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Photosynthetic gas exchange in leaves of wheat plants supplied with silicon and infected with *Pyricularia oryzae*

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Abstract Photosynthetic gas exchange in the leaves of wheat plants growing in a nutrient solution containing 0 or 2 mM silicon (Si) and inoculated with *Pyricularia oryzae* was investigated. The blast severity, the gas exchange parameters such as net carbon assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i) and transpiration rate (E) and the concentration of pigments (chlorophyll a, chlorophyll b and carotenoids) were determined. The blast severity was reduced by 67.66 % on +Si plants compared with the −Si plants. There were significant increases of 29.3, 17.7 and 45 % for A at 48, 72 and 96 h after inoculation (hai); 26.7 and 49 % for g_s at 48 and 96 hai; and 25.2 and 31.4 % for E at 48 and 96 hai, respectively, for +Si inoculated plants when compared with the −Si inoculated plants. The C_i was significantly lower for +Si inoculated plants than for −Si inoculated plants at 48, 72 and 96 hai. For inoculated plants, the concentrations of chlorophyll a and chlorophyll b were significantly higher for the +Si plants compared with the −Si plants at 72 and 96 hai. The results of this study clearly demonstrated that the supply of Si to the wheat plants was associated with lower blast severity in parallel with improved gas exchange performance, resulting in higher energy for mounting successful defense strategies against *P. oryzae* infection.

Keywords *Triticum aestivum* · Leaf gas exchange parameters · Mineral nutrition · Photosynthesis

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Introduction

Blast, caused by the fungus *Pyricularia oryzae* Sacc. (teleomorph: *Magnaporthe grisea* (Hebert) Barr), has become one of the most important disease of wheat (*Triticum aestivum* L.) in Brazil, considering that it can decrease yield by up to 70 %. On the leaves, the symptoms of this disease include gray–green and water-soaked lesions with dark green borders. Indeed, the fungus causes seedling blight, spike tip death and bright black spots on the rachis. The occurrence of gray–brown lesions on the spikes and spikelets significantly contributes to yield reduction due to low levels of nutrient translocation to the grains. Blast epidemics mainly occur during the rainy season, with temperatures ranging from 21 to 27 °C and high relative humidity (Goulart et al. 2007). The spraying of fungicides has demonstrated low efficiency for disease control (Goulart and Paiva 1993; Goulart et al. 2007), and few cultivars with desirable level of blast resistance are available (Urashima et al. 2004).

Although silicon (Si) is not considered to be an essential nutrient for plants, its beneficial effects on disease control have been very well documented (Datnoff et al. 2007). Plants absorb Si from the soil solution in the form of monosilicic acid, but differences in their ability to accumulate Si in their shoots differ among plant species (Datnoff et al. 2007). Dallagnol et al. (2009) demonstrated that low Si concentration in the tissues of the *lsi*1 mutant plants, which were defective in active Si uptake ability, affected the basal level of resistance to brown spot, suggesting that a minimum foliar Si concentration is necessary for increasing the resistance of rice to the disease. Sorghum plants supplied with Si and infected with *Colletotrichum sublineolum* were able to maintain carbon fixation and keep an efficient antioxidant system (Resende et al. 2012).

When plants are attacked by pathogens, several physiological processes, such as respiration, water and nutrient translocation, photosynthesis and transpiration are negatively impaired (Lucas 1998). Some studies have shown that attacks by pathogens reduce photosynthesis due to damage to the photosynthetic machinery (Bassanezi et al. 2002; Petit et al. 2006; Dallagnol et al. 2011). Bassanezi et al. (2002) measured gas exchange in the leaves of bean plants infected with *Uromyces appendiculatus*, *Pseudocercospora griseola* and *Colletotrichum lindemuthianum* and observed that reductions in photosynthesis caused by *U. appendiculatus* and *P. griseola* were due to a lower carboxylation capacity. In contrast, the reductions in internal CO_2 concentrations were due to increased stomatal resistance, which was the main factor associated with decreases in photosynthesis due to infection by *C. lindemuthianum*. Symptoms of esca disease on the leaves of vines were associated with stomatal closure and alterations in the photosynthetic apparatus due to decreases in the assimilation of CO_2 and a reduction in the concentration of chlorophyll (Petit et al. 2006).

