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RESEARCH ARTICLE

Bioagents and silicon promoting fast early upland rice growth

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Abstract

Upland rice can overcome major challenges through the insertion of silicate fertilization and the presence of plant growth-promoting microorganisms (PGPMs) during its cultivation, as these factors promote an increase in vigor and plant disease resistance. Two consecutive experiments were conducted to evaluate the beneficial effects of silicon fertilization combined with the PGPM, *Pseudomonas fluorensces*, *Burkholderia pyrrocinia*, and a pool of *Trichoderma asperellum*, in upland rice seedlings, cultivar BRS *Primavera* CL: (a) E1, selecting PGPM type and Si doses for rice growth promotion and leaf blast supression, and (b) E2, evaluating physiological characteristics correlated with mechanisms involved in the higher vegetative growth in highlighted treatments from E1. In E1, 2 Si t ha^{-1} combined with the application of *T. asperellum* pool or PGPM mixture increased 54% in root dry matter biomass and 35 and 65% in shoot and root lengths, respectively; it also suppressed 99% of rice blast severity. In E2, shoot and root dry matter biomass and length, photosynthetic rate, water use efficiency, total soluble sugar, and chloroplastidic pigments were superior in BRS Primavera CL seedlings treated with 2 Si t ha^{-1} and *T. asperellum* pool or PGPM mixture. Higher salicilic and jasmonic acid levels were found in seedlings treated with Si and *T. asperellum* pool, individually. These physiological characteristics may explain, in part, the higher vigor of upland rice seedlings promoted by the synergistic effect between silicate fertilization and beneficial microorganisms.

Keywords Beneficial microorganisms · Silicon · Physiological parameters · Vigor · Disease resistance

Introduction

Rice is the most important cereal crop cultivated worldwide, and its ecosystems are generally classified as irrigated, rain-fed lowland, deep-water, and rain-fed upland (Guimarães et al. 2016). The upland rice ecosystem constitutes 12% of the global rice production area and has a proportionally greater importance in Africa and Latin America, where it accounts for approximately 40 and 45% of rice-growing areas, respectively (Bernier et al. 2008). Upland rice presents advantages compared to lowland rice, such as a greater potential for saving water, reducing labor requirements, mitigating greenhouse gas emissions, and adapting to climatic risks (Kumar and Ladha 2011). However, its productivity is limited by almost 50% in relation to its productive potential, due to inadequate and irregular moisture supply, heavy weed infestation, lack of suitable cultivars, nutritional imbalance, inadequate cultural practices, and inefficient control of insect pests and diseases (Galinato et al. 1999). Among fungal diseases, rice blast

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caused by *Magnaporthe oryzae* [B Couch (anamorph: *Pyricularia oryzae* cavara)] (Couch and Kohn 2002) is of significant economic importance (Pooja and Katoch 2014).

Developing cultivars and management strategies to improve upland rice seedling vigor and disease resistance may contribute to reducing crop losses due to competition with weeds, drought, and diseases, since these factors constitute "the first stratum" of technical constraints to upland rice production (Namuco et al. 2009). Early vegetative vigor can be defined as a high relative growth rate (RGR) during exponential growth, before canopy closure (Dingkuhn et al. 1999). During the vegetative stage, rapid ground cover achieved with early vegetative vigor (Dingkuhn et al. 1999) can reduce soil evaporation and accelerate root access to soil, water, and nutrients (Zhao et al. 2010).

The potential use of bioagents or plant growth-promoting microorganisms (PGPMs) and silicated fertilization has been widely explored in recent decades. These factors contribute to both increasing resistance against pathogens and promoting plant growth. In addition to plant hormones, PGPMs also produce phosphate solubilization, nutrient mobilization, siderophore production, and release of various enzymes like lipases and proteases, physiological changes activation, and biocontrol of pathogens (Cassán et al. 2009; Mei and Flinn 2010). The application of PGPM in upland rice plants increases phytomass, modifies root anatomy, and suppresses leaf rice blast (Filippi et al. 2011; Silva et al. 2012; Rêgo et al. 2014; Lucas et al. 2014; Souza et al. 2015). In addition to the presence of PGPM, the application of silicon (Si) improves the growth and development of upland rice plants (Gomes et al. 2011) by increasing both the resistance and erectness of leaves and the mesophyll conductance (Detmann et al. 2012). Moreover, Si acts as a physical barrier after being deposited under the cuticle, resulting in a cuticle-Si double layer (Yoshida et al. 1962). This cuticle-Si double layer prevents or delays pathogen penetration, thereby prolonging the incubation and latent periods, which reduces disease severity in many plant species (Datnoff et al. 2007; Resende et al. 2009; Brunings et al. 2009; Shetty et al. 2012). We hypothesized that the joint application of biogents and silicate fertilization, in the management of rice crop, is promising for sustainable and environmentally friendly production.

The objective of this study was to elucidate the beneficial effects of *Pseudomonas fluorensces* (BRM 32111), *Burkholderia pyrrocinia* (BRM 32111), and *Trichoderma asperellum* pool (UFRA.T06; UFRA.T09; UFRA.T12; UFRA.T52), individually or in combination with silicated fertilization, on the vigor of upland rice seedlings. The study was divided into two experiments: (E1) selecting PGPM types and Si doses, individually or in combination, for greater vigor promotion and disease severity (rice blast) reduction in the upland rice seedlings and (E2) evaluating physiologic mechanisms associated with greater vigor in upland rice seedlings.

