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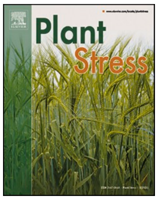

Silicon and bioagents pretreatments synergistically improve upland rice performance during water stress

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ABSTRACT

Rice (*Oryza sativa* L.) is one of the most important food crops worldwide. Upland rice growing areas are susceptible to adverse conditions and drought represents the main limiting factor for its production and yield stability. Soil management strategies (e.g., chemical and biological treatments) are often implemented to mitigate drought and improve crop production. However, morpho-physiological responses of upland rice to drought under such management strategies remains poorly understood. Here, we studied the effect of silicon and bioagents pretreatments under water stress on an upland rice landrace, *Samambaia Branco*. Our results unraveled that these pretreatments improved robustness of the root system in water stressed plants with increase in 40.9% of surface area, 11.5% on diameter, 53.8% on volume and 30.8% of length density when measured at 45 cm soil depth. Furthermore, these treatments increased number of thick roots by more than 14.0 and 45.0% at 25 and 45 cm soil depths, respectively; and fine root by more than 25.0% at 45 cm soil depth. Consequently, pretreated water stressed plants exhibited greater yield stability (reduction of 14.6% in grain yield compared to pretreated well-watered plants), root/shoot ratio (26.8%), photosynthesis (50.0%), stomatal conductance (14.4%), leaf water potential (61.0%) and water use efficiency (49.1%) than untreated water stressed plants. Thus, we conclude that silicon and bioagent pretreatments significantly improve root and shoot performance under water stress. Our results provide a first step towards understanding the relevance of these pretreatments in upland rice for improving adaptive root system as a response to suboptimal environmental conditions.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major cereal crops and it is considered as the staple food for more than half of the world's population (Gross and Zhao, 2014). Rice has been predominantly cultivated in flooded fields rather than in rainfed conditions. However, in the 21st century, more attention is being paid to the use of water-saving rice, i.e., research efforts focus on upland rice to cope with the increasing worldwide water shortage that will become more severe and ubiquitous under global climate change (Kato and Katsura, 2014; Liu et al., 2019).

Drought is one of the most severe abiotic stresses limiting rice yield worldwide and it poses a serious threat to rice sustainability in rainfed agriculture (Wu and Cheng, 2014). It occurs mostly due to the variation in quantity and distribution of rainfall during the rainy season and it may impact rice plants according to its timing, duration and intensity. In Brazil, upland rice cropped area has decreased by 70% in the last two decades partly due to high drought risk (Heinamann et al., 2019). At vegetative stage of upland rice, drought can affect development rate, plant height, leaf area and tillering; while, at reproductive stage, it mainly affects panicle branching, spikelet formation and pollen viability, and after flowering, it can affect grain setting and filling and their resulting grain number and mass (Lima et al., 2021). Choice of tolerant varieties, optimum sowing time, proper seed treatment and time of nitrogen and potassium application are some of the options to mitigate the adverse effect of drought stress in upland rice (Ray et al., 2016).

For upland rice, majority of the research efforts are focused on above ground physiology to make it stress resilient. However, roots play a

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critical role in plant growth and exhibit various adapted responses specific to the prevailing soil moisture stress conditions (Yamauchi et al., 1996). For instance, one of the adaptive responses of plants to drought conditions is the development of deep and extensive root systems (Fukai and Cooper, 1995; Serraj et al., 2004; Guimarães et al., 2020), which include thicker roots (Price et al., 2000), increased root length density (Siopongco et al., 2005) and rooting depth and distribution (Asch et al., 2005) as a result of the plasticity in lateral root development (Azhiri-Sigari et al., 2000; Bañoc et al., 2000; Kamoshita et al., 2000). These adaptations are perceived to be associated with increased water extraction (Kamoshita et al., 2000, 2004; Siopongco et al., 2005, 2006; Kato et al., 2007), increased nutrient uptake, escape from root diseases and being competitive to weeds (Richards, 2008). Rice roots are also known to produce signals in response to progressive drought, which regulates leaf stomatal conductance, transpiration and shoot growth (Siopongco et al., 2008; Burridge et al., 2022).

The application of bioagents, specifically plant growth-promoting rhizobacteria (PGPR), which produces phytohormones, volatile organic compounds, and secondary metabolites, play important role in influencing the root architecture and growth, improving the resource use efficiency of the root system and other rhizosphere effects (Grover et al., 2021). Other alternative technology is the supplementation with Silicon (Si), generally regarded as a beneficial element for plant growth, particularly for *Poaceae* crops such as rice (Garg et al., 2020). Due to continuous mono-cropping or intensive cultivation of cereal crops like rice, the soil Si concentration is depleted which can be one of the reasons for the declining rice yields. Rice is capable of absorbing and accumulating Si metabolically while many other upland crop plants appear to lack such capability. Besides rice yield increase, Si has other advantages including the increase in nutrient availability (N, P, K, Ca, Mg, S, Zn) and resistance to lodging, promoting the maintenance of the erect leaf, which allows better use of light through the rice canopy with positive responses in photosynthesis. Furthermore, this element decrease the nutrient toxicity (Fe, Mn, P, Al) and minimize the biotic and abiotic stress in plants by positively influencing the development of system root (Tamai and Ma, 2008; Garg et al., 2020; Verma et al., 2020). Beneficial effects of combined Si and bioagents in promoting growth and improve disease resistance in upland rice plants are reported in Cortês et al. (2015); Sperandio et al. (2017); Sousa et al. (2018); Souza et al. (2021). However, little attention has been paid to the responses of upland rice treated with bioagents and Si to combined abiotic stresses occurring frequently as drought, high temperature and high radiation.

