorophyll *a* (maximal photosystem II quantum yield (F_v/F_m), quantum yield of non-regulated energy dissipation [Y(NO)], photochemical yield [Y(II)], electron transport rate (ETR), and quenching non-photochemical [Y(NPQ)]) parameters were evaluated. The Exp. 2 was carried out to determine the effect of PS on blast control and also on the photosynthetic performance of plants. Plants at 35 days after emergence were sprayed with PS rate of 12.5 g·L⁻¹, which did not affect photosynthesis on plants from Exp.1. This experiment was a 2 × 4 factorial and arranged in a completely randomized design with six replications. The factors studied were plants non-inoculated or

inoculated plants and the spray of water, PS, fungicide (trifloxystrobin 10% + tebuconazole 20%; 0.75 L/ha), and fungicide + PS. There were no significant changes in the values of A, g_s, E, C_i, F_v/F_m, Y(NO), Y(II), Y(NPQ), and ETR for plants sprayed three times (every 96 h interval) as the PS rates increased from 2.5 to 12.5 g·L⁻¹. There was no significant relationship between the PS rates with either absorbance, reflectance or transmittance on the leaf blades. Linear regression model best described the foliar Si concentration-PS rates relationship. Foliar Si concentration significantly increased by 44 and 42%, respectively, for the PS and PS + fungicide treatments compared to water-sprayed plants. The area under disease progress curve was significantly lower by 64, 58, and 53%, respectively, for the fungicide, PS, and fungicide + PS treatments in comparison to water-sprayed plants. The photosynthetic process, primarily related to the F_v/F_m parameter, on wheat leaves was greatly impaired during the infection process of *P. oryzae*, but to a lesser extent on the leaves of PS-sprayed plants. In conclusion, the foliar spray of PS can be an environmentally friendly strategy to control wheat blast without causing perturbation to the photosynthetic machinery of wheat plants.

Key words: *Triticum aestivum* L., disease control, fungal disease, plant nutrition.

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Received: Oct. 14, 2018 – Accepted: Dec. 3, 2018



Blast, caused by the hemibiotrophic fungus *Pyricularia oryzae* Sacc. (teleomorph: *Magnaphorthe grisea* (T. T. Hebert) M. E. Barr), has limited wheat production in Brazil and other South America countries (Cruz and Valent 2017; Kohli et al. 2011). Blast was restricted to South America until its first report in Bangladesh in 2016 and more recently in India (Ceresini et al. 2018). On leaves, blast symptoms are characterized by elliptic lesions with a gray center and brown margin (Goulart et al. 2007). On infected spikes, grains are small, deformed and of reduced weight (Igarashi et al. 1986). Seed treatment with fungicides, foliar applied systemic fungicides and cultivars with a high level of partial resistance have been the major control methods used by growers to reduce the negative impact of blast on yield (Goulart et al. 2007).

Since fungicides application is not very efficient for blast control and obtaining resistant cultivars is currently difficult (Goulart et al. 2007; Cruz and Valent 2017), new alternative methods for disease control need to be investigated. Several plant species, mainly grasses and some dicotyledons, exposed to both abiotic and biotic types of stresses are positively benefited by Si application either through soil amendment or foliar spray (Rodrigues et al. 2015b; Dallagnol et al. 2012; Debona et al. 2017). Polymerization of Si from liquid foliar products on the leaf surface is believed to form a physical barrier that may affect spores germination, fungal penetration, and sporulation (Liang et al. 2005; Dallagnol et al. 2012; Cacique et al. 2013). Rice plants receiving foliar Si applications showed lower severity for both blast and brown spot (Rezende et al. 2009; Cacique et al. 2013). Powdery mildew severity on leaves of melon plants was reduced more by Si applied via the roots in contrast to foliarly applied (Dallagnol et al. 2015). Wheat plants grown in soilless potting mix amended with Si showed lower blast severity and had their photosynthetic performance less impaired (Debona et al. 2014; Rios et al. 2014; Aucique-Pérez et al. 2014). Debona et al. (2014) suggested that biochemical limitation related to a reduction in Rubisco activity was the primary factor associated with the low A values during the infection process by *P. oryzae*.

This study was conducted to determine if potassium silicate (PS) deposition on leaf blades of wheat plants could decrease blast symptoms without compromising photosynthesis.

The first experiment (Experiment 1) aimed to determine the effect of foliarly applied PS on the photosynthetic performance of wheat plants. Wheat seeds [cultivar BRS Guamirim, susceptible to blast (Cruz et al. 2010)] were