Material and methods

Experimental conditions

The experiments were carried out under greenhouse conditions by planting microbiolized seeds in eight rows (5.0 cm long each), in polyethylene trays (20 × 40 × 20 cm) filled with 3 kg of Oxisol soil collected from a non-cultivated area in the Cerrado ecosystem in Goiás, Brazil. This Oxisol soil was characterized by pH H_2O 5.4, 589 g clay kg^{-1}, 66 g silt kg^{-1}, 144 g sand kg^{-1}, 63 mg K^+ dm^{-3}, 4 mg P dm^{-3}, 0.4 mg Ca^{+2} dm^{-3}, 0.2 cmolc Mg^{+2} dm^{-3}, 0.1 cmolc Al^{+3} dm^{-3}, and 3 mg Si kg^{-1}. Additional substrate fertilization was performed by applying 5 g NPK (5-30-15) + Zn, and FTE at the sowing time. In addition, 3 g $(NH_4)_2SO_4$ + Fe and Bo were applied 19 days after sowing. Commercial calcium and magnesium silicate ($CaSiO_3 \cdot MgSiO_3$), in the registered form of Agrosilício®, containing 10.5% Si, 27% Ca, and 6% Mg, were used as a silicon source. The silicon doses used in this study were 1, 2, 4, and 8 Si t ha^{-1}. The SiCaMg doses were established according to the levels of Si in the soil and previous studies described by Prabhu et al. (2001). Before fertilization with silicon, the soil was corrected with lime and was incubated for 30 days, according to the recommendation of Korndörfer et al. (1999).

PGPM preparation and BRS Primavera CL seed microbiolization

The PGPM used in this study were the rhizobacterias *Pseudomonas fluorensces* (BRM 32111) and *Burkholderia pyrrocinia* (BRM 32113), which were obtained from the Microorganism Culture Collection of the Embrapa Rice and Bean Research Center, Goiás, Brazil. Additionally, a mixture composed of the following *T. aesperellum* strains was used, UFRA.T06, UFRA.T09, UFRA.T12, and UFRA.T52, obtained individually from the Fungal Culture Collection of the Plant Protection Laboratory of the Federal University of the Amazon. The BRS Primavera CL seeds were sterilized by immersion in 70% (*v*/*v*) ETOH and 2% (*v*/*v*) NaClO solution for 1 min, washed in distilled water, and placed on sterile filter paper for 1 h to eliminate excessive water just prior to the experimental setup. The method of applying the mixture of bioagents was performed according to Filippi et al. (2011) and Silva et al. (2012). The bacterial suspensions were prepared with water from cultures that had been growing for a 24 h period on solid medium 523 (Kado and Heskett 1970) at 28 °C, and the concentration was placed in a spectrophotometer set to $A_{540} = 0.5$ (10^8 CFU mL^{-1}). For the fungal suspension, each isolate of *T. asperellum* was grown in a Petri dish containing potato, dextrose, and agar (PDA) for 5 days and bioformulated as described by Silva et al. (2012).

Experiment 1: screening of PGPM type and Si doses

The soil was previously mixed (30 days before planting) with doses of Agrosilício® corresponding to 1, 2, 4, and 8 Si t ha^{-1}. This experiment was set up in a randomized block design forming a factorial scheme 5 × 5: four PGPM suspensions: BRM 32111, BRM 32113, *T. asperellum* pool (UFRA.T06, UFRA.T09, UFRA.T12, and UFRA.T52), and PGPM mixture (*T. asperellum* pool + BRM 32111 + BRR 32113), with the microbiolized seed as control, and five Si doses (0, 1, 2, 4, and 8 Si t ha^{-1}), with eight replications per treatment combination.

Shoot and root lengths and shoot and root dry matter of upland rice seedlings

Twenty-one days after being sown, the seedlings were harvested, and the shoot length (SL) and root length (RL) were determined. Next, the roots and shoots were oven-dried at 65 °C until reaching a constant mass to determine shoot dry matter biomass (SDMB) and root dry matter biomass (RDMB). After thinning, 40 seedlings per tray (10 each row) were considered an experimental replicate in all definitive experiments.

Blast severity

A single conidial isolate of *M. oryzae*, Py 10.900, compatible with cv. BRS Primavera CL, maintained on sterilized filter paper disks in the culture collection of the Embrapa Rice and Bean Research Center, was used to inoculate the upland rice seedlings. The fungal multiplication, sporulation, and plant inoculation were performed as as described by Filippi and Prabhu (2001). The 21-day-old plants were inoculated by spraying a spore suspension (3×10^5 conidia mL^{-1}) on the leaves until run-off, using an atomizer connected to an air compressor. The inoculated plants were incubated in a humid plastic chamber in the dark for 24 h and then transferred to greenhouse benches. The disease severity reaction was assessed 8 days after inoculation using a 10-grade visual rating scale (0, 0.5, 1, 2, 4, 8, 16, 32, 64, 82%) based on the percentage of the area infected as described by Notteghem (1981). Treatments that resulted in a higher amount of shoot and root dry matter biomass, greater shoot height and root length, and low disease severity were selected for the study of the physiological mechanisms associated with greater vigor of upland rice seedlings.

Experiment 2: physiological characteristics of the upland rice seedlings

A second greenhouse experiment was conducted using the best combinations of silicon dose and bioagents from the first experiment. The experiment was set in randomized blocks with six treatments and four replicates. The treatments were (1) control (bioagent-free and silicon-free), (2) *T. asperellum* pool, (3) PGPM mixture, (4) 2 Si t ha^{-1}, (5) 2 Si t ha^{-1} plus *T. asperellum* pool, and (6) 2 Si t ha^{-1} plus PGPM mixture. Comparisons between treatments were performed 21 days after planting (DAP). The seedlings were irrigated daily with 100 mL of distilled water per tray.