We hypothesize that silicon and bioagents pretreatments synergistically holds great potential for stabilizing the upland rice grain yield under suboptimal environmental conditions mainly due to increased root system. Therefore, understanding the architecture and morphological plasticity of roots, concurrently with the shoot responses, will be of paramount importance to understand the potential of optimizing root system for improving abiotic stress tolerance of upland rice.

2. Material and methods

2.1. Plant material

A Brazilian upland rice landrace variety named *Samambaia Branco* was used for all experiments in this study. It is an accession of Embrapa's GAB (Germoplasm Active Bank) and its geographical origin is Mantenópolis, Espírito Santo state, Brazil. Its phenotypic characteristics are as follows: plant cycle of 120–140 days, intermediate grain quality and moderate cooking quality (Embrapa Alelo System, 2023). This genotype was specifically chosen due to its sensitivity to water deficit (A.P. de Castro, personal communication, June 04, 2019) so the Si and bioagents pretreatments applied would show any visible effects.

2.2. Experimental design and treatments

We conducted two trials in this study: (1) preliminary trial in 2019–20 to choose bioagents from different plant growth-promoting rhizobacteria isolates to act in combination with *Serratia* sp. (*BRM 32114*), which was previously characterized as a multifunctional and beneficial microorganism for upland rice (Nascente et al., 2017; Sperandio et al., 2017, 2019). This trial included following bioagent treatments: no-microorganism (control), *Burkholderia cepacea* (*BRM32111*), *Bacillus thuringienses* (*BRM32110*) and *Serratia marcenses* (*BRM63523*), and (2) main trial in 2020–21 included following bioagent consortium treatments: no-microorganism (control), *Bacillus thuringienses* (*BRM32110*) + *Serratia* sp. (*BRM32114*) and *S. marcenses* (*BRM63523* + *Serratia* sp. (*BRM32114*). The combination of different bioagents allows the plant to benefit from the sum of the effects of each isolate, and also from the synergism between them. Thus, currently, investigations involving growth promotion, productivity enhancement and stress mitigation focus on maximizing the contribution of each microorganism to the best plant performance. Both trials included randomized block design with a triple factorial scheme with four replicates for each water treatment: well-watered, *WW*, as control and water stressed, *WS*. All above treatments, in both years 2019 and 2020, were performed in presence, (*+Si*, 2000 kg ha^{-1}) and absence of Si (*-Si*, 0 kg ha^{-1}, as control), a combinatorial application of Si and bioagents treatments. For the sake of brevity, we present data from trial 2020–21 in the main text and from trial 2019/2020 in the supplementary text.

2.3. Experimental conditions

The experiments were carried out under a greenhouse condition at the Integrated System for Drought-Induced Treatment (Portuguese acronym SITIS) plant phenotyping platform facility (Supplementary Fig. 1), from October 2019 to May 2020, and from November 2020 to Jun 2021. The SITIS is located at Embrapa Rice and Beans, Santo Antônio de Goiás, Goiás, Brazil (16°28′00″ S, 49°17′00″ W, with an altitude of 823 m). All treatments were performed in soil columns of diameter 25 cm and height 100 cm, placed over digital scales to monitor the water amount in each column. The chemical characteristics of the Oxisol soil were determined according to Donagema et al. (2011) and are shown in Supplementary Table 1. The soil was sieved using 125 mm mesh to remove any larger aggregates and was fertilized according to Silva et al. (2021). A commercial (Agrosilício®) calcium and magnesium silicate ($CaSiO_3.MgSiO_3$) containing 10.5% Si, 27% Ca and 6% Mg was applied as a source of Si. Two-ton ha^{-1} of $CaSiO_3.MgSiO_3$ was incorporated in the soil thirty days before the sowing as described in Souza et al. (2021). The hydric treatments consisted of two water levels: well-watered (*WW*, control) and water stressed (*WS,* stress), being that in the first (*WW*) the amount of soil water was initially established to 80–85% of field capacity (FC) and kept throughout the crop cycle. For the *WS* treatment, irrigation was performed as in the control treatment until the plants reached the reproductive stage (R2 – collar formation on flag leaf/R3 – panicle exsertion), followed by the suspension of irrigation for four days. After this period, 50% of the volume of evapotranspired water of *WW* columns was replaced at the plate of the respective *WS* columns, for six days in 2019/2020 and four days in 2020/2021.

The amount of evapotranspirated water was estimated based on the water quantity required to keep soil at FC 80 – 85% in the control treatment. After the water stress period, irrigation was restored until the end of the crop cycle R8 (at least one grain on the main stem panicle with a brown hull)/R9 (all grains that reached R6 have brown hulls). In the control columns, the evapotranspiration rate was determined daily (difference between the reference mass and the column/day mass) and restored through irrigation placed on the soil surface to achieve the initial mass (reference mass) again. Each column contained four plants. The quantity of the evapotranspirated water and the average daily transpiration rate, during the water stress, in all columns and meteorological conditions of the SITIS phenotyping platform (monitored by a datalogger Hobo® U12–12, Onset Computer Corp. Ltd, Cape. Cod, MA, USA), in 2019/2020 and 2020/2021, are shown in the Supplementary Table 2.