surface sterilized in 10% (vol·vol⁻¹) NaOCl for 2 min, rinsed in sterilized water for 3 min and sown in plastic pots filled with 1 kg of substrate (Tropstrato, Vida Verde, Mogi Mirim, SP, Brazil). A total of 1.63 g of calcium phosphate monobasic was added to each plastic pot. A total of nine seeds were sown per pot and at five days after seedling emergence, each pot was thinned to seven seedlings. Seedlings in each pot were weekly fertilized with a nutrient solution containing, in g·L⁻¹, 6.4 KCl; 3.48 K₂SO₄; 5.01 MgSO₄·7H₂O; 2.03 (NH₂)₂CO; 0.009 NH₄Mo₇O₂₄·4H₂O; 0.054 H₃BO₃; 0.222 ZnSO₄·7H₂O; 0.058 CuSO₄·5H₂O; and 0.137 MnCl₂·4H₂O (Xavier Filha et al. 2011). A volume of 15 mL of nutrient solution containing 0.27 g of FeSO₄·7H₂O and 0.37 g of EDTA bisodic·L⁻¹ was also applied after seedling emergence. The nutrient solution was prepared using deionized water and 30 mL per pot was applied after seedlings emergence. Plants were watered as needed. Plants were grown during 40 days in a greenhouse with temperature of 25 ± 3 °C, relative humidity of 70 ± 5% and natural photosynthetically active radiation of 950 ± 15 μmol photons·m⁻²·s⁻¹, which was measured at midday. Plants at growth stage 45 (Zadoks et al. 1974) were sprayed with PS solutions at the rates of 2.5, 5.0, 7.5, 10.0, and 12.5 g·L⁻¹ (Fertililício®, Plant Defender, São Paulo, SP; 12% soluble Si) three times with a 96 h interval between each application using a handheld manual sprayer. Plants sprayed with water served as the control treatment. At 24 h after application, the net carbon assimilation rate (A ; μmol CO₂·m⁻²·s⁻¹), stomatal conductance to water vapor (g_s ; mol H₂O·m⁻²·s⁻¹), internal CO₂ concentration (C_i ; μmol CO₂·mol⁻¹) and transpiration rate (E ; mmol H₂O·m⁻²·s⁻¹) were estimated from 09:00 to 12:00 h (solar time) on the fifth leaf, from the top to the base, of each plant per replication of each treatment using a portable open-system infrared gas analyzer (IRGA, LI-COR 6400 XT, LI-COR Biosciences Inc. Nebraska, USA). All measurements were conducted under artificial, saturating photon irradiance (1,000 μmol·m⁻²·s⁻¹) at the leaf level at 25 °C and under external CO₂ concentration of 400 μmol·mol⁻¹ air. The vapor pressure deficit was maintained at approximately 1.0 kPa while the amount of blue light was set to 10% of the photosynthetic photon flux density to optimize stomatal aperture. Previously dark-adapted (30 min) leaf tissues were illuminated with weak, modulated measuring beams (0.03 μmol·m⁻²·s⁻¹) to obtain the initial fluorescence (F_0). Saturating white light pulses of 8,000 μmol photons·m⁻²·s⁻¹ were applied for 0.8 s to ensure maximum fluorescence emissions (F_m) from which

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the variable-to-maximum chlorophyll fluorescence ratio, $F_v/F_m = [(F_m - F_0)/F_m]$, was calculated. In light-adapted leaves, the steady-state fluorescence yield (F_s) was measured following a saturating white light pulse ($8,000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.8 s) that was applied to achieve the light-adapted maximum fluorescence (F_m'). The actinic light was then turned off and far-red illumination was applied ($2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) to measure the light-adapted initial fluorescence (F_0'). Using these parameters, the capture efficiency of the excitation energy by the open PSII reaction centers (F_v'/F_m') was estimated as $F_v'/F_m' = (F_m' - F_0')/F_m'$. The coefficient for photochemical quenching (q_p) was calculated as $q_p = (F_m' - F_s)/(F_m' - F_0')$, while that for non-photochemical quenching (NPQ) was calculated as $\text{NPQ} = (F_m'/F_m) - 1$. The actual quantum yield of PSII electron transport (ΦPSII) was computed as $\Phi\text{PSII} = (F_m' - F_s)/F_m'$, from which the electron transport rate (ETR) was calculated as $\text{ETR} = \Phi\text{PSII} \times \text{PPFD} \times f \times \alpha$, where f is a factor that accounts for the partitioning of energy between PSII and PSI and is assumed to be 0.5, which indicates that the excitation energy is distributed equally between the two photosystems; and α is the leaf absorbance by the photosynthetic tissues and is assumed to be 0.84 (Maxwell and Johnson 2000). Reflectance (R) and transmittance (T) were measured at 24 h after spraying the leaves with PS rates of 0, 2.5, 5.0, 7.5, 10.0, and 12.5 $\text{g}\cdot\text{L}^{-1}$ (Fertilisício®, Plant Defender, São Paulo, SP; 12% soluble Si) using an Ocean Optics model USB2000 spectrometer (Ocean Optics Inc., Dunedin, FL, USA). This spectrometer had a 2048 element detector array, 0.5 nm sampling interval and 7.3 nm spectral resolution in the 350-1000 nm range. A software was designed for signal verification, adjustment of integration time, and data acquisition. The absorbance (A) values were obtained as following: $A = 100 - (R + T)$. At the end of the Experiment 1 (Exp. 1), leaves from plants from the replications of each treatment were collected, washed in deionized water, dried for 72 h at 65 °C, and ground to pass through a 40-mesh screen with a Thomas Wiley mill. The foliar Si concentration was determined by colorimetric analysis of 0.1 g of dried and alkali-digested tissue (Korndörfer et al. 2004).