Physiological and biochemical measurements

Vegetative structure growth

Shoot and root lengths and shoot and root dry matter biomass were determined as described previously.

Gas exchange

Measurements were carried out using a portable gas exchange analyzer in the infrared region (LCpro + ADC BioScientific) by analyzing the first leaf from the apex (completely expanded and with good sun exposure) and five seedlings per tray. The equipment was adjusted to use concentrations between 370 and 400 mol^{-1} CO_2 (reference C). The real flux density of photosynthetically active photons (FDPAP) used was 900 μmol [quanta] m^{-2} s^{-1}. The minimum equilibration time for the analysis was 2 min. The parameters measured were CO_2 liquid assimilation rate also known as photosynthetic rate (A) (μmol CO_2 m^{-2} s^{-1}), transpiration rate (E) (mmol H_2O m^{-2} s^{-1}), and stomatal conductance (gs) (mol H_2O m^{-2} s^{-1}). The measurements were carried out between 07:30 and 10:00 (solar time), and during measurements, the mean air temperature varied between 25 and 29 °C. The water use efficiency (WUE) (μmol CO_2 mol^{-1} H_2O) was expressed as the ratio between A and E (Doni et al. 2014).

Chloroplastid pigments

For the biochemical assay, leaf samples were collected and immediately frozen at − 80 °C until the assay. The chlorophyll (Chl) *a*, Chl *b*, Chl *a* + *b*, and total carotenoids (Car) were extracted from the leaf samples using 80% acetone and 0.1 g $CaCO_3$. The resulting slurry was centrifuged at 4000×*g* for 10 min at 4 °C. The supernatant was collected, and the extraction procedures were repeated three times. All supernatants were combined, and the final volume was adjusted to 25 mL. The absorbance of leaf extracts was recorded at 470, 646.8, and 663.2 nm in a UV-Visible spectrophotometer

(Genesys™ 10series, Thermo Electron Co., Madison, USA), and pigment concentrations were determined according to Lichthenthaler (1987). All procedures were carried out with the total absence of light.

Total soluble sugar

The leaflet samples were oven-dried until reaching constant mass (at 72 °C), and 0.1 g from the resultant grounded tissue was used for the assays. Starch was extracted using 80% ethanol (*v*/*v*), and its content was determined according to McCready et al. (1950).

Hormone level

The salicylic acid and jasmonic acid contents were determined according to Saikia et al. (2006) and Meher et al. (2012), respectively.

Statistical analysis

Experiment 1: The data were subjected to two cluster analyses. The first analysis used the average values of each individual SDMB and RDMB, and the second used SL and RL. For both cluster analyses, the degree of similarity was obtained from the standard Euclidean distance. The means of each class and rice blast severity (%) obtained were subjected to analysis of variance (ANOVA), and the means were compared by Duncan's test ($p \leq 0.05$). Experiment 2: Vegetative structures growth data, gas-exchanges traits, chloroplastid pigment concentrations, total soluble sugar content, and hormones level were combined after the determination of the homogeneity of variance by the Duncan test (Gomez and Gomez 1994). The data were subjected to an ANOVA, and the treatment means were compared by Duncan's test ($p < 0.05$). Then, the standard error was calculated ($p \leq 0.05$). The SPSS 21.0 software was used for all the analyses.

Results

Experiment 1: screening of PGPM type and Si doses

The grouping analysis, performed with the vegetative growth data (shoot dry matter biomass and root dry matter biomass, shoot length and root length) of the 25 treatments studied, defined the formation of three classes, as shown in Table 1. The plants of the treatments grouped in class 1 have vegetative structures significantly more robust, when compared to the plants of classes 2 and 3. The increase observed in SL, SDMB, RL, and RDB was of 35, 121, 60, and 54%, respectively, when compared to the control plants (class 3). Among the components of class 1, the doses 1, 2, and 4 Si t ha^{-1}, in combination with PGPM 32111, 32113, *T. asperellum* pool, and PGPM mixture were the most effective to increase the vigor of upland rice seedlings (Table 1). However, for leaf blast suppression, the dose of 2 Si t ha^{-1} was the most effective, and the most prominent PGPM type was the PGPM mixture (Table 2), presenting 0.59 of leaf blast severity as reported by Souza et al. (2015). Thus, for the study of the physiological mechanisms involved with the higher vigor of upland rice seedlings, the treatments of 2 Si t ha^{-1} plus PGPM mixture and 2 Si t ha^{-1} plus *T. asperellum* pool were selected.

Experiment 2: physiological characteristics of the upland rice seedlings

The effect of silicate fertilization (2 Si t ha^{-1}) and the PGPM *T. asperellum* pool and PGPM mixture, both individually and in combination, on the growth rates of upland rice vegetative structures showed an increase of 16% in SL, 71% in RL, 194% in SDMB, and 189% in RDMB when compared to the control plants (Figs. 1a, b and 2). The increase of vegetative structures in upland rice plants treated with Si and PGPM resulted from the significant increase of *A* (net CO_2 assimilation rate) (ca.70%) compared to the control plants (Fig. 3a). Other gas exchange variables as gs (stomatal conductance of water vapor) and *E* (transpiration rate) were higher in the control plants and were reduced by 55 and 52%, respectively, in plants treated with Si and PGPM (Fig. 3b, c). The water use efficiency (WUE), which corresponds to the ratio between the amount of CO_2 assimilated and the amount of H_2O transpired by the plant, was higher in rice plants treated with Si and PGPM, individually or in combination, when compared to control plants (Fig. 3d). In parallel with the increase of phytomass and photosynthetic rate (or net CO_2 assimilation rate), an increase of about 80% in the content of chloroplastidic pigments (Chl a, Chl b, Chl *a* + *b*, and total carotenoids) was found in rice plants treated with PGPM (Table 3). There was also an increase significant in the content of total soluble sugars in rice seedlings fertilized with 2 Si t ha^{-1} plus PGPM mixture, 2 Si t ha^{-1} plus *T. asperellum* pool, and 2 Si t^{-1} alone, compared to the control plants (Fig. 4). To confirm the effectiveness of the silicon and PGPM treatments on the resistance increase against blast, the levels of salicylic acid and jasmonic acid were determined. Upland rice seedlings fertilized with Si or inoculated with *T. asperellum* pool, alone, had salicylic acid contents higher than 35% compared to control plants. Regarding jasmonic acid, upland rice seedlings treated with *T. asperellum* pool showed an increase of 28% (Table 4).