2.4. Bioagent inoculation

Bioagents, as cell suspensions, were applied three times during the rice cycle: 1. Seed microbiolization; 2. Spray pulverization in the soil at 30 days after sowing (DAS); 3. Spray pulverization at rice shoots, 95 - 98 DAS (Nascente et al., 2017, 2019; Araújo et al., 2021, with modifications). In 2020, the consortia of bioagents *Bacillus thuringienses* + *Serratia* sp. (*BRM32110*+*BRM32114*) and *S. marcenses* + *Serratia* sp. (*BRM63523*+*BRM32114*) were used in seed microbiolization and soil pulverization; while only *Bacillus thurigienses* isolate (*BRM32110*) and *S. marcenses* isolate (*BRM63523*) were used in rice shoots pulverization. Bioagents were selected from upland rice fields and are currently stored and preserved in the Multifunction Microorganisms and Fungi Collection of Embrapa Rice and Beans. Their biochemical characteristics and taxonomic classification are available in Martins et al. (2020) and Faria (2021). The suspensions of bioagents were prepared in liquid medium 523 (nutrient broth) (Kado and Heskett, 1970), in a shaking incubator, for 24 h at 28 °C. The suspension concentration of each bioagent was adjusted in a spectrophotometer to A540 = 0.5, which corresponds to 1×10^8 colony-forming units (CFU) per mL. Before microbiolization, seeds were disinfected with immersion in 70% alcohol for one minute and 0.05% sodium hypochlorite for the same period, followed by drying at room temperature. Microbiolization was carried with the immersion of the seeds in the suspension of each bioagent and the control treatment, by immersing the seeds in distilled water, for 24 h at a temperature of 25 °C, under constant agitation (Sperandio et al., 2017; Martins et al., 2020). At 30 DAS, 100 mL suspension (10^8 CFU) of each bioagent or distilled water (control) was applied in the soil. At 95 - 98 DAS, 100 mL of bioagent suspension (10^8 CFU) or with distilled water (control) was applied directly to the rice shoot. The equipment used for the application of the bioagents was a manual sprayer, pressured with CO_2, using a conical type nozzle (TXVS2).

2.5. Agronomic and morphophysiological measurements

2.5.1. Morphological root traits

Root system in each column was evaluated according to Lanna et al. (2016). Briefly, acrylic tubes were installed inside the columns to take pictures and four rice plants were planted around the tube. Root images were taken at a depth of 5 to 25 cm (depth 1) and 25 to 45 cm (depth 2) at the end of the drought period. Root traits were assessed by measuring root length (*RL*; cm), root surface area (*RSA*; cm^2), root volume (*RV*; cm^3) and root diameter (*RD*; mm). Furthermore, we divided roots into two diameter classes: fine roots with a diameter ≤ 0.5 mm; and thick roots with $1.0 \text{ mm} \leq \text{diameter} \leq 2.5$ mm (Guimarães et al., 2020). Length, surface area and volume were calculated for each root type (fine and thick roots): fine root length (*FRL*; cm); thick root length (*TRL*; cm); fine root surface area (*FRSA*, cm^2); thick root surface area (*TRSA*, cm^2); fine root volume (*FRV*, cm^3) and thick root volume (*TRV*; cm^3). Thick roots were considered primary roots and fine roots as secondary or tertiary roots, which made possible to analyze the capacity of soil exploration vertically as well as laterally, respectively. Images were taken with a CI – 600 Cano Scan scanner (CID Bio - Science, Version 3.1.19), followed by automatic image processing with the WinRhizo software (Regent Instruments Inc, Version 2016). Root length density (*RLD*, cm^{-3}) was calculated as the ratio between *RL* and *RV* (Dusserre et al., 2012). Total root volume (TOT_{vol}) was calculated by adding root volume in each analyzed layer and was considered as a proxy of total root biomass (Guimarães et al., 2020).

2.5.2. Morphophysiological shoot traits

The gas exchange parameters were measured on the flag leaf. The net CO_2 assimilation (*A*, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}), intercellular CO_2 concentration (*Ci*), transpiration rate (*E*, mmol H_2O m^{-2} s^{-1}) and intrinsic water use efficiency (*WUE*, μmol CO_2 mol^{-1} H_2O) were measured between 08:00 and 10:00 a.m., on the last day of the water stress period using a portable gas exchange analyzer in the infrared region (LCpro+, ADC® Bioscientific, Hoddesdon, England) at an external CO_2 concentration of 400 μmol mol^{-1} of air and PAR of 1200 of photons m^{-2} s^{-1}. *WUE* was calculated as the ratio between *A* and *gs* (Rosales et al., 2012). Root/Shoot ratio (*R:S*) was calculated as TOT_{vol} divided by *SDMB*. Leaf water potential (*LWP*, MPa) was evaluated between 05:00 and 06:00 a.m. using a Scholander pressure chamber (Soilmoisture Equipment, model 3005) (Scholander et al., 1965). The reading was determined at the extremity (tip) of two flag leaves of the primary tiller of two upland rice plants at the end of the water stress period. Pressure was applied until exudation from the cut made in the leaf collar.

2.5.3. Agronomic traits

Shoot dry matter biomass (*SDM*B, g $plant^{-1}$) was achieved through drying samples at 65 °C until a constant mass was achieved; grain yield (*GY*, g of grain $plant^{-1}$, which means the total mass of grains, in grams, was obtained for one plant per column) and its components, such as 100-grain mass (*100GM*, g) and spikelet sterility (*SS*,%), estimated as $SS = (NEG \times 100)\ TG^{-1}$, where SS = spikelet sterility, NEG = number of empty grains, and TG = total number of grains, were determined on the harvest period.

Descriptions and abbreviations of the 32 traits (23 root traits and 9 shoot traits) are presented in Supplementary Table 3.

2.6. Statistical analyses

The data was subjected to an analysis of variance (three-way ANOVA with all main factors evaluated as fixed factors). All data obtained was analyzed to normality by the Shapiro-Wilk test. Comparison of means was done by Tukey's test at 5% significance level. Bar plots represent means ± the standard deviations. All the statistical analyses were performed using the R software version 3.6.0 (R Core Team, 2019) with the package "ExpDes.pt" (Ferreira et al., 2018).

3. Results

3.1. Preliminary trial identifies isolates other than BRM32114 to improve plant performance in Samambaia Branco cultivated with silicon

In our preliminary trial in 2019–20, the analysis of the root system of *Samambaia Branco* showed a significant difference ($p \leq 0.05$) for most variation sources (Supplementary Table 4). Furthermore, the environmental conditions of phenotyping platform SITIS were moderate to severe (Supplementary Table 2) in which the water deficit index was equal to 0.52 for the trial +Si, and 0.56 for the trials -Si, the maximum temperature was 32.8 °C and minimum relative humidity was 58%.