The Experiment 1 was arranged in a completely randomized design with six treatments (PS rates) and six replications. Each experimental unit corresponded to a plastic pot containing seven plants. The experiment was repeated once. Data from A , g_s , C_i , E , F_v/F_m , F_v'/F_m' , ETR, q_p , and q_n were separately used to calculate the area under the curve (AUC). Data from AUC for each parameter was submitted to analysis

of variance (ANOVA) using SAS (SAS, version 6.12; SAS Institute, Inc., Cary, NC). Data from AUC for each parameter, for reflectance variables, and foliar Si concentration from Exp. 1 and its repetition were analyzed using the MIXED procedure of the SAS software to determine if data from these experiments could be combined (Moore and Dixon 2015). Polynomial regression procedures were used to determine the relationship between PS rates and foliar Si concentration as well the reflectance variables using SAS.

Another experiment (Experiment 2) was carried out to determine the effect of PS on blast control and on the photosynthetic performance. Plants were grown as mentioned for the Exp. 1. The PS rate of 12.5 $\text{g}\cdot\text{L}^{-1}$, which did not affect photosynthesis from Exp. 1, was used on Experiment 2 (Exp. 2). Plants at growth stage 45 (Zadoks et al. 1974) were sprayed with PS (12.5 $\text{g}\cdot\text{L}^{-1}$), fungicide (trifloxystrobin 10% + tebuconazole 20%; 0.75 L/ha) and fungicide + PS at 24 h before inoculation with *P. oryzae* using a handheld manual sprayer. Plants sprayed with water served as the control treatment. An isolate of *P. oryzae* (UFV/DFP Po-01), obtained from spikes of wheat plants from cultivar BR-18, was used for plant inoculation. This isolate was preserved on strips of filter paper placed into glass tubes containing silica gel at 4 °C. Pieces of filter paper with fungal mycelia were transferred to Petri dishes containing potato dextrose agar (PDA). After three days, PDA plugs containing fungal mycelia were transferred to new Petri dishes containing oat media, which were kept in a growth chamber at 25 °C with a 24 h photoperiod for ten days. After this period, conidia were carefully removed from the Petri dishes with a soft bristle brush to obtain a conidial suspension, which was calibrated with a hemacytometer to obtain a concentration of 1×10^5 conidia·ml⁻¹. Thirty milliliters of the suspension were applied as a fine mist to the adaxial leaf blades of each plant until runoff with a VL Airbrush atomizer (Paasche Airbrush Co., Chicago, IL). Immediately after inoculation, plants were transferred to a growth chamber with a temperature of 25 ± 2 °C and a relative humidity of $90 \pm 5\%$ and were subjected to an initial 24 h dark period. After this period, plants were transferred to a plastic mist growth chamber (temperature of 25 ± 2 °C (day) to 20 ± 2 °C (night) and relative humidity of $92 \pm 3\%$ by using a misting system in which nozzles (model NEB-100; KGF Company, São Paulo, Brazil) sprayed mist every 30 min above the plant canopy) for the duration of the experiment.

The fourth and fifth leaves, from the top to the base, of each plant per replication of each treatment were marked and used to evaluate blast severity at 48, 72, 96, and 120 h after inoculation (hai) according to a diagrammatic scale proposed by Rios et al. (2013). The area under blast progress curve (AUBPC) for each leaf per plant was computed by using the trapezoidal integration of blast progress curves over time according to Shaner and Finney (1977). The leaf gas exchange and chlorophyll *a* fluorescence parameters, as well as the foliar Si concentration, were determined as previously described for Exp. 1. The Experiment 2 was a 2 × 4 factorial arranged in a completely randomized design with six replications. The factors studied were plants non-inoculated or inoculated with *P. oryzae* and products (plants sprayed with water, PS, fungicide, and fungicide + PS). Each experimental unit corresponded to a plastic pot containing seven plants. The experiment was repeated once. Data from A , g_s , C_i , E , F_v/F_m , $Y(NO)$, $Y(II)$, ETR , and $Y(NPQ)$ were separately used to calculate the AUC. Data from AUC for each parameter, AUDPC, and foliar Si concentration were submitted to ANOVA, and the treatment means were compared based on Tukey's test using SAS. Data from AUC for each parameter, AUDPC, and foliar Si concentration from Exp. 2 and its repetition were analyzed using the MIXED procedure of the SAS software to determine if data from these experiments could be combined (Moore and Dixon 2015).

For Exp. 1, there were no significant changes for A , g_s , E , and C_i as well as for F_v/F_m , $Y(NO)$, $Y(II)$, $Y(NPQ)$, and ETR regardless of the evaluation time and PS rates (data not shown). The linear regression model best described the foliar Si concentration-PS rates relationship ($Y = 0.80 + 0.073x$, $P = 0.0042$, $R^2 = 0.74$). The foliar Si concentration significantly increased by 166% at the highest PS rate. There was no significant relationship between the PS rates with absorbance, reflectance or transmittance (data not shown).

For Exp. 2, the foliar Si concentration significantly increased by 44% and 42%, respectively, for the PS and fungicide + PS treatments in comparison to the control treatment (Table 1). The AUDPC was significantly lower by 64%, 58%, and 53%, respectively, for the treatments fungicide, PS, and fungicide + PS in comparison to the control treatment (Table 1). For inoculated plants, A was significantly lower by 19%, 31%, 22%, and 35%, respectively, for the control, fungicide, PS, and fungicide + PS treatments in comparison to the non-inoculated plants (Fig. 1a). For non-inoculated

Table 1. Foliar silicon (Si) concentration and area under blast progress curve (AUBPC) for wheat plants submitted to different treatments and inoculated with *Pyricularia oryzae*.