Considering the lack of information on physiological changes on wheat leaves of plants supplied with Si during the infection process for *P. oryzae*, this study investigated the potential for this element to minimize the negative effects of *P. oryzae* infection on leaf gas exchange parameters and photosynthetic pigments concentration.

Materials and methods

Nutrient solution preparation

A nutrient solution was prepared based on Clark (1975), with some modifications. It included the following macronutrients: 1.04 mM $Ca(NO_3)_2 \cdot 4H_2O$, 1 mM NH_4NO_3, 0.8 mM KNO_3, 0.069 mM KH_2PO_4, 0.931 mM KCl and 0.6 mM $MgSO_4 \cdot 7H_2O$. It also included the following micronutrients: 19 μM H_3BO_3, 2 μM $ZnSO_4 \cdot 7H_2O$, 0.5 μM $CuSO_4 \cdot 5H_2O$, 7 μM $MnCl_2 \cdot 4H_2O$, 0.6 μM $Na_2MoO_4 \cdot 4H_2O$, 90 μM $FeSO_4 \cdot 7H_2O$ and 90 μM EDTA bisodium. Silicon (2 mM) was supplied to plants in the form of silicic acid, which was prepared by passing potassium silicate through a cation exchange resin (Amberlite IR-120B; H^+ form; Sigma-Aldrich). The pH of the nutrient solution was 5.6 and was not affected by the addition of silicic acid.

Plant growth

Wheat seeds from cv. BR-18 were germinated on distilled water-soaked germitest paper (Fisher Scientific Co., Pittsburgh, PA, USA) in a germination chamber at 25 °C for 6 days. Germinated seedlings were transferred to plastic pots with one-half strength nutrient solution without the presence of Si for 2 days. After this period, the plants were transferred to new plastic pots with 5 dm^3 of nutrient solution prepared with or without Si. The nutrient solution, with aeration, was changed every 4 days. The electrical conductivity and the pH of the nutrient solution were checked daily. The pH was kept at ≈5.6 by using NaOH or HCl (1 M) as needed.

Inoculation of plants with *P. oryzae*

A pathogenic isolate of *P. oryzae* (UFV/DFP-01), obtained from ears of wheat plants (cv. BR-18), was used to inoculate the leaves of the wheat plants. Pieces of filter paper with fungal mycelia were transferred to Petri dishes containing oatmeal agar medium. After 3 days, plugs of oatmeal agar medium containing fungal mycelia were transferred to new Petri dishes containing the same medium. These Petri dishes were kept in a growth chamber at 25 °C with a 12-h photoperiod for 10 days. After this period, conidia were carefully removed from the Petri dishes with a rubber policeman to obtain a suspension of conidia. Plants were inoculated with a conidial suspension of *P. oryzae* (10^5 conidia cm^{-3}) at 60 days after emergence (growth stage 65) (Zadoks et al. 1974). Twenty-five cm^3 of suspension was applied as a fine mist to the adaxial leaf blades of each plant until runoff using a VL Airbrush atomizer (Paasche Airbrush Co., Chicago, IL, USA). Gelatin (1 %, wt vol^{-1}) was added to the suspension to aid in conidial adhesion to the leaf blades. Immediately after inoculation, the plants were transferred to a growth chamber with a temperature of 25 ± 2 °C and a relative humidity of 90 ± 5 % and were subjected to an initial 24 h dark period. After this period, the plants were transferred to a plastic mist growth chamber (MGC) inside a greenhouse for the duration of the experiments. The MGC was made of wood (2 m wide, 1.5 m high and 5 m long) and was covered with 100-μm-thick transparent plastic. The temperature inside the MGC ranged from 25 ± 2 °C (day) to 20 ± 2 °C (night). The relative humidity was maintained at 92 ± 3 % using a misting system in which the nozzles (model NEB-100; KGF Company, São Paulo, Brazil) sprayed mist every 30 min above the plant canopy. The relative humidity and temperature were measured with a thermo-hygrograph (TH-508, Impac, Brazil). The maximum natural photon flux density at plant canopy height was approximately 900 μmol m^{-2} s^{-1}.