Table 1 Shoot dry matter biomassa and lenght (SDMB) and lenght, root dry matter biomassa (RDMB), shoot length (SL), and root length (RL) in upland rice seedlings from cultivar BRS Primavera CL in response to Si doses and PGPM types (experiment 1)

Class	Treatment	Dry matter (g)		Treatment	Length (cm)	
		SDMB	RDMB		SL	RL
1		2.3a	0.7a	1 Si	38.6a	15.1a
				1 Si + BRM 32111[b]		
				1 Si + *T. asperellum* pool		
	1 Si[e]			2 Si[a] + BRM 32111		
	2 Si + *T. asperellum* pool[a]			2 Si + BRM 32113		
	2 Si + PGPM mixture[d]			2 Si + *T. asperellum* pool		
	4 Si + BRM 32113[c]			2 Si + PGPM mixture		
	4 Si + *T. asperellum* pool			1 Si + PGPM mixture		
	4 Si + PGPM mixture			4 Si + BRM 32113		
				4 Si + *T. asperellum* pool		
				4 Si + PGPM mixture		
2	BRM 32113	1.6c	0.6c		34.0b	11.7b
	T. asperellum pool					
	PGPM mixture					
	1 Si + BRM 32113			BRM 32113		
	1 Si + BRM 32111			PGPM mixture		
	1 Si + *T. asperellum* pool			1 Si[a] + BRM 32113		
	1 Si + PGPM mixture			1 Si + PGPM mixture		
	2 Si			2 Si		
	2 Si + BRM 32113			8 Si + BRM 32111		
	2 Si + BRM 32111			8 Si + *T. asperellum* pool		
	4 Si			8 Si + PGPM mixture		
	8 Si + BRM 32113					
	8 Si + BRM 32111					
	8 Si + *T. asperellum* pool					
	8 Si + PGPM mixture					
3		1.1c	0.5c	Control	8.5c	9.4c
				BRM 32111		
	Control			*T. asperellum* pool		
	BRM 32111			4 Si		
	4 Si + BRM 32111			4 Si + BRM 32111		
	8 Si			8 Si[a]		
				8 Si + BRM 32113		
	CV (%)	26.78	18.96		12.64	23.08

Different lowercase letters in the column denote significant differences between treatments (Duncan's test, $p \leq 0.05$)

CV coefficient of variation

[a] *Trichoderma asperellum* pool (UFRA.T06 × 10^8 ; UFRA.T09 × 10^8 ; UFRA.T12 × 10^8 ; UFRA.T52 × 10^8 con mL^{-1})

[b] *Pseudomonas fluorensces* (BRM 32111 × 10^8 UFC)

[c] *Burkholderia pyrrocinia* (BRM 32113 × 10^8 UFC)

[d] PGPM mixture (BRM 32111 plus BRR 32113 plus *T. asperellum* pool)

[e] t ha^{-1}

Discussion

Although rice is generally a weak competitor against weeds, the identification or development of alternative management in the upland rice production system may be an attractive, cost-effective, and safe approach to sustaining upland rice productivity. The importance of early vigor in upland rice seedlings has been emphasized in terms of the crop's ability

Table 2 The effect of silicon fertilization and bioagents, both individually and in combination, on leaf blast severity (%) (E1)

Biopromotor	Si (t ha^{-1})				
	Control	1	2	4	8
Control	14.02 dD	3.61 cB	1.95 abC	3.05 bcC	1.30 aA
BRM 3211[1]	4.16 bA	1.14 aA	1.41 aB	1.27 aB	4.12 bC
BRM 3213[2]	8.06 dB	3.87 cB	1.01 aB	1.82 bB	2.31 bB
T. asperellum pool[3]	9.60 cBC	2.46 bB	1.24 aB	0.87 aA	1.60 bB
PGPM mixture[4]	9.63 dC	3,87aB	0.56 aA	1.94 bB	1.25 abA

Source: Souza et al. (2015). Different upper and lower case letters on the same line denote significant differences between treatments (Duncan's test, $p \leq 0.05$)

[a] *Pseudomonas fluorensces* (BRM 32111 × 10^8 UFC)

[b] *Burkholderia pyrrocinia* (BRM 32113 × 10^8 UFC)

[c] *T. Trichoderma asperellum* pool (UFRA.T06 × 10^8; UFRA.T09 × 10^8; UFRA.T12 × 10^8; UFRA.T52 × 10^8 con mL^{-1})