The *WS* plants pre-treated with Si and inoculated with *BRM32111, BRM32110* and *BRM63523* isolates showed *RSA* (22.0, 22.4 and 38.0%, respectively) and *RLD* (15.9, 22.5 and 55.0%, respectively) higher than non-inoculated plants. In addition, *WS* plants fertilized with only Si, at 25 and 45 cm layers, showed *RSA* (22.0 and 31.0%, respectively) and *RLD* (37.0 and 32.0%, respectively) superior to the non-fertilized plants. In relation to the shoot traits, under *WS* condition, plants showed lower agronomic performance (*GY*), regardless of the bioagents inoculation and Si fertilization, with equivalent to reduction of 25.8% (Supplementary Table 5). For *A*, the reduction was more accentuated in stressed/non-inoculated plants (51.6%) than in stressed/inoculated plants (19.8%). For *gs*, the reduction was also more accentuated in stressed/non-inoculated plants (61.5%) than in stressed/inoculated plants (23.5%). For *LWP*, the reduction was greater in stressed/non-inoculated plants (34.2%) than in stressed/inoculated plants (15.8%). In relation to *WUE*, in general, stressed plants exhibited values greater than that found in *WW* plants, regardless of the inoculation and Si fertilization. Overall, the plants pre-treated with Si and the bioagents *BRM32110* and *BRM63523* showed better results for a greater number of variables evaluated in the 2019–20 crop.

3.2. *Pretreatments: bioagents consortium and silicon improve root architecture and morphological plasticity during water stress*

Root system of *Samambaia Branco* showed a significant difference ($p \leq 0.05$) for most variation sources. Treatments of Si and bioagents consortium displayed large variations in the evaluated root traits across different layers and under two water conditions (Supplementary Table 4). For instance, the results revealed that no significant differences in root traits between inoculated *WW* plants and non-inoculated *WW* plants were found under non-stress conditions regardless of the bioagents treatment. However, *WW* plants +Si showed root system more robustness than *WW* plants -Si. The Fig. 1 shows representative images of the root *Samambaia Branco* plants under *WW* and *WS* condition. Among treatments, Si + *BRM63523*+*BRM32114* contributed to greater robustness of the root system, mainly at 45 cm.

WS plants pre-treated with Si + *BRM63523*+*BRM32114* significantly improved *RLD* (11.9%) at 25 cm; and *RSA* (40.9%), *RD* (11.5%), *RLD* (30.8%) and *RV* (53.8%) at 45 cm. Furthermore, Si +