Assessment of blast severity

The blast severity was assessed on the fourth, fifth and sixth leaves, from the base to the apex, of each plant, 96 h after inoculation (hai) using a standard area diagram sets (SADs) proposed by Rios et al. (2013). The SADs proposed by these authors has ten levels of blast diseased wheat leaves with a range of severity from 0.1 to 72 %.

Determination of the leaf gas exchange parameters

Gas exchange parameters were measured on the fifth leaf, from the base to the apex, of non-inoculated and inoculated plants at 48, 72 and 96 hai. The net carbon assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i) and transpiration rate (E) were estimated from 09:00 to 12:00 h under artificial and saturating photon irradiance (1,000 μmol m^{-2} s^{-1}) and an external CO_2 concentration of 400 μmol mol^{-1} using a portable open-system infrared gas analyzer (LI-6400, LI-COR Inc., Lincoln, NE, USA).

Determination of pigments concentration

The fourth and fifth leaves, from the base to the apex, of non-inoculated and inoculated plants were collected at 24, 48, 72 and 96 hai. Samples were kept in liquid nitrogen during sampling and were then stored at −80 °C until further analysis. A total of 200 mg of leaves was ground into a fine powder with liquid nitrogen using a mortar and pestle with the addition of 1 mg of calcium carbonate. Next, the fine powder was homogenized with 2 mL of 80 % acetone (v/v) for 1 min in a room with reduced light intensity. The suspension was filtered through a Whatman Number 1 filter paper and the residue was washed four times with 80 % acetone. The volume was increased to 25 ml with the same solvent in a volumetric flask. The absorbance of the samples was recorded at 470, 646.8 and 663.2 nm and the concentrations of photosynthetic pigments (chlorophyll a, chlorophyll b and carotenoids) were estimated according to Lichtenthaler (1987) and expressed in mg per gram of fresh matter.

Determination of foliar Si concentration

After the termination of the experiments, fourth and fifth leaves were collected from plants from each replication of each treatment, washed in deionized water, dried for 72 h at 65 °C and ground with a Thomas Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) until they could pass through a 40-mesh screen. The foliar Si concentration was determined by colorimetric analysis of 0.1 g of dried and alkali-digested tissue (Resende et al. 2012) and was expressed in g kg^{-1}.

Experimental design and data analysis

A 2 × 2 factorial experiment was performed consisting of two Si concentrations (0 and 2 mM, hereafter referred to as the −Si and +Si treatments, respectively) and plant inoculation was arranged in a completely randomized design with four replications. Each experimental unit corresponded to a plastic pot containing five wheat plants. The experiment was repeated once. Data from blast severity, foliar Si concentration, leaf gas exchange parameters and pigments concentration were combined for statistical analysis after determining the homogeneity of variance and the mean squares (Gomes and Garcia 2002). For leaf gas exchange parameters, the analysis of variance was considered to be a 2 × 2 × 3 factorial experiment consisting of two Si concentrations, plant inoculation and three evaluation times. The analysis of variance for pigments concentration was considered to be a 2 × 2 × 4 factorial experiment consisting of two Si concentrations, plant inoculation and four evaluation times. Data for all variables were subjected to analysis of variance and the mean from the treatments were compared using a t test ($P \leq 0.05$) using SAS software (SAS Institute Inc., Cary, NC, USA). The Pearson correlation was used to determine the relationships among the gas exchange parameters, foliar Si concentration and blast severity.

