CARLOS EDUARDO AUCIQUE PÉREZ

TROCAS GASOSAS E FLUORESCÊNCIA DA CLOROFILA a EM PLANTAS DE TRIGO SUPRIDAS COM SILÍCIO E INFECTADAS POR *Pyricularia oryzae*

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Fisiologia Vegetal, para obtenção do título de Magister Scientiae.

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APROVADA: 25 de março de 2013.

Renata Sousa Resende	Fábio Murilo da Matta

Fabricio de Ávila Rodrigues
(Orientador)

DEDICO,

A meus pais, Dilza Maria e Luis Eduardo, seu amor e ensinamentos, fizeram entender que as lutas da vida só podem ser vencidas com coragem e perseverança. Amo a vocês desde a eterna distância.

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"Há uma força motriz mais poderosa que
a eletricidade, o vapor e a energia atômica:
a vontade".

Albert Einstein (1879-1955)

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BIOGRAFIA

CARLOS EDUARDO AUCIQUE-PÉREZ, nasceu em Bogotá D.C., Colômbia, no dia 22 de dezembro de 1982.

No ano de 2007, obteve o titulo como Engenheiro Agrônomo da Universidade Nacional da Colômbia.

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Em 2011, iniciou estudos de mestrado em Fisiologia Vegetal na Universidade Federal de Viçosa, atuando na área de interação planta-patógeno sob a orientação do professor Fabrício de Ávila Rodrigues.

ÍNDICE

RESUMO

AUCIQUE-PÉREZ, Carlos Eduardo, M. Sc., Universidade Federal de Viçosa, Março de 2013. **Trocas gasosas e fluorescência da Clorofila a em plantas de trigo supridas com silício e infectadas por Pyricularia oryzae.** Orientador: Fabrício de Ávila Rodrigues.

A brusone, causada pelo fungo Pyricularia oryzae, tornou-se uma doença economicamente importante no trigo. Este estudo teve como objetivo determinar o efeito do silício (Si) sobre os parâmetros das trocas gasosas (taxa de assimilação líquida de CO_2 (A), condutância estomática ao vapor de água (g_s), a concentração interna de CO_2 (C_i) e taxa de transpiração (E)) e parâmetros de fluorescência da clorofila (eficiencia quântica máxima do fotosistema II (F_v/F_m e F_v'/F_m'), fotoquímica (q_P) e coeficiente de extinção não-fotoquimico (NPQ) e a taxa de transporte de eletrons (TTE)) em plantas de trigo crescendas em recipiente com solução nutritiva contendo 0 ou 2 mM de silício (Si) e inoculadas com P. oryzae. A concentração foliar de Si incrementou-se significativamente para plantas, contribuindo à dismunição da severidade da brusone. Para plantas inoculadas com +Si, A foi significativamente maior a 72 (14%), 96 (12%) e 120 (58%) hai do que em suas contrapartes inoculadas. A g_s e E foram significativamente maiores em 60 e 42%, respectivamente, às 120 hai para as plantas inoculadas +Si em comparação com as plantas inoculadas -Si. Diferenças significativas entre as plantas inoculadas e não inoculadas ocorreu entre as 48 a 120 hai para A, g_s e E e entre as 48 a 96 hai para C_i. Para as plantas inoculadas +Si, diferenças significativas para F_v/F_m entre os tratamentos –Si e +Si foram encontradas às 48, 96 e 120 dai e às 72, 96 e 120 hai para F_v'/ F_m'. Os valores de F_v/F_m diminuiram significativamente em 1, 3 e 5%, respectivamente, aos 48, 96 e 120 hai para plantas -Si, em comparação com as plantas de +Si. Reduções significativas de 10, 11 e 22%, respectivamente, às 72, 96 e

120 hai para F_v'/F_m' ocorreu para as plantas -Si, em comparação com as plantas +Si. Diferenças significativas entre as plantas inoculadas e não inoculadas ocorreu às 48 a 120 hai para F_v/F_m e F_v'/F_m'. Para as plantas inoculadas, diferenças significativas entre os tratamentos -Si e +Si ocorreu apenas às 96 hai para ambos q_P e NPQ e às 72 e 120 hai para TTE. Diferenças significativas entre as plantas inoculadas e não inoculadas só ocorreu em 120 hai para q_P e às 96 e 120 hai para TTE. A concentração de clorofila total (a + b), e a razão de clorofil a/b diminuiu significativamente para as plantas -Si, em comparação com as plantas de +Si. Os resultados deste estudo demonstraram claramente que a severidade da brusone diminuiu em plantas de trigo supridas com Si em paralelo a um melhor desempenho das trocas gasosas e menores perdas disfuncionais ao nível fotoquímico.

ABSTRACT

AUCIQUE-PÉREZ, Carlos Eduardo, M. Sc., Universidade Federal de Viçosa, March 2013. **Leaf Gas Exchange and Chlorophyll a Fluorescence in Wheat Plants Supplied with Silicon and Infected with Pyricularia oryzae**. Adviser: Fabrício de Ávila Rodrigues.

Blast, caused by the fungus Pyricularia oryzae, has become an economically important disease in wheat. The objective of this study was to determine the effect of silicon (Si) on the photosynthetic gas exchange parameters (net CO_2 assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i), and transpiration rate (E)) and chlorophyll fluorescence parameters (maximum quantum quenching (F_v/F_m and F_v'/F_m'), photochemical (q_P) and nonphotochemical (NPQ) quenching coefficients and electron transport rate (ETR)) in wheat plants grown in a nutrient solution containing 0 (-Si) or 2 mM Si (+Si) and inoculated with P. oryzae. The leaf Si concentration significantly increased for the +Si plants compared to the -Si plants and contributed to a decrease in the severity of blast symptoms. For the inoculated +Si plants, A was significantly higher at 72 (14%), 96 (12%) and 120 (58%) hours after inoculation (hai) when compared with their inoculated -Si counterparts. The g_s and E were significantly higher by 60 and 42% at 120 hai for the inoculated +Si plants compared with the inoculated -Si plants, respectively. Significant differences between non-inoculated and inoculated plants were observed from 48 to 120 hai for A, g_s and E and from 48 to 96 hai for C_i. For the inoculated +Si plants, significant differences of F_v/F_m between the -Si and +Si treatments occurred at 48, 96 and 120 hai and at 72, 96 and 120 hai of F_v'/F_m'. The values of F_v/F_m significantly decreased by 1, 3 and 5% at 48, 96 and 120 hai, respectively, in the -Si plants compared with the +Si plants. Significant decreases of 10, 11 and 22% at 72, 96 and 120 hai, respectively, were observed for F_v'/F_m' in the -Si plants when compared with the +Si plants. Significant differences between the non-inoculated and inoculated plants occurred from 48 to 120 hai for F_v/F_m and F_v'/F_m', respectively. For the inoculated plants, significant differences between the -Si and +Si treatments occurred at 96 hai for both q_P and NPQ and 72 and 120 hai for ETR. Significant differences between the non-inoculated and inoculated plants occurred at 120 hai for q_P and at 96 and 120 hai for ETR. The total chlorophyll content (a + b) and the chlorophyll a/b ratio significantly decreased for the -Si plants compared with the +Si plants. The results of this study clearly demonstrate that the severity of blast symptoms decreased in wheat plants supplied with Si. These plants also exhibited improved gas exchange performance and less dysfunctions at the photochemical level.