Treatments	Si (dag/kg)	AUBPC
Control	0.45 b	295.20 a
Fungicide	0.44 b	105.60 b
Potassium Silicate	0.65 a	125.52 b
Fungicide + Potassium Silicate	0.64 a	139.20 b
Coefficient of Variation (%)	9.99	45.98

Means within each column followed by the same letter are not significantly different ($P = 0.05$) as determined by Tukey's test. $n = 6$.

plants, A was significantly higher by 24% and 26% for the control and fungicide treatments, respectively, in comparison to the fungicide + PS treatment. For inoculated plants, A was significantly lower by 7% for the fungicide + PS treatment in comparison to the control treatment. For inoculated plants, C_i was significantly higher by 4% and 5%, respectively, for the control and fungicide treatments, and significantly lower by 8% for the fungicide + PS treatment in comparison to the non-inoculated plants (Fig. 1b). For non-inoculated plants, C_i was significantly lower by 7% for the PS treatment in comparison to the control treatment. For inoculated plants, C_i was significantly lower by 7% and 14%, respectively, for the PS and fungicide + PS treatments in comparison to the control treatment (Fig. 1b). For inoculated plants, g_s was significantly lower by 24% and 69%, respectively, for the fungicide and fungicide + PS treatments in comparison to the non-inoculated plants (Fig. 1c). For non-inoculated plants, g_s was significantly lower by 31% for fungicide + PS treatment in comparison to the control treatment. For inoculated plants, g_s was significantly lower by 26% and 57%, respectively, for the fungicide and fungicide + PS treatments in comparison to the control treatment (Fig. 1c). For inoculated plants, E was significantly lower by 55% for the fungicide + PS treatment in comparison to the non-inoculated plants (Fig. 1d). For inoculated plants, E was significantly lower by 49% for the fungicide + PS treatment in comparison to the control treatment (Fig. 1d). For inoculated plants, F_v/F_m was significantly lower by 10, 6, 5, and 4%, respectively, for the control, fungicide, PS, and fungicide + PS treatments in comparison to non-inoculated plants (Fig. 2a). The F_v/F_m was significantly lower for inoculated plants from the control treatment in comparison to the other treatments. For inoculated plants, $Y(NO)$ was significantly higher by 9% for the control treatment and significantly lower by 9% and 20%, respectively, for the PS and fungicide + PS

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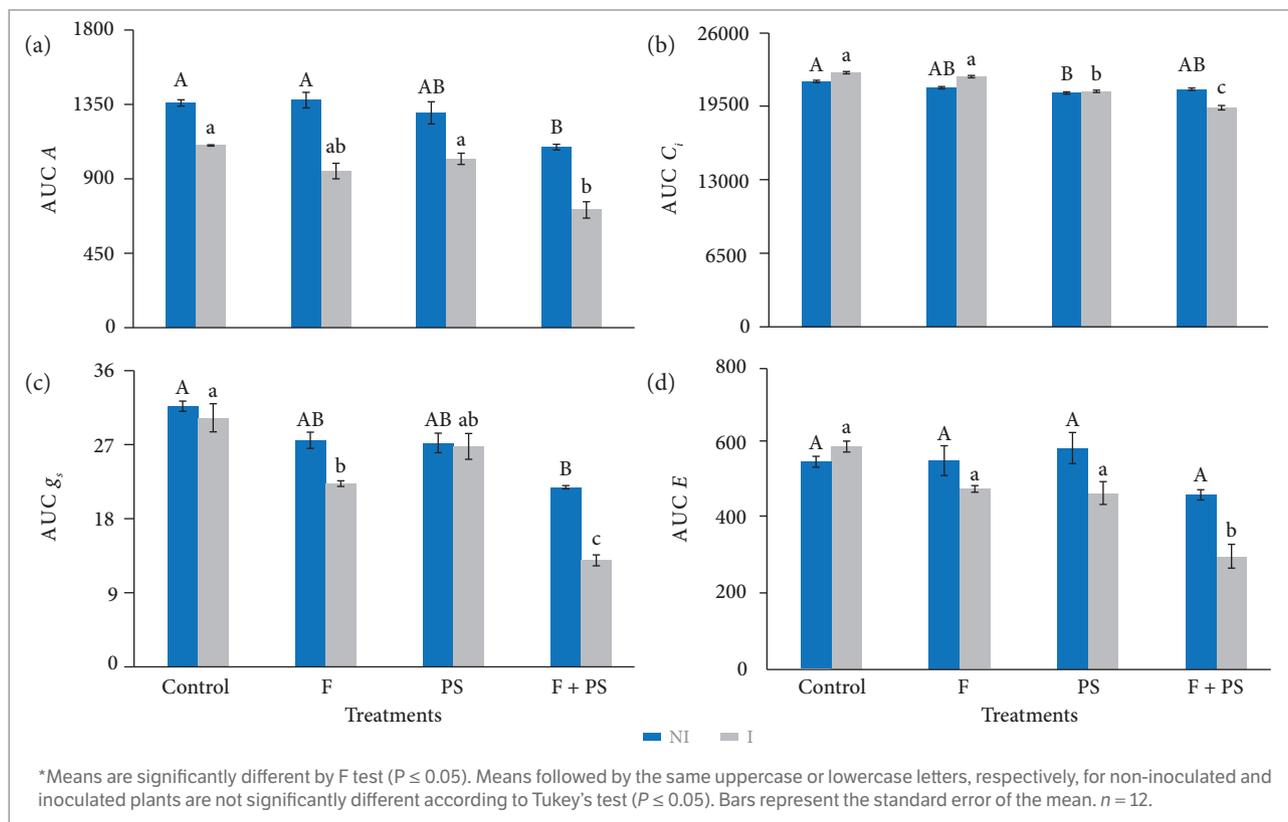