[d] PGM mixture (BRM 32111 plus BRM 32113 plus *T. asperellum* pool)

to outcompete weeds and accelerate root access to soil, water, and nutrients (Dingkuhn et al. 1999; Zhao et al. 2006, 2010). In this study, upland rice crop management with 2 Si t ha^{-1} plus *T. asperellum* pool (UFRA.T06, UFRA.T09, UFRA.T12, and UFRA.T52) and with 2 Si t ha^{-1} plus PGPM mixture (BRM 32111 + BRM 32113 + *T. asperellum* pool) was selected for physiological studies since they provided higher vigor to rice seedlings and the effects of these treatments resulted in higher biomass accumulation, higher seedling length, mainly in the roots, and increased resistance to the main culture pathogen (Tables 1 and 2; Figs. 1a, b and 2). These results indicate the existence of a synergistic effect between the silicate fertilization and the application of PGPM in upland rice cultivation. This synergism can be attributed to the enhanced growth of PGPM in the presence of Si, which in turn favors the increase of the rice root system, with a consequent increase in water and nutrient absorption, total enzymatic activity in the rhizosphere of the plant, phosphorus solubilization, hormone production, mineral oxidation, siderophore production, and increased Si availability. At the same time, silicate fertilization may have promoted the stability of the beneficial plant-microorganism interaction (Reddy et al. 1986; Ahemad and Kibret 2014; Mishra and Sundari 2013; Wang et al. 2015). For the rice plants, considering a Si-accumulating species, although it is not an essential element, Si may have benefited the growth/development of the crop, since it promotes changes in primary metabolism through amino acid remobilization (Detmann et al. 2012). Also, Si improves plant architecture, as a result of the lower opening of the leaf angle, which makes the leaves more upright, reducing auto-shading, especially under conditions of high population densities and high N doses (Mauad et al. 2003). It is known that upland rice production in Brazil occurs mainly in the Cerrado soils that is characterized by high acidity and low natural fertility, high aluminum saturation, low cation exchange capacity, with low phosphorus, potassium, and silicon contents available (Barbosa Filho et al. 2001). Si values below 2 mg L^{-1} in the soil solution are found in the Brazilian Cerrado region (Lima Filho 2009). This information highlights the value of the results from this study for upland rice crop management. Regarding the effects of PGPM on the rice plant, Rêgo et al. (2014) attributed a greater seedling vigor to a better morphoanatomic development of the root system (higher root length, changes in root architecture through cortex expansion, aerenchymal spaces, and vascular cylinder diameter). Nascente et al. (2016) also observed that for upland rice, the application of PGPM positively affects the growth of rice plants, increasing photosynthetic rate and nutrient absorption. In addition, Samolski et al. (2012) and Doni et al. (2014) reported the synthesis of cysteine rich proteins as a factor responsible for the change in architecture of rice roots colonized by *Trichoderma*, which led to a greater absorption of nutrients such as nitrogen, magnesium, and phosphorus.

Early vegetative vigor depends on the assimilate source (light capture and photosynthetic rate) as well as the sink constituted by structural growth (leaf appearance rate, potential size, and tiller outgrowth) (Sandhu et al. 2015). In this study, 2 Si t ha^{-1}, PGPM mixture, and *T. asperelum* pool, individually or in combination, promoted a significant increase of *A* (photosynthetic rate) and *WUE* (water use efficiency), while *E* (transpiratory rate) and gs (stomatal conductance) decreased markedly (Fig. 3a–d). Detmann et al. (2012) and Dallagnol et al. (2013) also reported that upland rice plants fertilized with silicon showed a 31% increase in *A* and 28% in WUE. According to Mauad et al. (2003), Soratto et al. (2012), and Qin et al. (2016), the increase in the photosynthetic rate can be attributed to the protection of the chloroplast, the increase in mesophyll conductance, and the alteration in the plant architecture that presents a better opening angle of the