1. INTRODUCTION

In Brazil, epidemics of blast caused by the fungus Pyricularia oryzae Sacc. (teleomorph Magnaporthe grisea (Hebert) Barr) have limited wheat (Triticum aestivum L.) production (Igarashi et al., 1986). On spikes and spikelets, where the blast symptoms are more pronounced, the occurrence of gray-brown lesions contributes to a reduced yield due to the reduced translocation of nutrients to the grains (Goulart et al., 2007). Gray-green and water-soaked lesions with dark green borders are blast symptoms that can be observed on the leaves (Igarashi et al., 1986). Seedling blight, spike tip death and bright black spots on the rachis are other common symptoms caused by P. oryzae (Goulart et al., 2007). Blast has been controlled using seed treatment with fungicides, the application of systemic fungicides at different plant growth stages and the use of cultivars that have various levels of resistance (Cruz et al, 2009; Cruz et al., 2012).

Several abiotic and biotic stresses that are imposed on plants may cause changes in their growth and development (Berger et al., 2007). Pathogens affect plant physiology by negatively impacting the leaf gas exchange due to losses in healthy leaf area or by lowering the efficiency of the photosynthetic process (Shtienberg, 1992). For different host-pathogen interactions, the reduction in pigment concentration, structural damage to the chloroplasts, impairments in energy dissipation via chlorophyll (Chl) a fluorescence and increases in leaf temperature are the most notable negative effects that result from this infection (Petit et al., 2006; Zhao et al., 2011; Resende et al., 2012). In addition to pathogen infection damaging a host’s photosynthesis capability, several studies have demonstrated that pathogens also cause leaf damage at the cuticular and stomatal levels, which can lead to changes in transpiration, plant water balance and ultimately canopy temperature (Ayres, 1981).

In healthy plants, silicon (Si) is believed to have a negligible effect on metabolism, which suggests a nonessential role for Si. However, recent studies have revealed a role for Si nutrition in promoting agronomic yields of unstressed crops, such as rice supplied with Si (Tamai & Ma, 2008; Detmann et al., 2012). Regardless, the most positive and consistent effects of Si nutrition have been found in the alleviation of both abiotic and biotic stresses in a wide variety of plant species (Epstein, 2009; Keeping & Reynolds, 2009). In particular, Si is distinguished by its potential to decrease the intensity of important diseases in several crops, especially in grasses and some dicots, such as beans, soybeans and cucumbers (Datnoff et al., 2007; Rodrigues et al., 2009). The biochemical and physiological mechanisms that are potentiated by Si include the high concentration of phenolics, lignin and phytoalexins, an increase in the activities of defense enzymes, such as chitinases and β-1,3-glucanases and the rapid, efficient transcription of genes associated with plant resistance (Rodrigues et al., 2003, 2004, 2005; Liang et al., 2006; Brunings et al., 2009). Furthermore, increased resistance to the pathogens of plants that have been supplied with Si has also been associated with a physical barrier that prevents or slows fungal penetration; such a barrier can result from an increase in the density of the long and short silicate cells in the leaf epidermis or to a thick silica layer below the cuticle, as noted in the case of the rice-**P. oryzae** pathosystem (Kim et al., 2002).

Regarding the wheat-P. oryzae pathosystem, Xavier-Filha et al. (2011) demonstrated that supplying Si to the wheat resulted in reduced levels of blast symptoms in the host plant. More recently, Debona et al. (2012) noted that the net carbon assimilation rate (A), stomatal conductance (g_s) and transpiration rate were all dramatically reduced in two wheat cultivars with contrasting degrees of resistance to the fungus, although such reductions occurred to a greater extent in the susceptible cultivar. The decreases in A were largely attributed to the biochemical limitations of

CO_2 fixation. The authors also suggested that A was impaired in asymptomatic leaf tissues, which suggested that the severity of blast symptoms is not a good indicator for predicting P. oryzae-induced reductions in A. Given the facts described above and considering that Si could help to maintain the photosynthetic rates in plants infected with pathogens (Resende et al., 2012; Dallagnol et al., 2013), it is hypothesized that the supply of Si could mitigate the deleterious effects of the P. oryzae infection on wheat plants by avoiding a functional loss of the photosynthetic apparatus. To test this hypothesis, the combined gas exchange and Chl a fluorescence measurements, along with an analysis of the Chl pools, were used to examine the effects of Si nutrition on the photosynthetic performance during the P. oryzae infection process in the leaves of wheat plants.

2. MATERIALS AND METHODS

Nutrient solution preparation. The nutrient solution used in this study was prepared as described by Clark, (1975) and included the following nutrients: 1.04 M $Ca(NO_3)_2.4H_2O$, 1 M NH_4NO_3, 0.8 M KNO_3, 0.6 M $MgSO_4.7H_2O$, 6.9 mM KH_2PO_4, 9.3 mMKCl, 2 mM H_3BO_3, 2 mM $ZnSO_4.7H_2O$, 7 mM $MnCl_2.4H_2O$, 0.5 mM $CuSO_4.5H_2O$, 0.6 mM $ZnSO_4.7H_2O$, 90 mM $FeSO_4.7H_2O$ and 90 mM disodium EDTA. Silicon was supplied as monosilicic acid and was obtained by passing potassium silicate through a column with a cation-exchange resin (Amberlite IR-120B, H^+ form; Sigma-Aldrich, São Paulo) (Ma et al., 2002). Silicon was applied at 2 mM while non-amended Si (0 mM) served as the control. The addition of monosilicic acid to the nutrient solution did not alter the pH.

Plant growth. Wheat seeds (TriticumaestivumL)from the cultivar BRS-Guamirim were surface-sterilized in 10% (vol/vol) NaOCl for 2 min, rinsed in sterilized water for 3 min and germinated on a sand substrate at 25°C for 8 days. The germination seedlings were transferred to plastic pots with one-half strength nutritive solution without Si for 7 days. Then, five plants were transferred to plastic pots containing 5 L of nutrient solution prepared with or without Si. The nutrient solution was changed every 4 days and its pH was measured daily. The pH was maintained at approximately 5.8 by adding NaOH or HCl (1 M) when necessary. The plants were grown in a greenhouse with a relative humidity of 70±5%, a temperature of 25±3°C and natural photosynthetically active radiation (PAR) of 900±15 µmol photons m^{-2} s^{-1}, which was measured at midday.