Figure 1. Area under the curve (AUC) for (a) net CO_2 assimilation rate (A), (b) internal CO_2 concentration (C_i), (c) stomatal conductance to water vapor (g_s), and (d) transpiration rate (E) for the leaves of wheat plants sprayed with water (Control), fungicide (f), potassium silicate (PS), and fungicide + potassium silicate (F+PS) and non-inoculated (NI) or inoculated (I) with *Pyricularia oryzae*.

treatments in comparison to non-inoculated plants. The $Y(\text{NO})$ was significantly lower for non-inoculated plants from the fungicide treatment in comparison to the PS and fungicide + PS treatments. For inoculated plants, $Y(\text{NO})$ was significantly lower by 14%, 11%, and 21%, respectively, for the fungicide, PS, and fungicide + PS treatments in comparison to the control treatment (Fig. 2b). For inoculated plants, $Y(\text{II})$ was significantly lower by 22%, 21%, 40%, and 21%, respectively, for the control, fungicide, PS, and fungicide + PS treatments in comparison to the non-inoculated plants. For inoculated plants, $Y(\text{II})$ was significantly lower by 2% for the PS treatment in comparison to the control treatment and by 2% in comparison to the fungicide treatment (Fig. 2c). For inoculated plants, ETR was significantly lower by 23%, 21%, 41%, and 21%, respectively, for the control, fungicide, PS, and fungicide + PS treatments in comparison to the non-inoculated plants. For inoculated plants, ETR was significantly lower by 27%, 27%, and 24%, respectively, for PS treatment in comparison to the control, fungicide and fungicide + PS treatments (Fig. 2d). For inoculated plants, $Y(\text{NPQ})$ was significantly higher by 23%, 31%, 89%, and 60%,

respectively, for the control, fungicide, PS, and fungicide + PS treatments in comparison to the non-inoculated plants (Fig. 2e). The $Y(\text{NPQ})$ was significantly lower for non-inoculated plants from the PS treatment in comparison to the control and fungicide treatments. For inoculated plants, $Y(\text{NPQ})$ was significantly higher by 33% and 25%, respectively, for PS and fungicide + PS treatments in comparison to the control treatment (Fig. 2e).

The present study provided, to the best of authors' knowledge, novel evidence that leaf gas exchange (A, C_i , g_s , and E) and chlorophyll *a* fluorescence (F_v/F_m) parameters or the optical properties of the wheat leaf blades were not affected by foliar applications of PS. The PS did not impair CO_2 influx from the environment into the carboxylation sites or impede the photosynthetic process. These findings are important since any impact on photosynthesis may deploy plants of energy to be used in the biochemical routes involved in defense to counteract pathogens infection (Debona et al. 2017). The possibility of using PS foliarly to control blast on wheat has never been reported. In the present study, a higher foliar Si concentration for PS-sprayed plants contributed