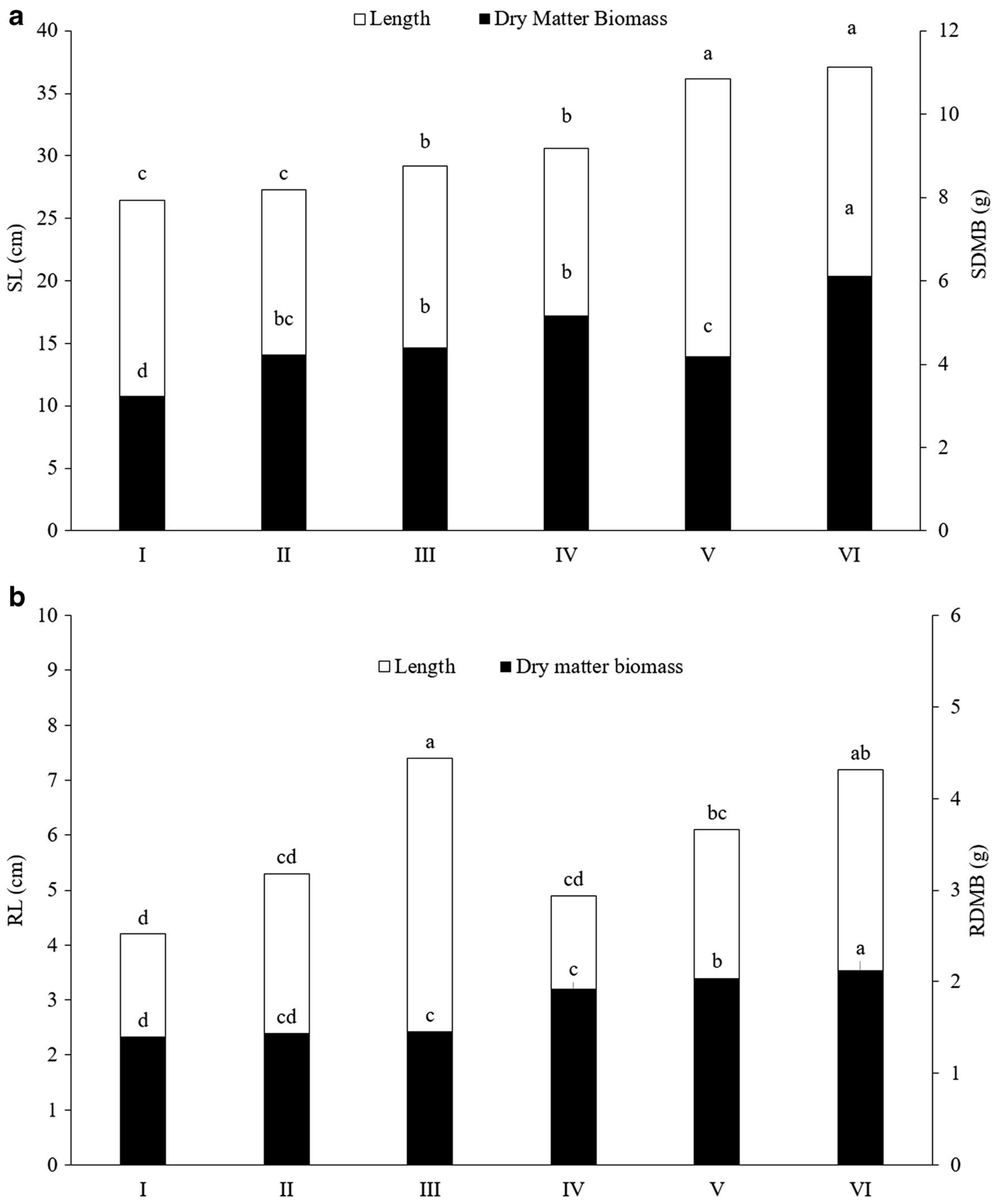

Fig. 1 Treatments: I, control; II, *Trichoderma asperellum* pool; III, PGPM mixture; IV 2 Si t ha^{-1}; V, 2 Si t ha^{-1} + *Trichoderma asperellum* pool; VI, 2 Si t ha^{-1} + PGPM mixture. **a** Shoot dry matter biomass (SDMB) and length (SL). **b** Root dry matter biomass (RDMB) and length (RL) of upland rice seddlings in response to Si (2 t ha^{-1}), *Trichoderma asperellum* pool (UFRA.T06 × 10^{8}; UFRA.T09 × 10^{8}; UFRA.T12 × 10^{8}; UFRA.T52 × 10^{8} con mL^{-1}) and PGPM mixture (BRM 32111 × 10^{8} UFC plus BRM 32113 × 10^{8} UFC plus *Trichoderma asperellum* pool). Different letters in the bars represent significant difference ($p \leq 0.05$) according to Duncan's test. Coefficient of variation (%) of SDMB = 17.10%; SL = 4.75%; RDMB = 17.32%; RL = 2.42%

leaves. This angle keeps the leaf erect and, consequently, affords greater light interception and increased photosynthetic capacity in upland rice seedlings fertilized with silicon. In addition to the presence of PGPM, several studies have reported that the phytomass increase may be due to the increase in the photosynthetic rate (Makino 2011; Naveed et al. 2014; Nascente et al. 2016). This change in the photosynthetic rate results from the increased efficiency of photochemical machinery (Thakur et al. 2010; Poupin et al. 2013) and also from the higher expression of genes associated with photosynthesis,

Fig. 2 Upland rice seddlings (21 DAP) from cultivar BRS Primavera CL in response to Si dose and PGPM types: (A) Control, (B) *T. asperellum* pool, (C) PGPM mixture, (D) Si, (E) 2 Si t ha^{-1} plus *T. asperellum* pool, and (F) 2 Si t ha^{-1} plus PGPM mixture

including two forms of Rubisco, Rubisco Activase, and proteins of photosystem II (Shoresh and Harman 2008; Naveed et al. 2014; Segarra et al. 2007). The significant reduction in *E* and gs can be explained by the existence of a double layer of silica-cellulose, which is formed by Si accumulation in the leaf blades. This accumulation promotes both reduction of water vapor permeability and, consequently, limits the loss of water through the cuticle and increase water flow in the