Results

Foliar Si concentration and blast severity

The foliar Si concentration was significantly higher for the +Si plants compared with the −Si plants (4.30 and 45.8 g kg^{-1}, respectively). The blast severity was significantly lower on the leaves of the +Si plants than on the leaves of the −Si plants (9.22 and 28.53 %, respectively).
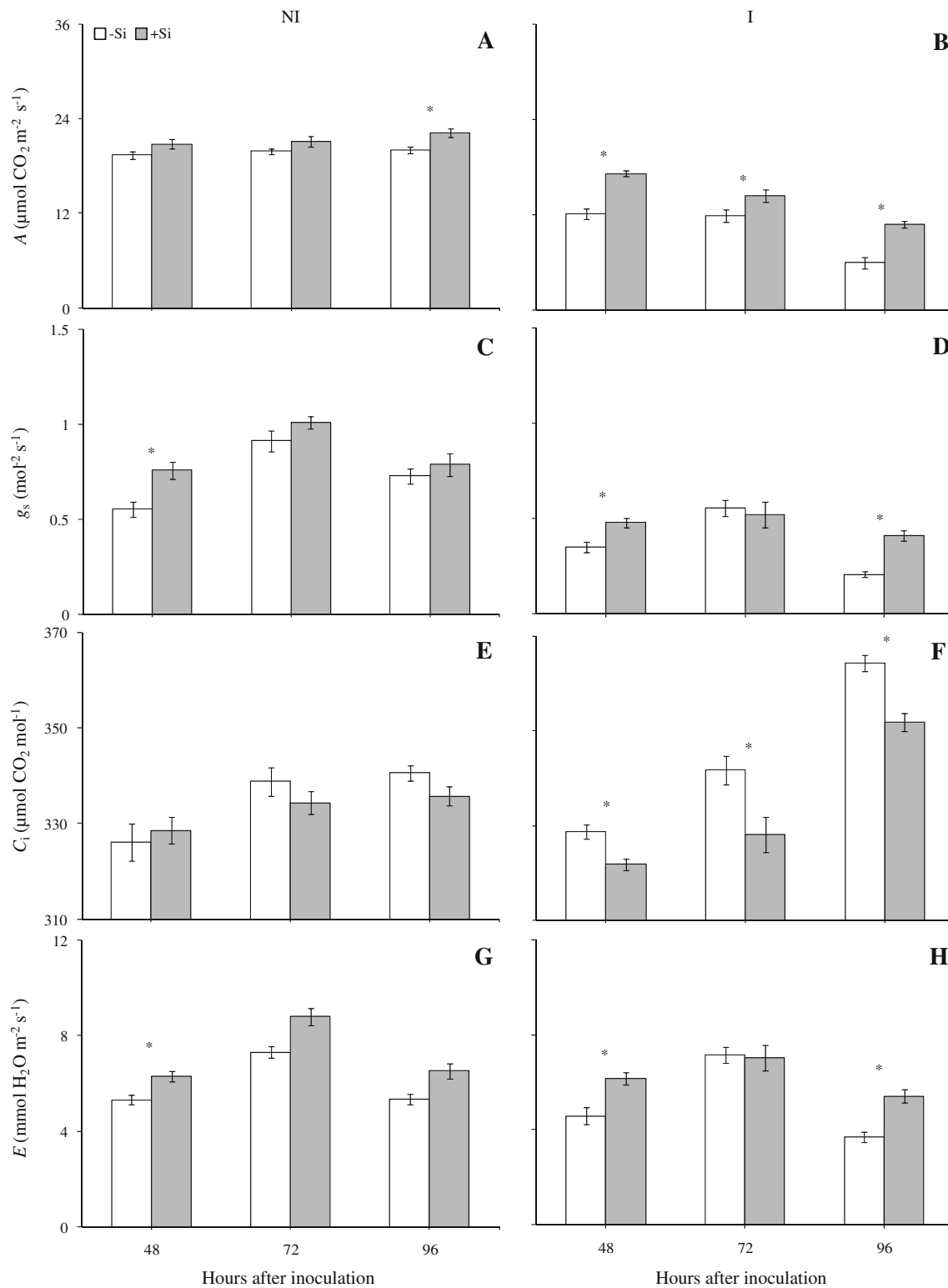
Leaf gas exchange parameters

At least one of the factors Si concentrations, plant inoculation and evaluation times and some of their interactions was significant for the parameters A, g_s, C_i and E (Table 1).