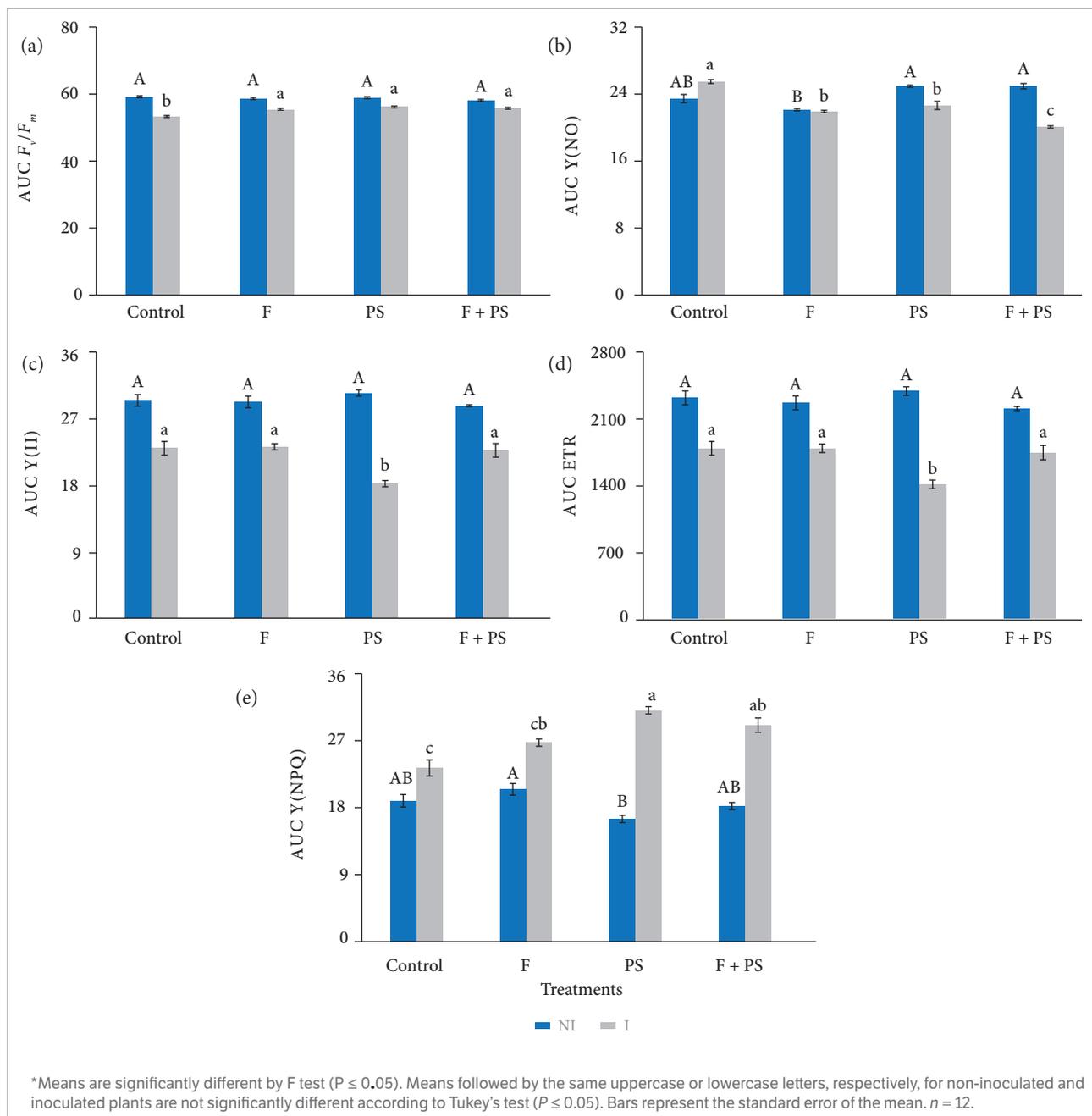


Figure 2. Area under the curve (AUC) for (a) maximal photosystem II quantum yield (F_v/F_m), (b) quantum yield of non-regulated energy dissipation [Y(NO)], (c) photochemical yield [Y(II)], (d) electron transport rate (ETR), and (e) quenching non-photochemical [Y(NPQ)] for the leaves of wheat plants sprayed with water (Control), fungicide (f), potassium silicate (PS), and fungicide + potassium silicate (F+PS), non-inoculated (NI) or inoculated (I) with *Pyricularia oryzae*.

to decrease blast severity, but no gain on disease control was achieved when PS was mixed with fungicide. One plausible explanation for a decrease in blast symptoms on PS-sprayed leaves can be linked to the osmotic effect of its alkaline solution on conidia viability or even on their germ tube growth. Moreover, *P. oryzae* pre-penetration through an appressorium can be prevented after the PS dries over

the leaf blades. On the other hand, for wheat plants having Si-supplied to the roots, blast symptoms were lowered due to the potentiation of host defense mechanisms (Rodrigues et al. 2015b; Debona et al. 2017). Foliar spray of Si to wheat plants was not as effective as root-applied Si to slow powdery mildew development because Si deposition on the leaf surface was not homogeneous (Guével et al. 2007). In the

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melon-*Podosphaera xanthii* interaction, Si application to roots was more efficient to reduce the rate of fungal colonies expansion, fungal colonies area and conidia production in contrast to foliar-applied Si (Dallagnol et al. 2012). In rice, the efficacies of both leaf and root Si-applications were compared for blast and brown spot control. For the brown spot, the foliar-applied Si decreased disease intensity; however, the level of control achieved was not as great as that obtained when Si was supplied to the roots (Rezende et al. 2009). For the blast, the lesion size, the number of lesions per cm² of leaf area and the area under the blast progress curve were reduced for both methods of applying Si, but Si supplied to the roots tended to be more effective in suppressing blast development than applied foliar (Cacique et al. 2013). The foliar spray of Si-containing products for powdery mildew control in cucumber, eggplant, and melon plants was efficient in reducing the number of fungus colonies on the leaves (Rodrigues et al. 2015b).

In the present study, the photosynthetic process for wheat leaves was greatly impaired during the infection by *P. oryzae*, but to a lesser extent for leaves of PS-sprayed plants. The F_v/F_m values, which represent the maximum potential quantum efficiency of PSII if all capable reaction centers were open, for inoculated plants sprayed with PS, fungicide or with their combination were less affected in comparison to non-sprayed plants. This finding suggests that the components associated with the photosynthetic machinery suffered minor damage for leaves of these treated plants. A F_v/F_m value in the range of 0.79 to 0.84 is known to be the approximate optimal value for many plant species, with lowered values indicating plant stress (Maxwell and Johnson 2000).