Inoculum production and inoculation procedure. A pathogenic isolate of P. oryzae (UFV/DFP Po-01) obtained from the wheat spikes of the BR-18 cultivar was used to inoculate the plants. Filter paper containing mycelial growth was transferred to Petri dishes containing oat-agar medium. After growing the mycelial disks, the media containing the fungus were transferred to new Petri dishes containing the same medium. The dishes were incubated in a growth chamber at 25°C with a 24 h photoperiod for 10 days. After this period, the conidia of the fungus were carefully removed from the Petri dishes with a soft bristle brush using water containing gelatin (1% w/v).The conidial suspension was calibrated with a hemacytometer to obtain a concentration of 1×10^5 conidia mL^{-1}. The conidial suspension was sprayed with an atomizer (Paasche Airbrush Co., Chicago, IL, USA) on the adaxial surface of the wheat plant leaves at stage 39 (Lancashire et al., 1991). After inoculation, the plants were kept in the dark in a mist chamber at 25°C for 24 h. The plants were then transferred to a greenhouse with a relative humidity of 80 ± 5% with a temperature of 25 ± 3°C.

Blast severity assessment. The fourth and fifth leaves (from the top) of each plant (per replication for each treatment) were marked and used to evaluate the severity of blast symptoms at 48, 72, 96 and 120 hours after inoculation (hai) using the scale proposed by Rios et al. (2012). The area under the blast progress curve (AUBPC) for each leaf was computed using the trapezoidal integration of the blast progress curve over time using the formula proposed by Campbell & Madden (1990).

Photosynthetic measurements. The leaf gas exchange parameters were simultaneously determined via conducting the measurements of Chl a fluorescence by using a portable open-flow gas exchange system (LI-6400XT, LI-COR, Lincoln, NE, USA) equipped with an integrated fluorescence chamber head (LI-6400-40, LI-COR Inc.). The net CO_2assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i) and transpiration rate (E) were measured from the attached leaves (fourth from the top of the plant per replication for each treatment) at 48, 72, 96 and 120 hai from 09:00 to 11:00 hours (solar time), which is when A was at its maximum under artificial PAR, i.e., 1,000 µmol photons m^{-2} s^{-1} at the leaf level and 400 µmol atmospheric CO_2 mol^{-1}. All of the measurements were performed at 25°C, and 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 (PPFD) to optimize the stomatal aperture.

After registering the gas exchange parameters, the steady-state fluorescence yield (F_s) was measured following a saturating white light pulse (8,000 µmol m^{-2} 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 µmol m^{-2} 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 $NPQ = (F_m/F_m') - 1$. The actual quantum yield of PSII electron transport (Φ_{PSII}) was computed as $\Phi_{PSII} = (F_m' - F_s)/F_m'$, from which the electron transport rate (ETR) was calculated as $ETR = \Phi_{PSII}{*}PPFD{*}f{*}\alpha$, 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 absorptance by the photosynthetic tissues and is assumed to be 0.84 (Maxwell & Johnson 2000). Additionally, the 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 8000 µmol m^{-2} s^{-1} were applied for 0.8 s to ensure maximum fluorescence emissions (F_m) from which the variable-to-maximum Chl fluorescence ratios $F_v/F_m = [(F_m - F_0)/F_m)]$ were calculated.

Determination of pigment concentrations. The leaf discs (1.0 cm in diameter) obtained from the fourth and fifth leaves (from the top) were collected at 120 hai. The leaf discs were quickly frozen in liquid nitrogen and then stored at -80°C until needed. The chlorophylls (a + b) were separated on an end-capped, C_{18}, Spherisorb ODS-2 reversed-phase column (particle size 5µm, 250 mm × 4.6 mm) and quantified using HPLC (Dionex Ultimate 3000, Thermo Fisher Scientific, Vantaa, Finland), as described previously (Matos et al., 2009).

Leaf area (LA) and leaf dry mass (LDM) determinations. At 132 hai, five plants were randomly collected from the replications of each treatment to determinate the leaf area (cm^2) of each plant using a leaf area meter (model LI-COR 3100, Li-Cor, Lincoln, NE, USA). The leaf dry mass was obtained by placing the samples in an oven with forced air circulation at 70°C until a constant weight was obtained.

Determination of foliar Si concentration. After the end of the experiment that was performed to evaluate the severity, the leaves were collected from the plants of each replication of each treatment, 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 (Thomas Scientific, Swedesboro, NJ, USA). The foliar Si concentration was determined by colorimetric analysis of 0.1 g dried and alkali-digested tissue (Korndörfer et al., 2004) and was expressed in dag kg^{-1}.

Experimental design and data analysis. A 2 × 2 factorial experiment, consisting of two Si concentrations (0 and 2 mM; hereafter referred to as the -Si and +Si treatments, respectively) and non-inoculated or inoculated plants, was arranged in a completely randomized design with five replications. The experiment was repeated once. Each experimental unit corresponded to a plastic pot containing five wheat plants. The data for all of the variables were subjected to an analysis of variance (ANOVA) and the means from the treatments were compared by a t test ($P \leq 0.05$) using the SAS software (SAS Institute Inc., Cary, NC). For the leaf Si concentration, LA, LDM and pigments, ANOVA was used and considered to be a 2 × 2 factorial experiment consisting of two Si concentrations and non-inoculated or inoculated plants. To assess the photosynthetic parameters and the blast severity, ANOVA was used and considered to be a 2 × 2 × 4 factorial experiment consisting of two Si concentrations, non-inoculated or inoculated plants and four sampling times. The Pearson correlation was used to determine the relationships among the gas exchange parameters: foliar Si concentration and the blast severity.

3. RESULTS

Foliar Si concentration. Only the factor Si concentrations was significant ($P \leq 0.05$) (Table 1). The leaf Si concentration was significantly higher in the +Si plants (1.40 dag kg^{-1}) compared with the -Si plants (0.09 dag kg^{-1}). The foliar Si concentration showed a similar trend across treatments based on a preliminary experiment (data not shown).

Blast severity and AUBPC. The blast severity on the leaves of the +Si plants was significantly lower at 96 and 120 hai compared with the -Si plants (Fig. 1A). The factor Si concentrations was significant ($P \leq 0.05$) for the AUBPC. For the +Si plants, the AUBPC was significantly reduced by78% compared with the -Si plants (Fig. 1B). The blast severity showed a similar trend across treatments based on a preliminary experiment (data not shown).