Table 1 Analysis of variance of the effects of silicon concentrations, plant inoculation and evaluation times for net carbon assimilation rate (A), internal CO_2 concentration (C_i), stomatal conductance to water vapor (g_s) and transpiration rate (E)

Sources of variation	df	F values[a]			
		A	C_i	g_s	E
Silicon (Si)	1	76.84*	13.15*	19.80*	39.59*
Plant inoculation (PI)	1	679.84*	15.27*	227.41*	26.57*
Evaluation times (ET)	2	24.49*	58.22**	33.96*	65.05*
Si × PI	1	9.78*	9.39**	0.19[ns]	0.24[ns]
Si × ET	2	2.42[ns]	1.54[ns]	2.65[ns]	1.68[ns]
PI × ET	2	46.71*	25.55[ns]	7.20*	2.26[ns]
Si × PI × ET	2	0.57[ns]	0.02[ns]	2.93[ns]	3.99[ns]

[a], [ns], and * Indicates non-significant and significant at 0.05 level of probability, respectively

Fig. 1 Leaf gas exchange parameters net carbon assimilation rate (A) (**a, b**), stomatal conductance to water vapor (g_s) (**c, d**), internal CO_2 concentration (C_i) (**e, f**) and transpiration rate (E) (**g, h**) determined on the leaves of wheat plants grown in hydroponic culture containing 0 mM (−Si) or 2 mM (+Si) of silicon and non-inoculated (NI) or inoculated (I) with *Pyricularia oryzae*. The mean for the −Si and +Si treatments followed by an *asterisk* at each evaluation time are significantly different using Student's *t* test ($P \geq 0.05$). *Bars* represent the standard errors of the mean. $n = 8$

Table 2 Analysis of variance of the effects of silicon concentrations, plant inoculation and evaluation times for the concentrations of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and carotenoids (Car)

Sources of variation	df	F values[a]		
		Chl *a*	Chl *b*	Car
Silicon (Si)	1	30.31**	6.62**	0.49[ns]
Plant inoculation (PI)	1	80.58**	40.30**	3.76*
Evaluation times (ET)	3	13.59**	7.85**	0.41[ns]
Si × PI	1	1.65[ns]	0.75[ns]	2.34[ns]
Si × ET	3	4.42*	4.05*	2.51[ns]
PI × ET	3	4.42*	2.40[ns]	2.09[ns]
Si × PI × ET	3	8.16*	4.41*	6.36*

[a], [ns], * and ** Indicates non-significant, significant at 0.05 and 0.01 levels of probability, respectively

For the non-inoculated plants at 96 hai, A was significantly higher for the +Si plants than for the −Si plants (Fig. 1). For the inoculated plants supplied with Si, A significantly increased by 29.3, 17.7 and 45 % at 48, 72 and 96 hai, respectively, compared with the −Si plants (Fig. 1). For the non-inoculated plants, the g_s was significantly higher for the +Si plants in comparison to the −Si plants at 48 hai (Fig. 1). For the inoculated plants supplied with Si, the g_s significantly increased by 26.7 and 49 % at 48 and 96 hai, respectively, compared with the −Si plants. For C_i on the non-inoculated plants, there was no significant difference between the −Si and +Si treatments (Fig. 1). For the inoculated plants supplied with Si, the C_i was significantly lower than for the −Si plants at 48, 72 and 96 hai (Fig. 1). The E was significantly higher for non-inoculated +Si plants than for the −Si plants at 48 hai. For the inoculated plants, the E was significantly higher at 48 and 96 hai for the +Si plants than for the −Si plants (Fig. 1).

Pigments concentration

At least one of the factors Si concentrations, plant inoculation and evaluation times and some of their interactions was significant for the concentrations of chlorophyll *a*, chlorophyll *b* and carotenoids (Table 2). For non-inoculated plants, the concentration of chlorophyll *a* was significantly higher at 24, 48 and 96 hai for the +Si plants when compared with the −Si plants (Fig. 2). There was no significant difference between the −Si and +Si treatments regardless of plant inoculation for the concentrations of chlorophyll *b* and the carotenoids (Fig. 2). For the inoculated plants, the concentrations of chlorophyll *a* and chlorophyll *b* were significantly higher at 72 and 96 hai for the +Si plants in comparison to the −Si plants (Fig. 2). The concentration of carotenoids was significantly higher at 48 and 96 hai for the −Si plants compared with the +Si plants (Fig. 2).

Pearson correlation

The correlation between blast severity and foliar Si concentration was negatively significant (Table 3). Parameter A was negatively correlated with the C_i and blast severity, but positively correlated with the g_s, E and foliar Si concentration (Table 3). The g_s parameter correlated significantly and positively with the E but significantly and negatively with the C_i (Table 3). The correlation of the C_i with the E was significantly negative (Table 3). Parameter E was positively correlated with the foliar Si concentration and negatively correlated with blast severity.