Some studies on the wheat-*P. oryzae* interaction reported that Si-supplied plants through the roots showed that changes in the values of F_v/F_m , F_v'/F_m' , q_p and ETR were minimal indicating, therefore, that their ability to capture, explore and dissipate light energy were less affected in contrast to non Si-supplied plants (Aucique-Pérez et al. 2014; 2017).

Rodrigues et al. (2015a) reported no significant alterations in the values of C_i , g_s , and E for common bean plants sprayed with PS, but a significant reduction on anthracnose severity and an increase on yield were achieved. According to Ramos et al. (2013), the high rates of different Si sources used to control powdery mildew on pumpkin plants should be taken into account since leaf gas exchange parameters and yield may be affected. Interestingly, the combination of PS with fungicide caused an adverse effect on the photosynthetic performance of wheat plants in this study. Even though fungicides application is the most important control strategy to reduce blast impact on wheat yield (Rodrigues et al. 2017), growers should pay careful attention when mixing fungicides and Si sources for foliar spray aiming to control the disease.

In conclusion, the foliar spray of PS can be an environmentally friendly strategy to reduce blast development on wheat without causing any impact on photosynthesis.

AUTHOR'S CONTRIBUTION

Conceptualization, Oliveira T. B., Aucique-Pérez C. E. and Rodrigues F. A.; Methodology, Oliveira T. B., Aucique-Pérez C. E. and Rodrigues F. A.; Investigation, Oliveira T. B. and Aucique-Pérez C. E.; Writing – Original Draft, Oliveira T. B.; Writing – Review and Editing, Rodrigues F. A.; Funding Acquisition, Rodrigues F. A.; Resources, Rodrigues F. A.; Supervision, Rodrigues F. A.

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REFERENCES

Aucique-Pérez, C. E., Rodrigues, F. A., Moreira, W. R. and DaMatta, F. M. (2014). Leaf gas exchange and chlorophyll *a* fluorescence in wheat plants supplied with silicon and infected with *Pyricularia oryzae*. *Phytopathology*, 104, 143-149. <https://doi.org/10.1094/PHTO-06-13-0163-R>

Aucique-Pérez, C. E., Silva, P. E. M., Moreira, W. R., DaMatta, F. M. and Rodrigues, F. A. (2017). Photosynthesis impairments and excitation energy dissipation on wheat plants supplied with silicon and infected with *Pyricularia oryzae*. *Plant Physiology and Biochemistry*, 121, 196-205. <https://doi.org/10.1016/j.plaphy.2017.10.023>