Photosynthetic parameters. At least one of the factors silicon concentrations (Si), plant inoculation (PI) or sampling times as well as some interactions between these factors were significant for A, g_s, C_i, E and Sev (Table 1). For the non-inoculated plants, significant differences between the -Si and +Si treatments for A occurred only at 48 hai (Fig. 2A) and at 72, 96 and 120 hai for the inoculated plants (Fig. 2B). For the non-inoculated plants, A was significantly reduced by 7% for the +Si treatment compared with the -Si treatment at 48 hai. For the inoculated +Si plants, A was significantly higher at 72 (14%), 96 (12%) and 120 (58%) hai than in their inoculated -Si counterparts. The g_s and E were significantly higher by 60 and 42%, respectively, at 120 hai (Fig. 2D-H) for the inoculated +Si plants compared to inoculated -Si plants. Significant differences between the non-inoculated and inoculated plants occurred from 48 to 120 hai for A, g_s and E (Fig. 2 A-B, C-D and G-H) and from 48 to 96 hai for C_i (Fig. 2E and F).

At least one of the factors Si, PI or ST as well as some interactions between these factors were significant for F_v/F_m, F_v'/F_m', q_P, NPQ and ETR (Table 1). For the inoculated +Si plants, significant differences for F_v/F_m between the -Si and +Si treatments occurred at 48, 96 and 120 hai (Fig. 3B) and at 72, 96 and 120 hai for F_v'/F_m' (Fig. 3D). The values of F_v/F_m significantly decreased by 1, 3 and 5%, respectively, at 48, 96 and 120 hai in the -Si plants compared with the +Si plants (Fig. 3B). Significant decreases of 10, 11 and 22%, respectively, occurred at 72, 96 and 120 hai for F_v'/F_m' in the -Si plants compared to the +Si plants (Fig. 3D). Significant differences between the non-inoculated and inoculated plants occurred from 48 to 120 hai for F_v/F_m and F_v'/F_m' (Fig. 3A-D). For the non-inoculated plants, significant differences between the Si and +Si treatments occurred at 96 hai for q_P (Fig. 3E) and at 48 hai for ETR (Fig. 3I). For the inoculated plants, significant differences between the -Si and +Si treatments occurred at 96 hai for both q_P (Fig. 3F) and NPQ (Fig. 3H) and at 72 and 120 hai for ETR (Fig. 3J). Significant differences between the non-inoculated and inoculated plants occurred at 120 hai for q_P (Fig. 3E and F) and at 96 and 120 hai for ETR (Fig. 3I and J). A preliminary experiment to determine the photosynthetic parameters was performed and showed a similar trend for the treatments discussed above (data not shown).

Leaf pigments. At least one of the following factors Si or PI as well as their interactions were significant for the total Chl (a + b) and Chl a/b ratio (Table 1). Both the total Chl concentrations and the Chl a/b ratio significantly decreased at 120 hai; notably, such decreases were stronger in the-Si plants than in the +Si plants (Table 2).

Pearson correlation. There was a positive correlation of A with g_s and E, which was negatively correlated with C_i and the blast severity (Table 3). The g_s was negatively correlated with C_i and the blast severity, but positively correlated with A and E (Table 3). There was a positive correlation between C_i and the blast severity, but C_i correlated negatively with A. A significant negative correlation occurred between E and the blast severity, but the correlation of E with A and g_s was not significantly negative. The correlation of the severity of blast symptoms with A and with g_s was significantly negative, but was significantly positive between C_i and E (Table 3).

Variables LA and LDM Only the Si and PI factors were significant for LA and LDM (Table 1). The LA and the LDM significantly increased by 27.6 and 21.7%, respectively, in the +Si plants compared with the -Si plants, whereas they were significantly reduced by 23 and 19.3%, respectively, for the inoculated plants compared with the non-inoculated plants (Table 4).

4. DISCUSSION

In support of previous findings that Si can improve the resistance of several monocots against foliar pathogens (Datnoff et al., 2007), including the wheat-*P. oryzae* pathosystem (Xavier-Filha et al., 2011), the present study is the first to describes the physiological features that are associated with the increase in resistance of wheat plants supplied with Si to *P. oryzae* infection. Notably, regardless of the Si supply, *P. oryzae* exerted its deleterious effect on the physiology of the wheat plants by reducing both A and g_s, a fact additionally corroborated by the negative correlations between the blast severity and these two parameters. However, Si could to a large extent minimize the decreases in gas exchange capacity upon fungal infection as noted by the significantly higher values of A, g_s and E in the +Si plants in comparison to the -Si plants. Furthermore, the Si supply allowed the infected plants to maintain their total leaf areas at values similar to the non-infected plants. Taken together, the results from the present study suggest that the positive effects of Si can be translated into improved whole-plant photosynthetic productivity, which ultimately may decrease the negative impacts of blast on wheat growth.

Despite many efforts to elucidate the mechanisms by which pathogens are capable of affecting plant photosynthetic capacity, these mechanisms remain elusive (Bassanezi et al., 2002; Dallagnol et al., 2011; Debona et al., 2012). Debona et al. (2012) have previously demonstrated that the photosynthesis of wheat plants not supplied with Si was dramatically reduced during the infectious process of *P. oryzae* due chiefly to the biochemical constraints linked to an apparently lower Rubisco activity. Here, it is proposed that the mechanism by which *P. oryzae* affected the photosynthetic performance clearly depended on the presence of Si (highly significant Si × inoculation interaction for A and g_s and for C_i and F_v/F_m). Indeed, in the +Si plants, despite the early decreases in A, g_s and C_i at 48 hai, there were no major changes in these traits from 48 hai onwards. In sharp contrast, the -Si plants displayed proportionally larger decreases in A than in g_s concomitantly with an unchanging C_i at 120 hai; this result suggests that the anticipated lower influx of CO_2 into the leaves caused by a decreased stomatal aperture was not a primary factor associated with the reduction in A in the -Si plants infected by P. oryzae. Therefore, decreases in A during the infectious process of P. oryzae should be accounted for by non-stomatal factors. While some diffusive limitations imposed by the mesophyll could not be excluded (Flexas et al., 2012), the most likely explanation for the observed decreases in A were associated with dysfunctions at the level of the biochemical reactions involving CO_2 fixation and this explanation is in agreement with the results of Debona et al. (2012).