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 describes the first physiological features associated with the increase in resistance to *P. oryzae* infection of wheat plants supplied with Si. Several studies have demonstrated the efficiency of Si in reducing the negative effects of pathogen infections on plant photosynthesis (Fortunato et al. 2012; Resende et al. 2012). However, to the best of our knowledge, the effects of Si on enhancing the resistance of wheat to *P. oryzae* infection, specifically at the level of photosynthesis, have never been investigated.

The high Si concentration in the wheat leaves contributed to decreased blast severity. Supplying Si to plants has become an important strategy for reducing the intensity of diseases in many economically important crops, such as bananas, barley, beans, cucumbers, oats, rice and wheat (Dallagnol et al. 2009; Xavier Filha et al. 2011; Polanco et al. 2012; Fortunato et al. 2012). The mechanisms, however, are not completely understood. Originally, it was proposed that Si increased plant disease resistance by the deposition of silica in the leaves, which was believed to act as a physical barrier that hampers pathogen penetration into epidermis (Jones and Handreck 1967). Indeed, Kim et al. (2002) suggested that Si-induced cell wall fortification of rice leaves was closely associated with enhanced resistance to blast. Although important recent evidences suggest that the passive role of Si is not solely determinant for the Si-mediated resistance to pathogens. Therefore, some studies have demonstrated that Si potentiates inducible defense responses. Wheat plants supplied with Si produced phytoalexins in response *Blumeria graminis* f.sp. *tritici* infection (Rémus-Borel et al. 2005). According to Xavier Filha et al. (2011), the wheat resistance to blast was reduced by Si primarily due to an increase in the concentration of lignin-thioglycolic acid derivatives and higher activities of the
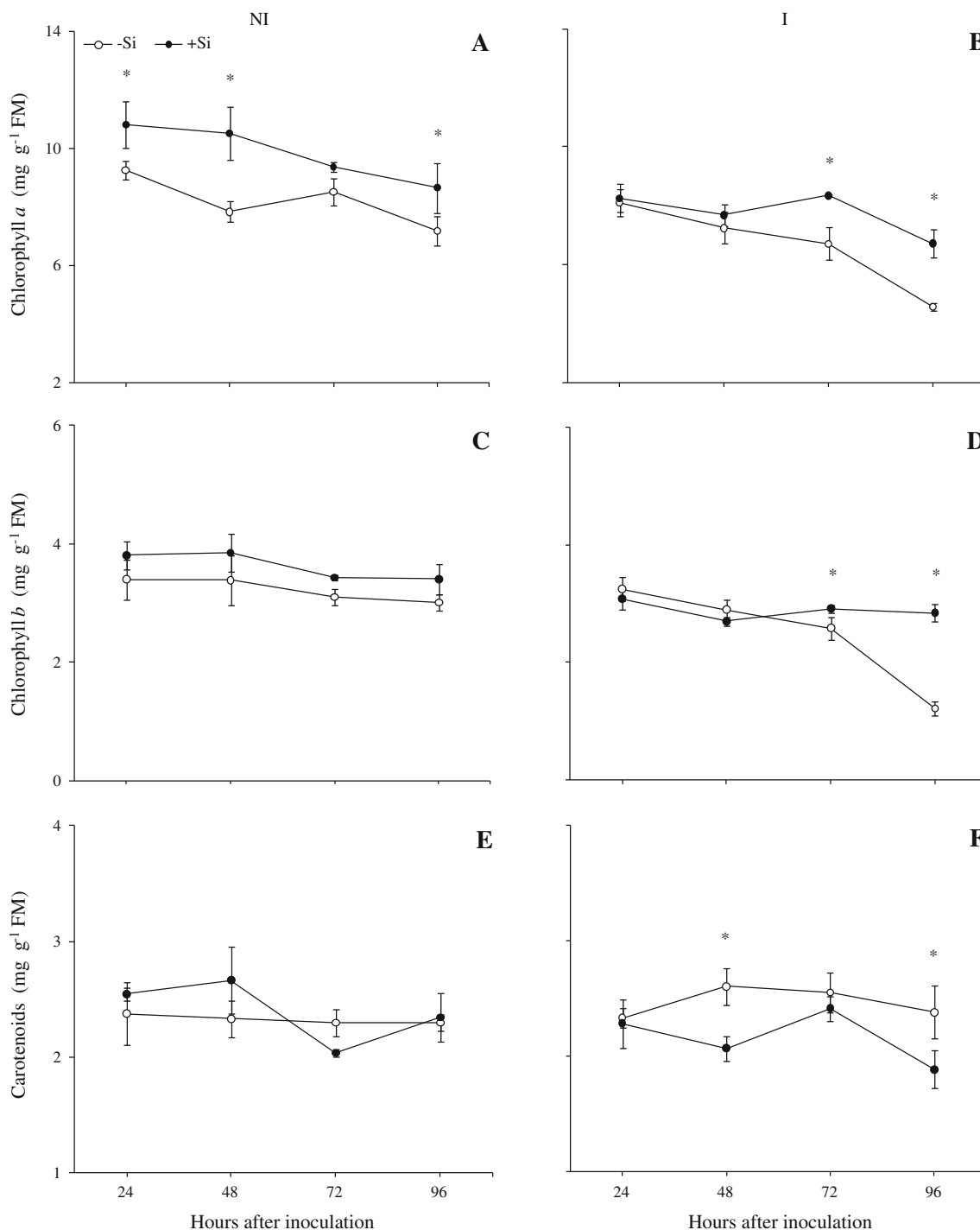
Fig. 2 Concentrations of chlorophyll *a* (**a**, **b**), chlorophyll *b* (**c**, **d**) and carotenoids (**e**, **f**) in the leaves of wheat plants grown in hydroponic culture containing 0 mM (−Si) or 2 mM (+Si) of silicon and non-inoculated (NI) or inoculated (I) with *Pyricularia oryzae*. The mean for the −Si and +Si treatments followed by an *asterisk* at each evaluation time are significantly different using Student's *t* test ($P \geq 0.05$). *Bars* represent the standard errors of the mean. *FM* fresh matter. $n = 8$