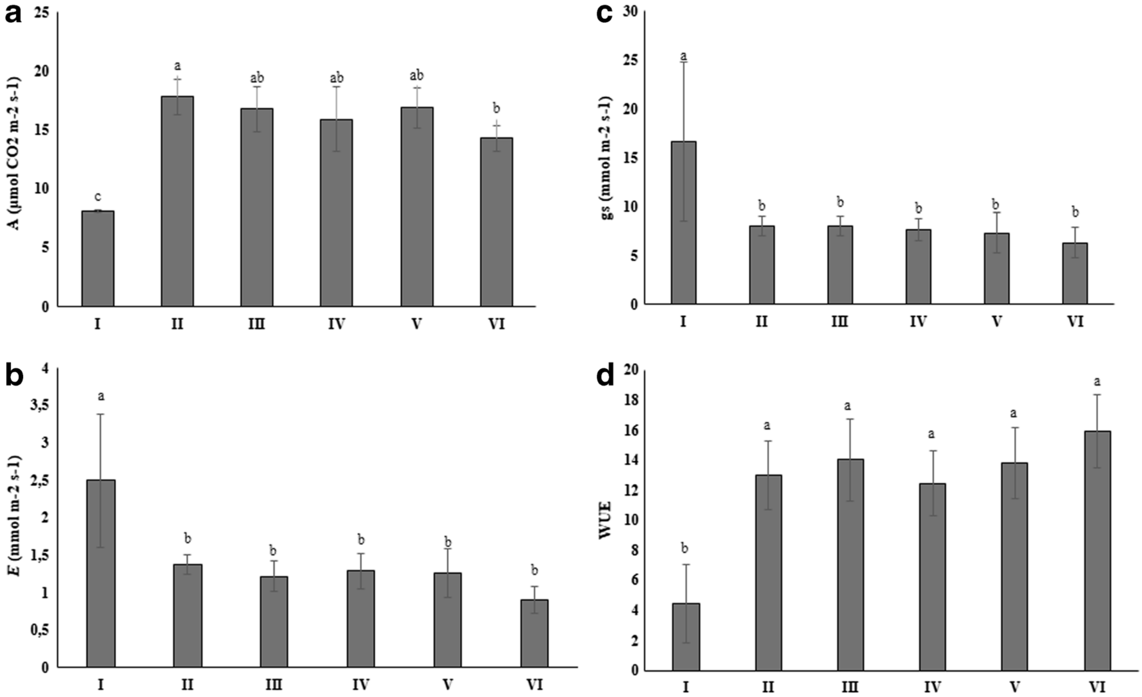

Fig. 3 Treatments: I, control; II, *Trichoderma asperellum* pool; III, PGPM mixture; IV, 2 Si t ha^{-1}; V, 2 Si t ha^{-1} + *Trichoderma asperellum* pool; VI, 2 Si t ha^{-1} + PGPM mixture. Leaf gas exchange variables: **a** In net CO_2 assimilation rate or photossyntetic rate (*A*), **b** transpiration rate (*E*), **c** stomatal conductance to water vapor (gs), and **d** water use efficiency (WUE), determined on leaves of upland rice seedlings from cultivar BRS Primavera CL in response to Si (2 t ha^{-1}), *Trichoderma asperellum* pool (UFRA.T06 × 10^8; UFRA.T09 × 10^8; UFRA.T12 × 10^8; UFRA.T52 × 10^8 con mL^{-1}) and PGPM mixture (BRM 32111 × 10^8 UFC plus BRM 32113 × 10^8 UFC plus *Trichoderma* asperellum pool). Different letters in the bars present significant difference ($p \leq 0.05$), according to Duncan's test. Coefficient of variation of *A* = 10.02%; *E* = 21.42%; gs = 27.55%; WUE = 17.10%

Table 3 Leaf pigment (chlorophyll *a*, Chl *a*; chlorophyll *b*, Chl *b*; total chlorophyll, Chl *a* + *b*; and total carotenoids, Car) concentrations determined on leaves of upland rice seedlings from cultivar BRS Primavera CL in response to Si (2 t ha^{-1}), *Trichoderma asperellum* pool and PGPM mixture

Treatment	Chl *a* (g kg^{-1} DM)	Chl *b* (g kg^{-1} DM)	Chl *a* + *b* (g kg^{-1} DM)	Car (g kg^{-1} DM)
Control	7.70 ± 1.18 b	2.77 ± 0.32 b	10.47 ± 1.49 b	1.53 ± 0.28 b
T. asperellum pool[a]	14.02 ± 1.09 a	5.09 ± 0.23 a	19.11 ± 1.31 a	2.89 ± 0.23 a
PGPM mixture[b]	13.30 ± 0.29 a	4. 78 ± 0.51 a	18.08 ± 0.24 a	2.84 ± 0.15 a
2 Si t ha^{-1}	8.19 ± 1.16 b	3.05 ± 0.31 b	11.24 ± 1.47 b	1.74 ± 0.24 b
2 Si t ha^{-1}+ *T. asperellum* pool[a]	8.91 ± 2.19 b	3.15 ± 0.66 b	12.06 ± 2. 85 b	1.88 ± 0. 54 b
2 Si t ha^{-1} + PGPM mixture[b]	8.25 ± 0.54 b	2.88 ± 0.20 b	11.14 ± 0.74 b	1.82 ± 0.61 b

Different letters in the column denote significant differences between treatments (Duncan's test, $p \leq 0.05$)

[a] *Trichoderma asperellum* pool (UFRA.T06 × 10^{8} ; UFRA.T09 × 10^{8} ; UFRA.T12 × 10^{8} ; UFRA.T52 × 10^{8} con mL^{-1})

[b] PGPM mixture (BRM 32111 × 10^{8} UFC plus BRM 32113 × 10^{8} UFC plus *T. asperellum* pool)

xylem vessels (Yoshida et al. 1962; Gharineh and Karmollachaab 2013), and stomatal closure due to a higher concentration of ABA in PGPM-treated plants (Contreras-Cornejo et al. 2014).

WUE increased in the upland rice seedlings treated with Si and PGPM, which are results similar to those obtained by Mishra and Salokhe (2011). The increase in WUE in upland rice plants is an invaluable gain, since the cultivation of upland rice occurs under total dependence on rainfall and during the summer, which is very common in the Brazilian Cerrado region. Concomitant to the phytomass increase and photosynthetic rate in upland rice seedlings, there was a significant increase in the chloroplastidic pigments content (Table 3) and total soluble sugars (Fig. 4). For the chloroplastidic pigments, it is suggested that the PGPM may be involved with mechanisms associated with the preservation of the photochemical machinery of photosynthesis, since the role of photosynthetic pigments is to capture and transfer energy during the photochemical phase of photosynthesis (Nelson and Yocum 2006). Kang et al. (2012), Lucas et al. (2014), and Shukla et al. (2015) obtained similar results with tomato, rice, and wheat plants, respectively, treated with bioagents. For the total soluble sugars, it is suggested that the increase in the photosynthetic rate triggered by Si and PGPM provided the increase in photoassimilates as well as their translocation (Dallagnol et al. 2013).