In addition to likely compromising the biochemical ability for CO_2 fixation, the infection by P. oryzae provoked a range of dysfunctions at the photochemical level, particularly at the later stages of fungal infection in the -Si plants. These dysfunctions could largely be avoided by supplying Si to the plants. Compared to the +Si plants, the maximum photochemical efficiency of photosystem II (analyzed as F_v/F_m) decreased to below 0.80 for the-Si plants, which suggested the occurrence of chronic photoinhibition to photosynthesis (Krause and Weis, 1991). Concomitant decreases in the efficiency of the excitation energy captured by the open PSII reaction centers (estimated as F_v'/F_m') and in the fraction of absorbed light that is dissipated photochemically (estimated as q_P) were also observed, which suggested that the infected plants were likely unable to fully capture and exploit the absorbed energy. Similar photochemical dysfunctions have been reported for other pathosystems, such as that of Eucalyptus-Puccinia psidii (Alves et al., 2011). The decreases in q_P can also be interpreted as an increased proportion of oxidized Q_A and thus represent a fraction of the PSII centers that are prone to suffer photoinhibitory damage (Lima et al., 2002). These results were accompanied by much lower decreases in ETR than in A, which potentially created an excess of reducing power that can trigger a range of photoinhibitory and photoxidative effects (Maxwell & Johnson, 2000; Baker, 2008). In the present study, the infected plants cope with such an excess by the reducing power via heat dissipation, as evidenced by the increased NPQ (Krause & Weis, 1991; Logan et al., 2006). Nevertheless, heat dissipation was demonstrated as not sufficient to prevent photoinhibition, given the observed decreases in F_v/F_m. Additionally, these photochemical impairments are unlikely to directly constrain A, as A decreased much more than ETR. However, these impairments contributed to blast progress through an anticipated generation of reactive oxygen species, which is consistent with the stronger decreases in the total Chl pools that occurred in parallel with the preferential loss of Chl a (that resulted in a lower Chl a/b ratio) in the -Si plants in comparison to the +Si plants at 120 hai. In fact, under photoxidative conditions, Chl a is more prone to photobleaching than Chl b (Murchie & Horton, 1997). Regardless, it must be emphasized that the wheat plants were grown under relatively low photon irradiances; had they been grown under field conditions where the irradiances can reach values as high as 2,000 µmol photons m^{-2} s^{-1} or even higher, the photoinhibitory damages caused by blast would be expected to be greatly exacerbated.

In conclusion, the results of this study clearly demonstrated that Si supplied to wheat plants resulted in a lower blast symptoms as well as an improved gas exchange performance and less dysfunctions at the photochemical level. These ameliorative effects of Si combined with the use of wheat cultivars that have a basal level of resistance to blast (Cruz et al., 2010; Debona et al., 2012), may be translated into useful tools to enhance the agronomic yields of wheat plants challenged with P. oryzae.

5. LITERAURE CITED

Alves, A. A., Guimaraes, L. M., Chaves, A. R. DaMatta, F. M. and Alfenas, A. C. 2011. Leaf gas exchange and chlorophyll a fluorescence of Eucalyptus urophylla in response to Puccinia psidii infection. Acta Physiologia Plantarum 33:1831-1839.

Ayres, P. G. 1980. Responses of stomata to pathogenic microorganisms. Pages 205-221 in: Stomatal Physiology. P. G. Jarvis, and T.A. Mansfield, eds., vol. 8, S.E.B. Sem., Cambridge University Press.

Baker, N. R. 2008. Chlorophyll Fluorescence: A Probe of Photosynthesis in vivo. Annual Review of Plant Biology 59:89-113.

Bassanezi, R.B.; Yamamoto, P.T.; Gimenes-Fernandes, N. 2002. Progresso dos de “morte súbita” em pomares de laranjeiras Valência e Pêra. Summa Phytopathologica 28:23.

Berger, S., Sinha, A. K. and Roitsch, T. 2007. Plant physiology meets phytopathology: plant primary metabolism and plant-pathogen interactions. Journal of Experimental Botany 58:4019-4026.

Brunings, A. M.; Datnoff, L. E.; Ma, J. F.; Mitani, N.; Nagamura, Y.; Rathinasabapathi, B.; Kirst, K. 2009. Differential gene expression of rice in responses to silicon and the rice blast fungus Magnaporthe oryzae. Annals of Applied Biology 155:161-170.

Campbell, C. L., and Madden, L. V. 1990. Introduction to Plant Disease Epidemiology. Wiler-Interscience, NY, John Wiley & Sons. 532 p.

Clark, R. B. 1975. Characterization of phosphates in intact maize roots. Journal of Agricultural and Food Chemistry 23:458-460.

Cruz, M. F. A., Prestes, A. R., Maciel, J. L. and Scheeren, P. 2010. Resistência parcial à brusone de genótipos de trigo comum e sintético nos estádios de planta jovem e de planta adulta. Tropical Plant Pathology 25:24-25.

Cruz, C. D., Bockus, W. W., Stack, J. P., Tang, X. and Valent, B. 2012. Preliminary assessment of resistance among U.S. wheat cultivars to the Triticum pathotype of Magnaporthe oryzae. Plant Disease 96:1501-1505.

Dallagnol, L. J., Rodrigues, F. A., Chaves, A. R. M., Vale, F. X. R. and DaMatta, F. M. 2013. Photosynthesis and sugar concentration are impaired by the defective active silicon uptake in rice plants infected with Bipolaris oryzae. Plant Pathology 62:120-129.

Dallagnol, L. J., Rodrigues, F. A., Martins, S. C. V., Calvette, P. C. and DaMatta, F. M. 2011. Alterations on rice leaf physiology during infection by Bipolaris oryzae. Australasian Plant Pathology 40:360-365.

Datnoff, L. E., Rodrigues, F. A. andSeebold, K. W. 2007. Silicon and Plant Disease. In: Datnoff LE, Elmer WH, Huber DM (eds). Mineral Nutrition and Plant Disease. The American Phytopathological Society, St Paul, pp. 233-246.

Debona, D., Rodrigues, F. A., Rios, J. A. and Telles, K. J. N. 2012. Biochemical changes in the leaves of wheat plants infected by Pyricularia oryzae. Phytopathology 102:1121-1129.

Detmann, K. C., Araújo, W. L., Martins, S. C. V., Sanglard, L. M. V. P., Reis, J. V., Detmann, E., Rodrigues, F. A., Nunes-Nesi, A., Fernie, A. R. and DaMatta, F. M. 2012. Silicon nutrition increases grain yield, which, in turn, exerts a feed-forward stimulation of photosynthetic rates via enhanced mesophyll conductance and alters primary metabolism in rice. New Phytologist 196:752-762.

Epstein, E. 2009. Silicon: its manifold roles in plants. Annals of Applied Biology 155:155-160.

Flexas, J., Barbour, M. M., Brendel, O., Cabrera, H. M., Carriquí, M., Díaz-Espejo, A., Douthe, C., Dreyer, E., Ferrio, J. P., Gago, J., Gallé, A., Galmés, J., Kodama, N., Medrano, H., Niinemets, Ü., Peguero-Pina, J. J., Pou, A., Ribas-Carbó, M., Tomás, M., Tosens, T. and Warren, C. R. 2012. Mesophyll diffusion conductance to CO2: An unappreciated central player in photosynthesis. Plant Science 193-194:70-84.

Goulart, A. C. P.; Sousa, P. G.; Urashima, A. S. 2007. Danos em trigo causados pela infecção de *Pyricularia grisea*. Summa Phytopathologica 33:358-363.