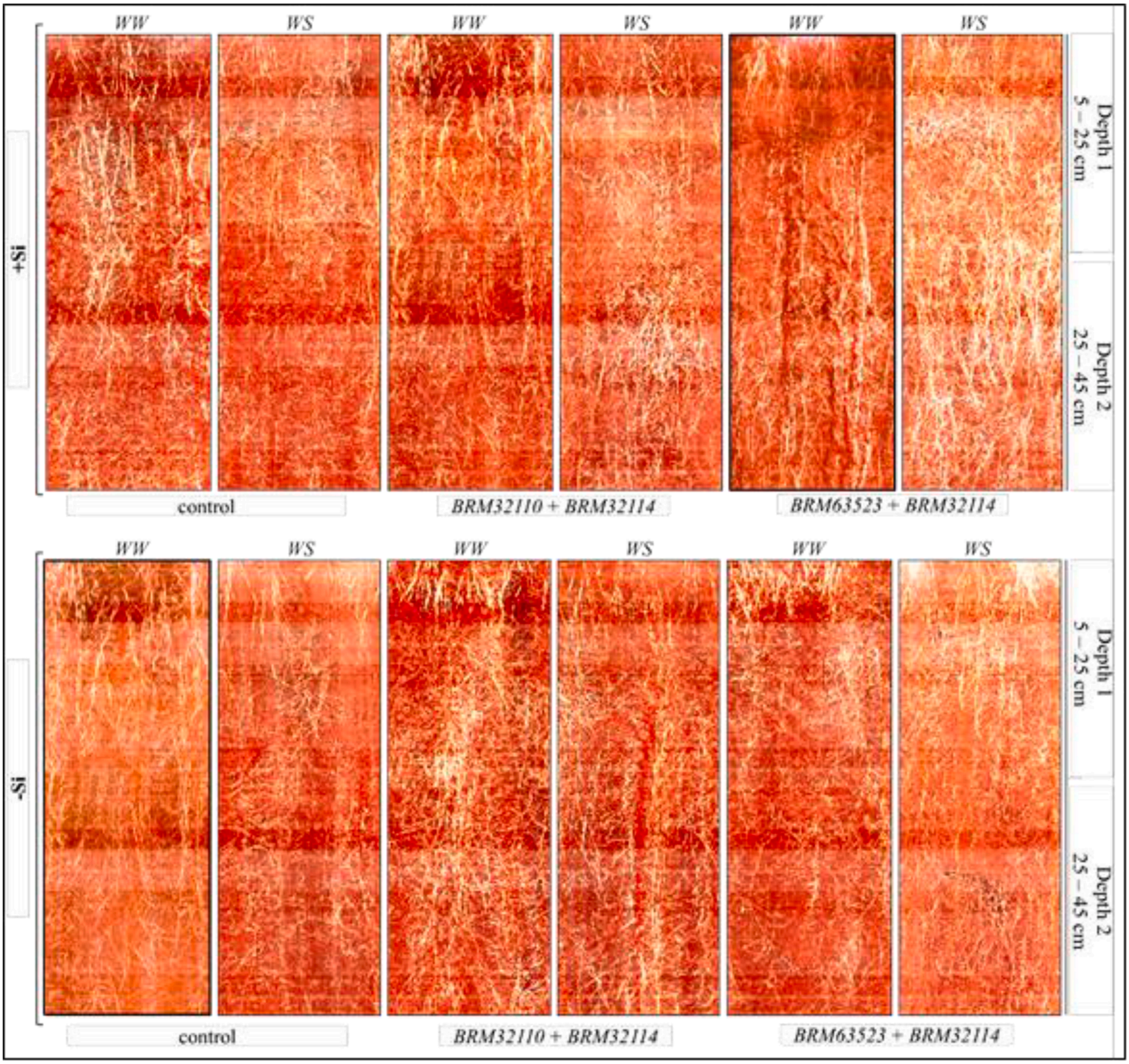

Fig. 1. Root system images of the *Samambaia Branco* plants at depth 1 (5 to 25 cm) and depth 2 (25 to 45 cm) of the soil at the water stress period end. The plants were submitted a combinatorial application of Si (+*Si*, 2000 kg ha^{-1} and -*Si*, 0 kg ha^{-1}) and bioagents (control, no microorganism; *Bacillus thuringienses* (*BRM 32110)* + *Serratia* sp (*BRM 32114)*; and *Serratia marcenses* (*BRM 63523)* + *Serratia* sp (*BRM 32114)*, under two hydric treatments: well-watered (*WW*) and water stressed (*WS*).

BRM63523+BRM32114 significantly improved *RL* (14.6 and 45.2%), *RSA* (19.9 and 46.6%) and *RV* (25.6 and 53.7%) of thick roots (1.0 mm ≤ diameter ≤ 2.5 mm) at 25 and 45 cm, respectively; and *RL* (26.0%) and *RSA* (25.9%) of fine roots (diameter ≤ 0.5 mm) at 45 cm of *WS* plants (Fig. 2).

3.3. Pretreatments: bioagents consortium and silicon improve shoot performance of Samambaia Branco during water stress

The effects of water treatments, Si fertilization and bioagents inoculation on shoot physiological traits of *Samambaia Branco* were assessed by *A, gs, WUE* and *LWP* (Fig. 3).

As expected, water stress significantly affected the gas exchange and water status of *Samambaia Branco plants*. For *A* (net CO_2 assimilation), inoculated plants showed 18.5% reduction under *WS* compared to *WW* condition. However, the *A* reduction was more accentuated in stressed/non-inoculated plants (29.9%). For *gs* (number and activity of stomata), *WS* plants, inoculated with both consortia *BRM32110+BRM32114* and *BRM63523+BRM32114*, showed average value equal to 0.11 mol H_2O m^{-2} s^{-1}, a reduction of 4% compared to *WW* plants. For the stressed/non-inoculated plants, *gs* value was 0.08 mol H_2O m^{-2} s^{-1}, a reduction of 44.4% compared to *WW* plants, regardless of Si fertilization. For *LWP*, the reduction was greater in stressed/non-inoculated plants (232.6%) than in stressed/inoculated plants (141.9%) compared to the corresponding *WW* plants.

In general, *WS* plants exhibited *WUE* values greater than that found in *WW* plants, regardless of the inoculation and Si fertilization. Interestingly, *WUE* of the *WS* plants inoculated with *BRM63523+BRM32114* and fertilized with Si (49.1%) was higher than plants inoculated with *BRM63523+BRM32114* without Si fertilization (14.4%) compared to their respective *WW* plants.