defense enzymes chitinase and peroxidase. The production of two diterpenoids phytoalexins in response to *P. grisea* infection has been potentiated in rice plants supplied with Si (Rodrigues et al. 2004).

As reported by several authors, photosynthesis in several crops is impaired by foliar diseases (Scholes and Rolfe 1996; Chou et al. 2000; Berger et al. 2007; Dallagnol et al. 2011; Resende et al. 2012). In the present study, infection

Table 3 Correlation coefficients (below diagonal) and their respective t values (above diagonal) among the net carbon assimilation rate (A), stomatal conductance to water vapor (g_s), internal CO_2 concentration (C_i), transpiration rate (E), foliar Si concentration (Si) and blast severity (Sev)

Variables[a]	A	g_s	C_i	E	Si	Sev
A	–	17.24*	−5.41*	47.37*	3.70*	−2.35*
g_s	0.91	–	−12.58*	17.21*	1.52[ns]	−1.45[ns]
C_i	−0.85	−0.57	–	−5.53*	0.42[ns]	−0.40[ns]
E	0.91	0.98	−0.58	–	3.19*	−2.98*
Si	0.19	0.38	0.05	0.38	–	−21.56*
Sev	−0.18	−0.36	−0.05	−0.36	−0.94	–

[a], [ns], and * Indicates non-significant and significant at 0.05 level of probability, respectively