Igarashi, S., Utiamada, C. M., Igarashi, I. 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.

Keeping, M. G. and Reynolds, O. L. 2009. Silicon in agriculture: new insights, new significance and growing application. Annals of Applied Biology 155:153-154.

Kim, S. G., Kim, K. W., Park, E. W. and Choi, D. 2002. Silicon-induced cell wall fortification of rice leaves: a possible cellular mechanism of enhanced host resistance to blast. Phytopathology 92:1095-1103.

Korndörfer, G. H., Pereira, H. S. and Nolla, A. (2004) Análise de Silício: Solo, Planta e Fertilizante Uberlândia MG, Grupo de Pesquisa em Silício, ICIAG-Universidade Federal de Uberlândia (Boletim Técnico 1). 28 pp.

Krause, G. H. and Weis, E. 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annual Review of Plant Physiology and Plant Molecular Biology 42:313-349.

Lancashire, P. D., Bleiholder, H., Langelüddecke, P., Stauss, R., Van Den Boom, T., Weber, E. and Witzenberger, A. 1991.An uniform decimal code for growth stages of crops and weeds. Annals of Applied Biology 119:561-601.

Liang, Y., Sun, W., Zhu, Y.G. and Christie, P. 2006. Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: A review. Environmental Pollution 147:422-428.

Lima, A. L. S., DaMatta, F. M., Pinheiro, H. A., Totola, M. R. and Loureiro, M. E. 2002. Photochemical responses and oxidative stress in two clones of Coffea canephora under water deficit conditions. Environmental and Experimental Botany 47:239–247

Logan, B. A., Kornyeyev, D., Hardison, J. and Holaday, A. S. 2006. The role of antioxidant enzymes in photoprotection. Photosynthesis Research 88:119-132

Ma, J. F., Tamai, K., Ichii, M. and Wu, G. F. 2002. A rice mutant defective in Si uptake. Plant Physiology 130:2111-2117.

Matos, F. S., Wolfgramm, R., Gonçalves, F. V., Cavatte, P. C.; Ventrella, M. C., DaMatta, F. M. 2009. Phenotypic plasticity in response to light in the coffee tree. Environmental and Experimental Botany 67:421-427.

Maxwell, K. and Johnson, G. N. 2000. Chlorophyll fluorescence – A practical guide. Journal of Experimental Botany 51:659-668.

Murchie, E. H. and Horton, P. 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: Chlorophyll content, photosynthetic capacity and habitat preference. Plant, Cell & Environment 20:438-448.

Petit, A. N., Vaillant, N., Boulay, M., Clément, C. and Fontaine, F. 2006. Alteration of photosynthesis in grapevines affected by esca. Phytopathology 96:1060-1066.

Resende, R. S., Rodrigues, F. A., Cavatte, P. C., Martins, S. C. V., Moreira, W. R., Chaves, A. R. M. and Damatta, F. M. 2012. Leaf gas exchange and oxidative stress in sorghum plants supplied with silicon and infected by Colletotrichum sublineolum. Phytopathology 102:892-898.

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. DOI 10.1007/s10658-013-0191-x.

Rodrigues, F. A., Duarte, H. S. S., Domiciano, G. P., Souza, C. A., Korndörfer, G. H. and Zambolim, L. 2009. Foliar application of potassium silicate on the control of soybean rust. Australasian Plant Pathology 38:366-372.

Rodrigues, F. A., Jurick, W. M., Datnoff, L. E., Jones, J. B. and Rollins, J. A. 2005. Silicon influences cytological and molecular events in compatible and incompatible rice-Magnaporthe grisea interactions. Physiological and Molecular Plant Pathology 66:144-159.

Rodrigues, F. A., McNally, D. J., Datnoff, L. E., Jones, J. B., Labbé, C. and Benhamou, N. 2004. Silicon enhances the accumulation of diterpenoid phytoalexins in rice: a potential mechanism for blast resistance. Phytopathology 94:177-183.

Rodrigues, F. A., Benhamou, N., Datnoff, L. E., Jones, J. and Bélanger, R. R. 2003. Ultrastructural and cytochemical aspects of silicon mediated rice blast resistence. Phytopathology 93:535-546.

Shtienberg, D. 1992. Effects of foliar diseases on gas exchange: A comparative study. Phytopathology 82:760-765.

Tamai, K. and Ma, J. F. 2008. Reexamination of silicon effects on rice growth and production under field conditions using a low silicon mutant. Plant and Soil 307:21-27.

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.

Zhao, D., Glynn, N. C., Glaz, B., Comstock, J. C. and Sood, S. 2011. Orange rust effects on leaf photosynthesis and related characters of sugarcane. Plant Disease 95:640-647.

6. TABLES AND FIGURES

TABLE 1. Analysis of variance of the effects of silicon concentrations (Si), plant inoculation (PI) and sampling times (ST) and their interactions on Si concentration in leaf tissue (Leaf Si), blast severity (blast), area under blast progress curve (AUBPC), leaf area (LA), leaf dry mass (LDM), photosynthetic gas exchange parameters (net CO_2 assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i) and transpiration rate (E)), chlorophyll fluorescence parameters (maximum quantum quenching (F_v/F_m and F_v'/F_m'), photochemical (q_P) and nonphotochemical (NPQ) quenching coefficients and electron transport rate (ETR)) and concentrations of total chlorophylls (Chl),Chl a/b ratio.

Variables	Si	PI	ST	Si × PI	Si × ST	PI × ST	Si × PI × ST
	P values						
Leaf Si	< 0.001	0.086	-	0.535	-	-	-
Blast	< 0.001	-	< 0.001	-	< 0.001	-	-
AUBPC	< 0.001	-	< 0.001	-	< 0.001	-	-
LA	< 0.001	0.008	-	0.697	-	-	-
LDM	< 0.001	0.015	-	0.910	-	-	-
A	< 0.001	< 0.001	< 0.001	0.167	0.003	< 0.001	< 0.001
g_s	< 0.001	< 0.001	< 0.001	0.376	0.029	0.028	0.001
C_i	0.560	< 0.001	< 0.001	0.249	0.998	< 0.001	0.459
E	0.013	< 0.001	< 0.001	< 0.001	0.641	0.074	0.175
F_v/F_m	< 0.001	< 0.001	< 0.001	0.160	0.049	0.001	< 0.001
F_v'/F_m'	0.018	< 0.001	0.001	0.463	0.540	< 0.001	0.025
q_P	0.067	0.001	0.082	0.022	0.609	0.001	0.110
NPQ	0.487	0.002	< 0.001	0.157	0.016	0.024	0.057
ETR	0.017	< 0.001	-	0.005	0.529	< 0.001	0.025
Total Chl	0.023	< 0.001	-	0.007	-	-	-
Chl a/b	< 0.001	< 0.001		< 0.001	-	-	-

TABLE 2. Concentrations of total chlorophylls (Chl) and Chl a/b ratio on the leaves of wheat plants grown in hydroponic culture containing 0 (-Si) or 2 (+Si) mM silicon (+Si) and non-inoculated (NI) and inoculated (I) with *Pyricularia oryzae*.