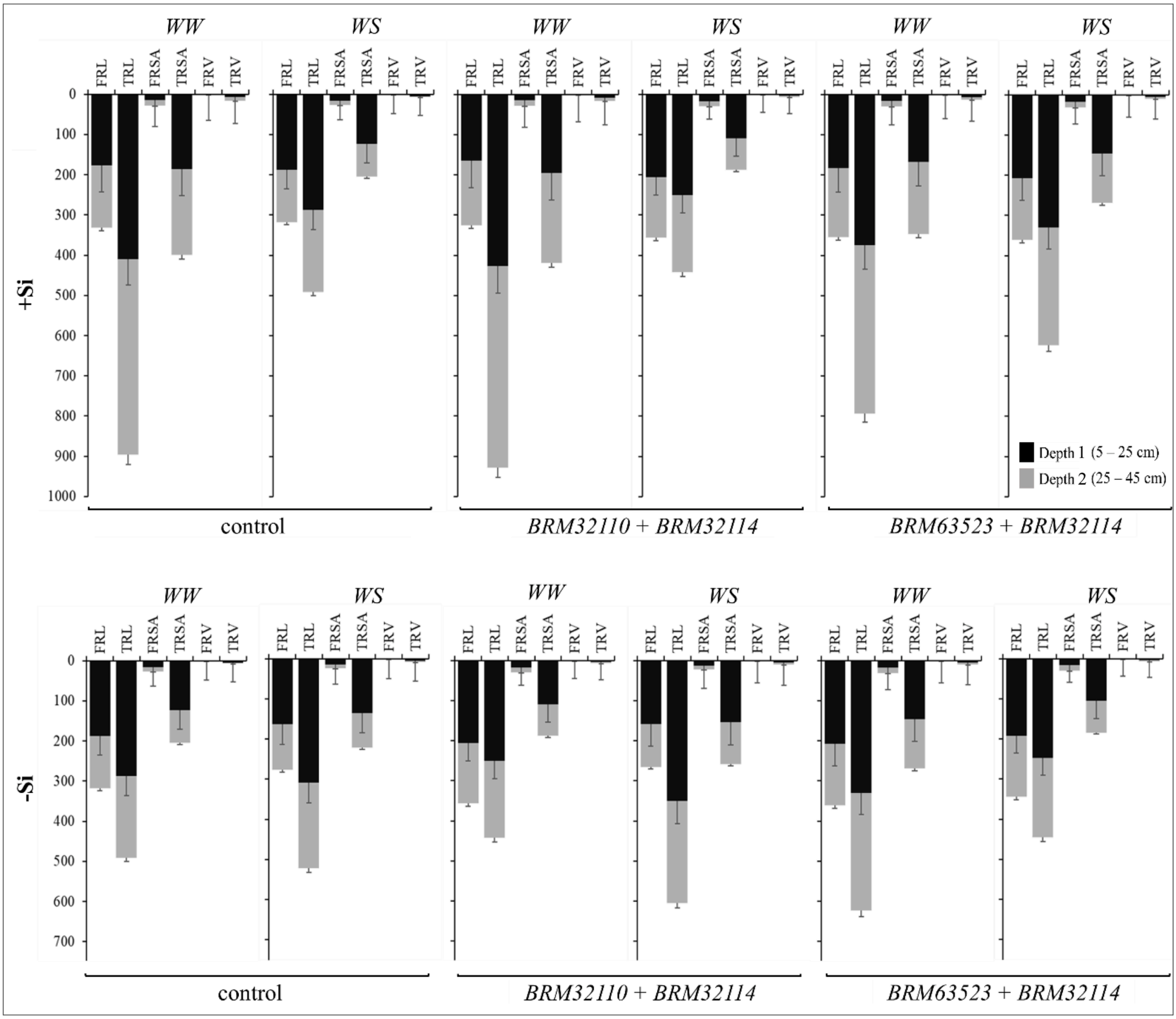

Fig. 2. Root performance of the *Samambaia Branco* plants pre-treated with silicon (Si) and bioagens under *WW* and *WS* ($n = 4$). Roots were divided into two diameter classes: fine roots (diameter ≤ 0.5 mm) and thick roots (1.0 mm ≤ diameter ≤ 2.5 mm) at depth 1 (5 – 25 cm) and depth 2 (25 – 45 cm). Fine root length – FRL (cm $plant^{-1}$), thick root length – TRL (cm $plant^{-1}$), fine root surface area – FRSA (cm^2 $plant^{-1}$), thick root surface area – TRSA (cm^2 $plant^{-1}$), fine root volume – FRV (cm^3 $plant^{-1}$) and thick root volume – TRV (cm^3 $plant^{-1}$). Vertical bars denote mean ± SE.

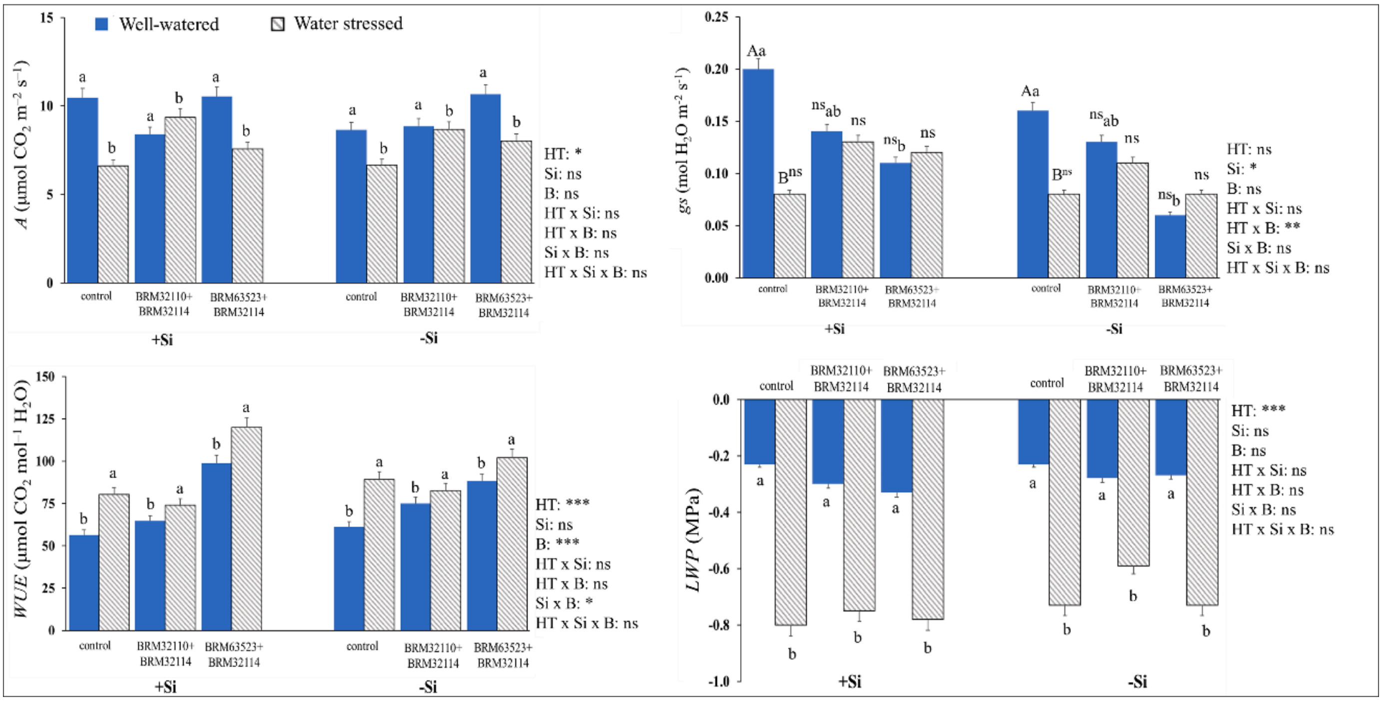

Fig. 3. Shoot performance of the *Samambaia Branco* pre-treated with silicon (Si) and bioagents under *WW* and *WS* ($n = 4$). A = net CO$_2$ assimilation, gs = stomatal conductance, *WUE* = intrinsic water use efficiency, and *LWP* = leaf water potential. Vertical bars denote mean ± SE. *, **, and ***, indicate significance levels at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. ns, indicates non-significant. HT = Hydric Treatments, Si = Silicon and B = Bioagent. The means following same letters has no significant difference at $p \leq 0.05$ (Tukey's test). For gs, wherein double interaction was detected, the capital letters represent the difference between the HT, and the lowercase letters between the B.