- Cacique, I. S., Domiciano, G. P., Moreira, W. R., Rodrigues, F. A., Cruz, M. F. A., Serra, N. S. and Català, A. B. (2013). Effect of root and leaf applications of soluble silicon on blast development in rice. *Bragantia*, 72, 304-309. <https://doi.org/10.1590/brag.2013.032>
- Ceresini, P. C., Castroagudín, V. L., Rodrigues, F. A., Rios, J. A., Aucique-Pérez, C. E., Moreira, S. I., Croll, D., Alves, E. and Maciel, J. L. N. (2018). Wheat Blast: past, present, and future. *Annual Review of Phytopathology*, 56, 427-456. <https://doi.org/10.1146/annurev-phyto-080417-050036>
- Cruz, M. F. A., Prestes, A. M., Maciel, J. L. N. and Scheeren, P. L. (2010). Resistência parcial à brusone de genótipos de trigo comum e sintético nos estádios de planta jovem e de planta adulta. *Tropical Plant Pathology*, 35, 24-31. <https://doi.org/10.1590/S1982-56762010000100004>
- Cruz, C. D. and Valent, B. (2017). Wheat blast disease: danger on the move. *Tropical Plant Pathology*, 42, 210-222. <https://doi.org/10.1007/s40858-017-0159-z>
- Dallagnol, L. J., Rodrigues, F. A., Pascholati, S. F., Fortunato, A. A. and Camargo, L. E. A. (2015). Comparison of root and foliar applications of potassium silicate in potentiating post-infection defences of melon against powdery mildew. *Plant Pathology*, 64, 1085-1093. <https://doi.org/10.1111/ppa.12346>
- Dallagnol, L. J., Rodrigues, F. A., Tanaka, F. A. O., Amorim, L. and Camargo, L. E. A. (2012). Effect of potassium silicate on epidemic components of powdery mildew on melon. *Plant Pathology*, 61, 323-330. <https://doi.org/10.1111/j.1365-3059.2011.02518.x>
- Debona, D., Rodrigues, F. A. and Datnoff, L. E. (2017). Silicon's role in abiotic and biotic plant stresses. *Annual Review of Phytopathology*, 55, 85-107. <https://doi.org/10.1146/annurev-phyto-080516-035312>
- Debona, D., Rodrigues, F. A., Rios, J. A., Martins, S. C. V., Pereira, L. F. and DaMatta, F. M. (2014). Limitations to photosynthesis in leaves of wheat plants infected by *Pyricularia oryzae*. *Phytopathology*, 104, 33-39. <https://doi.org/10.1094/PHYTO-01-13-0024-R>
- Goulart, A. C. P., Sousa, P. G. and Urashima, A. S. (2007). Danos em trigo causados pela infecção de *Pyricularia grisea*. *Summa Phytopathologica*, 33, 358-363. <https://doi.org/10.1590/S0100-54052007000400007>
- Guével, M. H., Menzies, J. G. and Bélanger, R. R. (2007). Effect of root and foliar applications of soluble silicon on powdery mildew control and growth of wheat plants. *European Journal of Plant Pathology*, 119, 429-436. <https://doi.org/10.1007/s10658-007-9181-1>
- Igarashi, S., Ultimada, C. M., Igarashi, L. C., Kazuma, A. H. and Lopes, R. S. (1986). *Pyricularia* em trigo. 1. Ocorrência de *Pyricularia* sp. no estado do Paraná. *Fitopatologia Brasileira*, 11, 351-352.
- Kohli, M. M., Mehta, Y. R., Guzman, E., Viedma, L. and Cubilla, L. E. (2010). *Pyricularia* Blast – a threat to wheat cultivation. *Czech Journal of Genetic and Plant Breeding*, 47, S130-S134. <https://doi.org/10.17221/3267-CJGPB>
- Korndörfer, G. H., Pereira, H. S. and Nolla, A. (2004). Análise de silício: solo, planta e fertilizante. Uberlândia: Universidade Federal de Uberlândia.
- Liang, Y. C., Sun, W. C., Si, J. and Römheld, V. (2005). Effects of foliar- and root-applied silicon on the enhancement of induced resistance to powdery mildew in *Cucumis sativus*. *Plant Pathology*, 54, 678-685. <https://doi.org/10.1111/j.1365-3059.2005.01246.x>
- Maxwell, K. and Johnson, G. N. (2000). Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany*, 51, 659-668. <https://doi.org/10.1093/jexbot/51.345.659>
- Moore, K. J. and Dixon, P. M. (2015). Analysis of combined experiments revisited. *Agronomy Journal*, 107, 763-771. <https://doi.org/10.2134/agronj13.0485>
- Ramos, A. R. P., Santos, R. L., Amaro, A. C. E., Fumes, L. A. A., Boaro, C. S. F. and Cardoso, A. I. I. (2013). Eficiência do silicato de potássio no controle do oídio e no desenvolvimento de abobrinha de moita. *Horticultura Brasileira*, 31, 432-438. <https://doi.org/10.1590/S0102-05362013000300014>
- Rezende, D. C., Rodrigues, F. A., Carré-Missio, V., Schurt, D. A., Kawamura, I. K. and Korndörfer, G. H. (2009). Effect of root and foliar application of silicon on brown spot development in rice. *Australasian Plant Pathology*, 38, 67-73. <https://doi.org/10.1071/AP08080>
- Rios, J. A., Debona, D., Duarte, H. S. S. and Rodrigues, F. A. (2013). Development and validation of a standard area diagram set to assess blast severity on wheat leaves. *European Journal of Plant Pathology*, 136, 603-611. <https://doi.org/10.1007/s10658-013-0191-x>
- Rios, J. A., Rodrigues, F. A., Debona, D. and Silva, L. C. (2014). Photosynthetic gas exchange in leaves of wheat plants supplied with silicon and infected with *Pyricularia oryzae*. *Acta Physiologiae Plantarum*, 36, 371-379. <https://doi.org/10.1007/s11738-013-1418-3>
- Rodrigues, F. A., Polanco, L. R., Duarte, H. S. S., Resende, R. S. and Vale, F. X. R. (2015a). Photosynthetic gas exchange in common bean

- submitted to foliar sprays of potassium silicate, sodium molybdate and fungicide and infected with *Colletotrichum lindemuthianum*. *Journal of Phytopathology*, 163, 554-559. <https://doi.org/10.1111/jph.12353>
- Rodrigues, F. A., Dallagnol, L. J., Duarte, H. S. S. and Datnoff, L. E. (2015b). Silicon control of foliar diseases in monocots and dicots. In F. A. Rodrigues and L. E. Datnoff (Eds.), *Silicon and Plant Diseases* (p. 67-108). Switzerland: Springer International Publishing.
- Rodrigues, F. A., Rios, J. A., Debona, D. and Aucique-Pérez, C. E. (2017). *Pyricularia oryzae*-wheat interaction: physiological changes and disease management using mineral nutrition and fungicides. *Tropical Plant Pathology*, 42, 223-229. <https://doi.org/10.1007/s40858-017-0130-z>
- Shaner, G. and Finney, R. E. (1977). The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. *Phytopathology*, 67, 1051-1056. <https://doi.org/10.1094/Phyto-67-1051>
- Xavier Filha, M. S., Rodrigues, F. A., Domiciano, G. P., Oliveira, H. V., Silveira, P. R., and Moreira, W. R. (2011). Wheat resistance to leaf blast mediated by silicon. *Australasian Plant Pathology* 40:28-38. <https://doi.org/10.1007/s13313-010-0010-1>
- Zadoks, J. C., Chang, T. T. and Konzak, C. F. (1974). A decimal code for the growth stages of cereals. *Weed Research*, 14, 415-421. <https://doi.org/10.1111/j.1365-3180.1974.tb01084.x>