To verify whether the treatments Si and PGPM alter the hormonal status of rice plants during the "priming stage," the levels of AS and AJ were quantified. These two

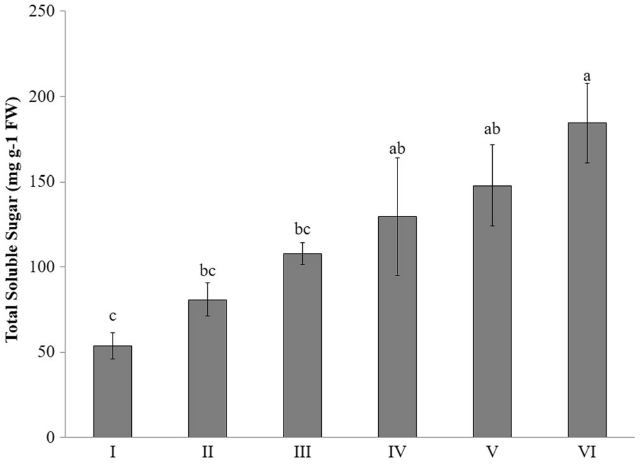

Fig. 4 Treatments: I, control; II, *Trichoderma asperellum* pool; III, PGPM mixture; IV, 2 Si t ha^{-1}; V, 2 Si t ha^{-1} + *Trichoderma asperellum* pool; VI, 2 Si t ha^{-1} + PGPM mixture. Total soluble sugar in determined on leaves of upland rice seedlings from cultivar BRS Primavera CL in response to Si (2 t ha^{-1}), *Trichoderma asperellum* pool (UFRA.T06 × 10^{8}; UFRA.T09 × 10^{8}; UFRA.T12 × 10^{8}; UFRA.T52 × 10^{8} con mL^{-1}) and PGPM mixture (BRM 32111 × 10^{8} UFC plus BRM 32113 × 10^{8} UFC plus *Trichoderma asperellum* pool). Different letters in the bars represent significant difference ($p \leq 0.05$) Coefficient of variation = 14.97%

Table 4 Changes in the hormonal profile of salicylic acid and jasmonic acid in upland rice seedlings from cultivar BRS Primavera CL in response to 2 Si t ha^{-1}, *Trichoderma asperellum* pool and PGPM mixture

Treatment	Acid salicylic	Jasmonic acid
Control	590.78 ± 81.55 b	4.55 ± 0.343 b
T. asperellum pool[a]	794.00 ± 118.87 a	5.81 ± 0.225 a
PGPM mixture[b]	686.09 ± 33.74 ab	ND
2 Si t ha^{-1}	811.85 ± 129.59 a	4.73 ± 0.121 b
2 Si t ha^{-1} + *T. asperellum* pool	575.75 ± 30.79 b	ND
2 Si t ha^{-1} + PGPM mixture	708.54 ± 41.75 ab	4.44 ± 0.347 b

Different letters in the column denote significant differences between treatments (Duncan's test, $p \leq 0.05$)

ND not detectable

[a] *Trichoderma asperellum* pool (UFRA.T06 × 10^{8} ; UFRA.T09 × 10^{8} ; UFRA.T12 × 10^{8} ; UFRA.T52 × 10^{8} con mL^{-1})

[b] PGPM mixture (BRM 32111 × 10^{8} UFC plus BRM 32113 × 10^{8} UFC plus *T. asperellum* pool)

hormones play important roles in plant defense against phytopathogens, as has been reported for other crops (Móran-diez et al. 2012; Martinez-Medina et al. 2013). The increase in salicylic acid content (AS) was confirmed in upland rice seedlings treated with 2 Si t ha^{-1} and *T. asperellum* pool alone, while the increase in jasmonic acid content (AJ) occurred only in the upland rice seedlings treated with *T. asperellum* pool (Table 4). The priming defense is related to the increase of AS and AJ contents in the plant, due to stimuli coming from the soil, such as the interaction with PGPM. When the plant is in the priming state, the initial stimulation is stored and potentiated by increasing the contents of these hormones, which initiate a signaling cascade when the plant is challenged by an agent (Martinez-Medina et al. 2016). Studies conducted by Móran-diez et al. (2012) and Martinez-Medina et al. (2013) showed that melon plants treated with *Trichoderma asperellum* synthesized levels of SA and JA in greater quantities and, consequently, obtained greater growth and resistance to diseases. The fungus *T. asperellum* causes a wide range of responses in plants, resulting in an increase in defense capacity in both root and shoot (Móran-Diez et al. 2012; Martinez-Medina et al. 2013). In summary, growth promoting in the early development stage of upland rice plants resulted in a greater seedling vigor, allowing competition with weeds and other limitations to be attenuated. In addition, increased biomass may result in a higher number of tillers and more panicles, key components of rice grain production (Li et al. 2007; Fageria 2007; Poletto et al. 2011).

Conclusion

Si fertilization (2 t ha^{-1}) and PGPM presence increased vigor and resistance to pathogens in upland rice seedlings.

Si fertilization (2 t ha^{-1}) mainly increased A, WUE, and total soluble sugar content.

The PGPM acted mainly by increasing A, WUE, chloroplastidic pigment content, and hormones related to plant disease responses.

Si and PGPM can be used as viable alternatives in the management of rice cultivation to make it more sustainable.

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