3.4. *Pretreatments: bioagents consortium and silicon improve agronomic performance of Samambaia Branco during water stress*

The effects of water treatments, Si fertilization and bioagents consortium inoculation on *Samambaia Branco* plants grown at SITIS phenotyping platform were assessed by *GY* and its components: *100GM* and *SS*, and *R:S* (Fig. 4 and Supplementary Table 5).

In the *WW* condition, there was no *GY* difference among the treatments ($p < 0.05$) and the global mean was 16.91 g grain plant^{-1}. However, under *WS, Samambaia Branco* plants showed reduced agronomic performance (*GY*), regardless of the inoculation with bioagents consortium and fertilization with Si, with global mean was 14.11 g grain plant^{-1}, equivalent to a reduction of 16.6%. Nonetheless, *WS* plants, fertilized with Si and inoculated with *BRM63523+BRM32114* consortium, showed greater yield stability (reduction of 14.6% in grain yield compared to pretreated *WW* plants), while the *GY* of the control plants and plants fertilized with Si and inoculated with *BRM32110+BRM32114* consortium was 27% lower. In addition, these plants showed *GY* (33%) higher than plants without Si and inoculated with *BRM63523+BRM32114*.

For the yield components, the average value of *SS* (spikelet sterility) was 11.41 and 20.58% under *WW* and *WS* conditions, respectively. While the average value of *100GM* was 3.16 and 2.99 g under *WW* and *WS* conditions, respectively. In 2020/21, the water deficit index was equal to 0.62 for the trial with Si and 0.66 for the trials without Si, the maximum temperature was 35.7 °C and minimum relative humidity was 39% (Supplementary Table 2).

Regarding the root and shoot growth of *Samambaia Branco* plants, the *R:S* of the stressed plants, fertilized with Si and inoculated with both consortia *BRM32110+BRM32114* (68%) and *BRM63523+BRM32114* (27%) were superior to non-inoculated plants. Without Si, stressed plants inoculated with *BRM32110+BRM32114* presented *R:S* (12%) higher than non-inoculated plants.

4. Discussion

Roots play critical role in plant health, growth and survival through water and nutrients uptake (Zhu et al., 2011; Takehisa et al., 2012; Sozzani and Iyer-Pascuzzi, 2014; Bhosale et al., 2018; Giri et al., 2018). Root length, surface area and volume together determine the root system architecture (Smith and De Smet, 2012), which is the spatial arrangement of the root system that is crucial for optimal use of the available resources (Lynch, 1995; Koevoets et al., 2016). The architecture of the root system exhibits plasticity and responds to external environmental conditions such as soil moisture, temperature, pH, nutrients and microbial communities (Bao et al., 2014).

In this study, we particularly focused on understanding the combinatorial effect of Si and bioagents pretreatments on root system architecture of *Samambaia Branco* and their relevance in improving resilience and plant performance during water stress. We identified that pretreatments of combination of Si and bioagents have beneficial effects on root as well as shoot growth during water stress. Particularly, our consortium of *BRM63523+BRM32114* bioagents promoted biggest root growth pattern of the *Samambaia Branco* roots. *Samambaia Branco* plants fertilized with Si and inoculated with *BRM63523+BRM32114*, under *WS* condition, showed the ability to change its root system by increasing the surface area (40.9%), diameter (11.5%), volume (53.8%) and length density (30.8%), mainly at 45 cm depth (Supplementary Tables 4 and 5). Furthermore, stressed plants of *Samambaia Branco* inoculated with *BRM63523+BRM32114* and fertilized with Si showed higher *WUE* (49.1%) in relation to their respective control plants (Fig. 3). These results are consistent with the previous report (Etesami and Jeong 2018) suggesting that bioagents act synergistically with Si to reduce water stress in plants e.g., rice (Chen et al., 2011) and sorghum (Sonobe et al., 2010; Ahmed et al., 2014) and by expanding the root system and, consequently, increasing the capacity to obtain water and nutrients.

The architecture and morphological plasticity of the root system are considered as key traits driving the adaptive response of plants to water