Treatments	Total Chl (mg g^{-1} FW)		Chl a/b ratio	
	NI	I	NI	I
-Si	7.87 Aa	1.98 Bb	3.38 Aa	0.88 Bb
+Si	7.56 Aa	4.85 Ba	3.24 Aa	2.67 Ba

Means within each column followed by the same lower-case letter or means within a row followed by the same upper-case letter are not significantly different (P = 0.05) as determined by ANOVA and Tukey's test. n = 5. FW = fresh weight.

TABLE 3. Pearson correlation coefficients among the net CO_2 assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i), transpiration rate (E) and blast severity (Sev) on leaves of wheat plants grown in hydroponic culture containing 0 (-Si) or 2 (+Si) mM silicon.

Variables	A	g_s	C_i	E	Sev
A	-	0.810^*	-0.367^*	0.528^*	-0.770^*
g_s	0.866^*	-	0.035^{ns}	0.752^*	-0.613^*
C_i	-0.373^*	-0.036^{ns}	-	0.165^{ns}	0.534^*
E	0.608^*	0.761^*	0.010^{ns}	-	0.432^*
Sev	-0.780^*	-0.667^*	0.611^*	-0.531^*	-

Values below and above the diagonal correspond to the -Si and +Si treatments, respectively.* = significant at $P \leq 0.01$ by t-test.

TABLE 4. Leaf area (LA), leaf dry mass (LDM) of wheat plants grown in hydroponic culture containing 0 (-Si) or 2 (+Si) mM silicon (+Si) and non-inoculated (NI) and inoculated (I) with *Pyricularia oryzae*.

Treatments	LA (cm^2 $plant^{-1}$)	LDM (g $plant^{-1}$)
-Si	384.50	1.80
+Si	531.10	2.30
Student´s t-test	-6.20*	-4.70*
NI	497.1	2.12
I	383.1	1.71
Student´s t-test	-2.69*	-2.47*
CV (%)	19.90	18.00

* significant at $P \leq 0.05$. CV = coefficient of variation. n = 5.

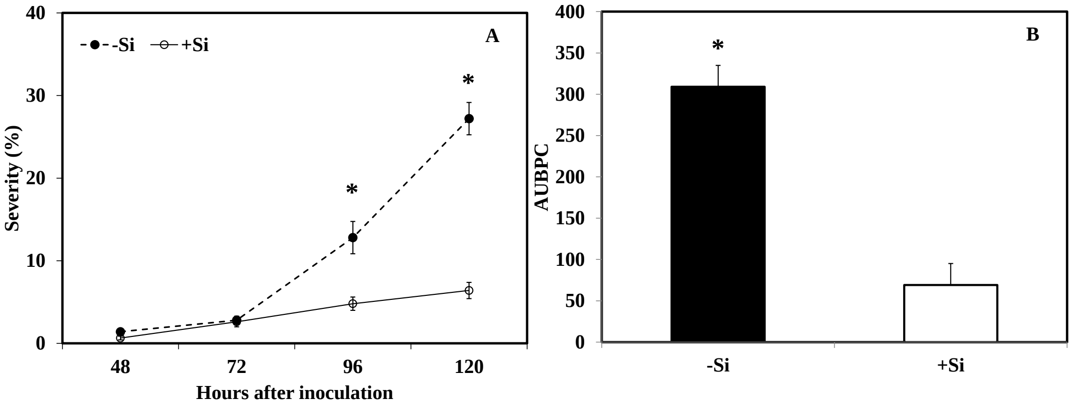

Fig. 1. Blast progress curves (A) and area under blast progress curve (AUBPC) (B) for wheat plants grown in hydroponic culture containing 0 (-Si) or 2 (+Si) mM silicon. For blast progress, the means for the -Si and +Si treatments followed by an asterisk (*) for each evaluation time are significantly different by Student´s t-test ($P \leq 0.05$). The bars represent the standard error of the mean. n = 5.