by *P. oryzae* on wheat leaves caused devastating effects on photosynthetic gas exchange in the plants not supplied with Si. As the wheat blast progressed, the A values dramatically decreased, but they decreased more slowly in the +Si plants. The reduction of A due to an increase in the severity of diseases has been demonstrated in other studies (Godoy et al. 2001; Meyer et al. 2001). One cause by which pathogens reduce photosynthesis is related to the stomatal closure impeding CO_2 inflow, in addition to directly affecting the chloroplasts (Erickson et al. 2003). Stomatal closure due to low water availability in diseased tissues compromises the electron transport chain and reduces the entry of CO_2 into the Calvin cycle in chloroplasts, increasing the photo-oxidation of photosystem antennae (Bacelar et al. 2006). Even at 48 hai, when the incubation period for blast had not yet occurred, there was some reduction of A in the −Si plants, which might be explained by lower photosynthetic efficiency in the asymptomatic tissues due to stomatal resistance. Meyer et al. (2001) showed that the infection of bean leaves with *C. lindemuthianum* caused stomatal closure in areas of apparently healthy tissues, thus reducing photosynthesis, even when the anthracnose severity remained at low levels. The reduction in the g_s is a major factor affecting photosynthesis in diseased plants because of the reduction in CO_2 influx (Erickson et al. 2003). The g_s values were dramatically lower in the −Si plants upon infection by *P. oryzae*. However, the higher C_i values suggest that the reduced CO_2 influx was not the main factor associated with the reduction in the A, in contrast to some limitations at the chloroplast level. Decreases in the A might be due to the low activities of photosynthetic enzymes such as the Rubisco (Guo et al. 2005), carbonic anhydrase, which converts CO_2 to HCO_3 or enzymes involved in the degradation of photoassimilates (Baker et al. 1997). In soybean plants subjected to an abiotic stress, it was showed Si increased the photosynthesis due to higher activities of photosynthetic enzymes (Shen et al. 2010) and this may explain the higher A values observed in the present study for the

inoculated +Si plants relative to their −Si counterparts. A recent study showed that Si increased the mesophyll conductance in rice plants (Detmann et al. 2012), which also may have occurred in the present study explaining the higher values of A for the +Si plants.

Reductions in the E for the −Si plants infected with *P. oryzae* can be linked to reductions in the g_s values and, therefore, can be associated with stomatal closure. Some studies have also demonstrated concomitant reductions in both E and g_s for the pathosystems wheat-*Puccinia triticina* (McGrath and Pennypacker 1990), common bean–*Uromyces appendiculatus*, common bean–*Phaeoisariopsis griseola* and common bean–*Colletotrichum lindemuthianum* (Duniway and Durbin 1971; Bassanezi et al. 2002), eucalyptus–*Puccinia psidii* (Alves et al. 2011) and rice–*Bipolaris oryzae* (Dallagnol et al. 2011). Moreover, the reductions in the E might be the result of the symptoms of wilting and drying observed in the leaves due to the massive colonization of the leaf tissue by *P. oryzae*. According to Resende et al. (2012), in sorghum plants not supplied with Si and infected by *C. sublineolum*, there were decreases of 60 % for the A, 61 % for the g_s and 57 % for the E in comparison to plants supplied with Si at 8 days after inoculation. Those authors showed that the reduction in the leaf gas exchange parameters caused by the *C. sublineolum* infection was attenuated in the +Si plants which was associated to the increased activity of some antioxidant enzymes such as superoxide dismutase, catalase, ascorbate peroxidase and glutathione reductase, limiting, therefore, the cellular damage in those plants compared to the −Si ones.

Infection with *P. oryzae* negatively affected the concentration of pigments, especially in the −Si plants. This finding can be linked to the actions of lytic enzymes or to non-selective toxins released by the pathogen during tissue colonization. Reductions in pigments concentration are typical features of the oxidative stresses caused by pathogen infections and might be a consequence of accelerated chlorophyll degradation or reductions in its synthesis due

to changes in the composition of the thylakoid membrane (Smirnoff 1995). The higher concentration of carotenoids in the −Si plants infected by *P. oryzae* might be interpreted as a strategy to protect the photosynthetic apparatus against damage by photoinhibitory singlet oxygen produced by the excited triplet state of chlorophyll (Bacelar et al. 2006).

In conclusion, the results of this study clearly demonstrated that Si supplied to the wheat plants was associated with lower blast severity in parallel with improved gas exchange performance, giving the plants more energy for mounting successful defense strategies against *P. oryzae* infection.

Author contribution Jonas Alberto Rios: Graduate student that conducted the experiments and analyzed the data. Fabrício de Avila Rodrigues: Advisor of the Ph.D. students Jonas A. Rios and Daniel Debona. Conceived the idea and helped to write the manuscript. Daniel Debona: Graduate student that conducted the experiments and analyzed the data. Leandro Castro Silva: Undergraduate student that helped on the experiments and on data analysis.

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