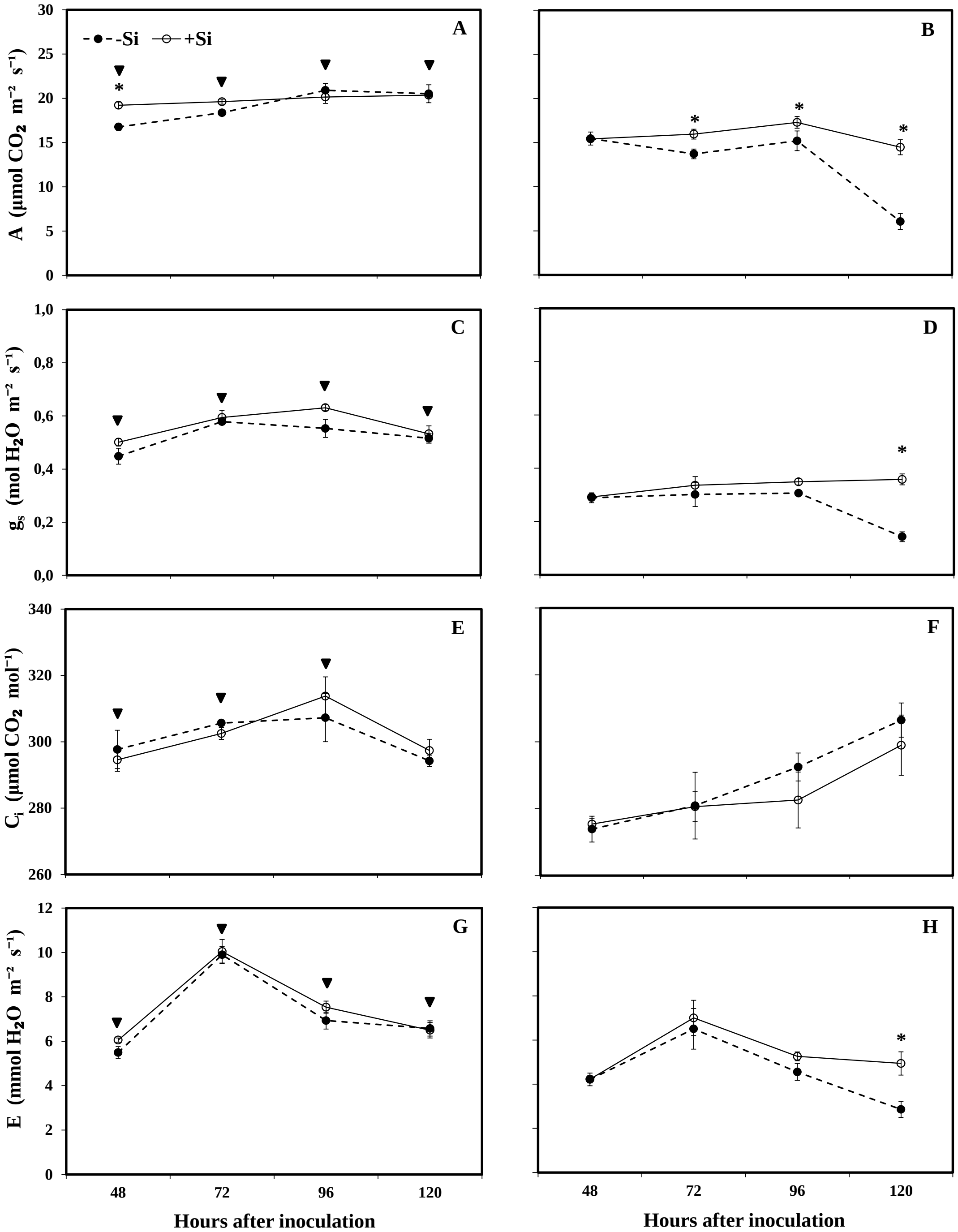

Fig. 2. The net CO_2 assimilation rate (A) (A and B), stomatal conductance to water vapor (g_s) (C and D), internal CO_2 concentration (C_i) (E and F) and transpiration rate (E) (G and H) for the leaves of wheat plants grown in hydroponic culture containing 0 (-Si) or 2 (+Si) mM silicon and non-inoculated (NI) (A, C, E and G) or inoculated (I) (B, D, F and H) with *Pyricularia oryzae*. The means for the NI and I treatments followed by an inverted triangle and for the -Si and +Si treatments followed by an asterisk (*) for each evaluation time are significantly different by Student´s t-test ($P \leq 0.05$). Bars represent the standard error of the mean. n = 5.

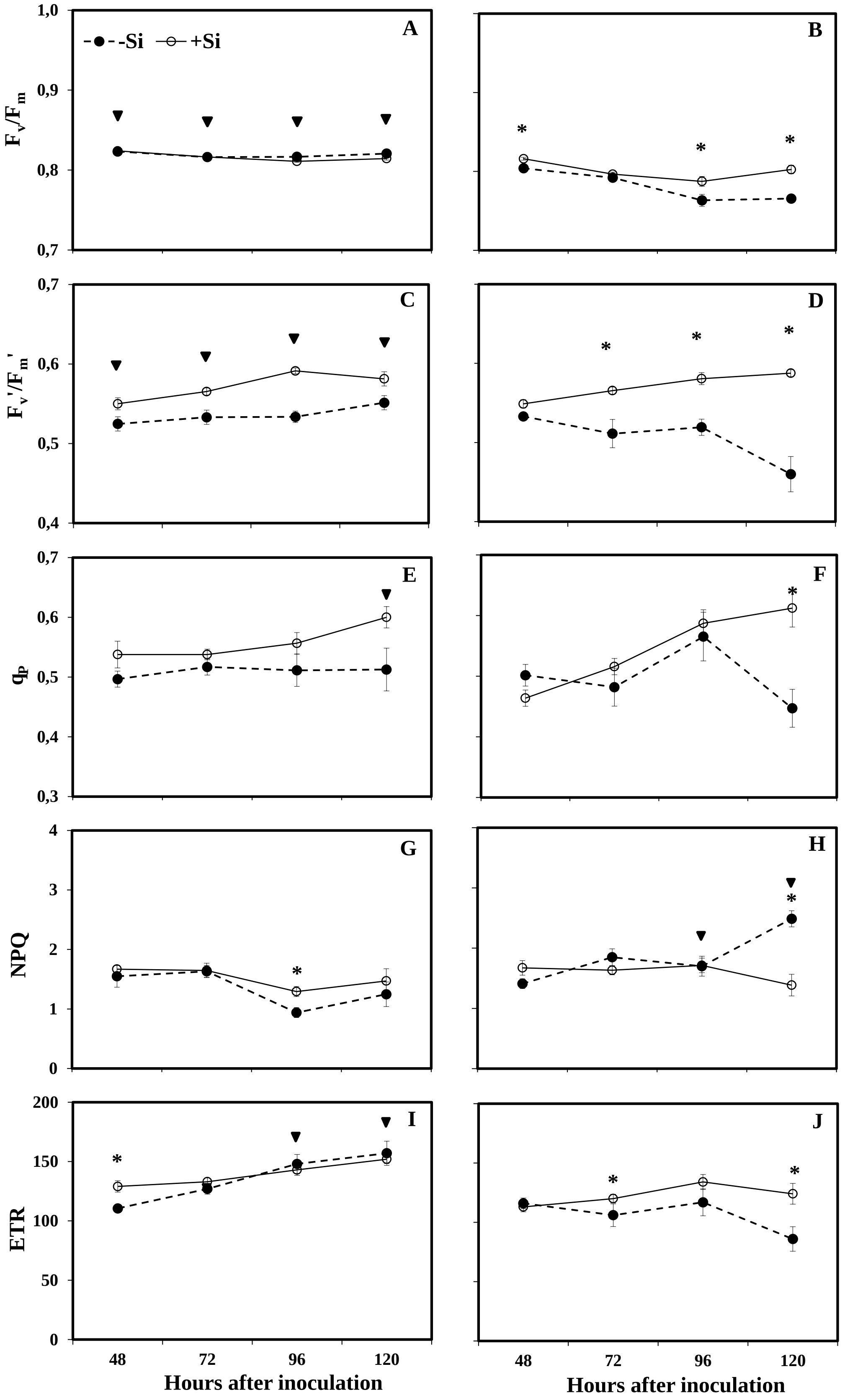
A
B
C
D
E
F
G
H
I
J
-Si
+Si
Fv/Fm
Fv'/Fm'
qP
NPQ
ETR
1,0
0,9
0,8
0,7
0,6
0,5
0,4
0,3
4
3
2
1
0
200
150
100
50
48
72
96
120
Hours after inoculation
Hours after inoculation

Fig. 3. The maximum PSII quantum efficiency (F_v/F_m) (A and B), capture efficiency of excitation energy by open PSII reaction centers (F_v'/ F_m') (C and D), photochemical (q_P) and non-photochemical (NPQ) quenching coefficients and electron transport rate (ETR) for plants grown in hydroponic culture containing 0 (-Si) or 2 (+Si) mM silicon and non-inoculated (NI) (A, C, E, G and I) or inoculated (I) (B, D, F, H and I) with Pyricularia oryzae. The means for the NI and I treatments followed by an inverted triangle and for the -Si and +Si treatments followed by an asterisk (*) for each evaluation time are significantly different by Student´s t-test ($P \leq 0.05$). Bars represent the standard error of the mean. n = 5.