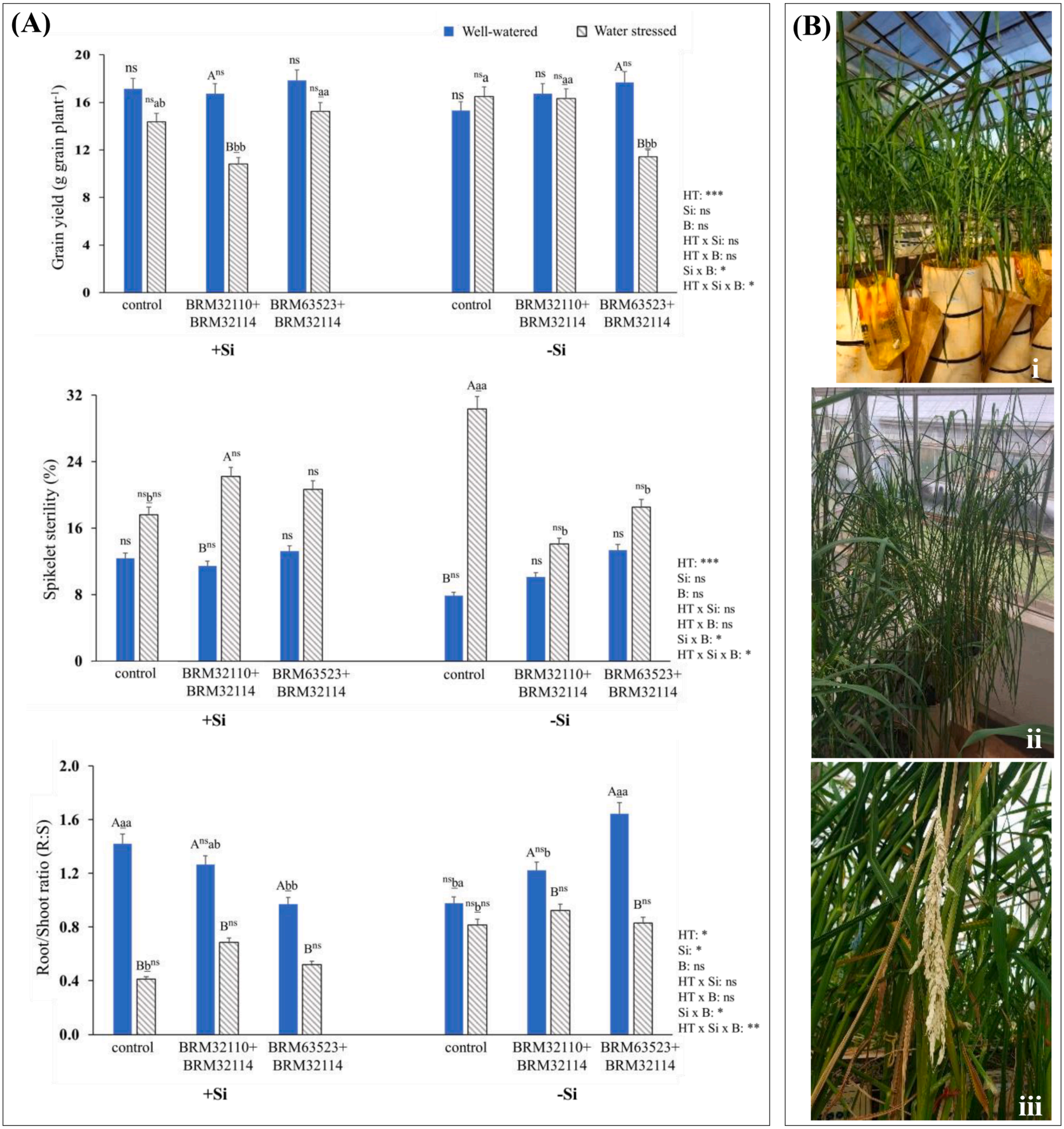

Fig. 4. Agronomic performance of the *Samambaia Branco* pre-treated with silicon (Si) and bioagents under *WW* and *WS* ($n = 4$). (A) Grain yield (*GY*, g grain plant^{-1}). (B) Spikelet sterility (*SS*,%). (C) Root/Shoot ratio (*R:S*). (D) i) *WW* plants, ii) *WS* plants, and iii) sterile panicle due to water restriction. Vertical bars denote mean ± SE. *, **, and ***, indicate significance levels at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. ns, indicates non-significant. HT = Hydric Treatments, Si = Silicon and B = Bioagent. The means following same letters has no significant difference at $p \leq 0.05$ (Tukey's test). The capital letters represent the difference between the HT, underlined lowercase letters between the Si, and the lowercase letters between the B.

stress (Henry, 2013; Brunner et al., 2015; Muthurajan et al., 2018; Bristiel et al., 2019; Chaichi et al., 2019). Thus, we characterized the root architecture of the *Samambaia Branco* plants under water stress in presence and absence of Si and bioagent pretreatments. We observed an increase of 20% of the thick roots at 25 cm depth combined to a higher density of thick roots (73.4%) and fine root (21.5%) at 45 cm depth (Fig. 2). Similar results were observed by Ambreetha et al. (2018), who found an increase the number of lateral roots, thickness, area and volume of rice root as compared to uninoculated plants. This finding is especially important as the fine roots are associated with water and nutrient uptake, in particular low-mobile nutrients such as phosphorus (Blouin et al., 2007; Henry et al., 2011; Comas et al., 2013; Gu et al., 2017) and thicker roots are associated with deep volume exploration and greater soil penetration ability, mainly through hardpans under drought (Yu et al., 1995; Clark et al., 2008; Bengough et al., 2011; Lynch, 2014; Guimarães et al., 2020).

Overall, our results suggest that *Samambaia Branco* plants fertilized with Si and inoculated with the *BRM63523+BRM32114* consortium, produced deeper root systems and thus had access to deep-stored water as the topsoil dried out. This may also be linked to reduced synthesis of ethylene, a hormone that impairs plant growth and yield (Salazar et al., 2015); although this component was not evaluated in our study. Under stress, plants produce high levels of 1-aminocyclopropane-1-carboxylate (ACC), an ethylene precursor, and certain bioagents act as a drain of ACC, promoting its hydrolysis to ammonia and α-ketobutyrate. Therefore, the *BRM63523+BRM32114* consortium may have contributed to the reduction of ethylene level in upland rice plants as such isolates exhibit high ACC deaminase activity (Faria, 2021). It has been known for a long time that the increased ethylene production in plants subjected the drought induces the photosynthesis reduction (Rajala and Peltonen-Sainio, 2001), the root growth inhibition, the shoot/leaf expansion reduction (Pierik et al., 2007) and the grain yield reduction by grain abortion (Wilkinson and Davies, 2002).

In general, under *WS* condition, the basic functional role of root plasticity is to efficiently capture the available moisture during progressive soil drying to maintain shoot function (Suralta et al., 2016). Therefore, it is essential to determine the influence of bioagents on plant physiology, particularly the ones with prominent performance under stress conditions (Ahemad and Kilbret, 2014). Our results showed that the use of Si in combination with *BRM63523+BRM32114* consortium promoted higher ratio *R:S* (26.8%) than control plants (Fig. 4). With the reduced shoot demand, assimilates are derived to root system, for growth and storage, which explains in turn the *R:S* increase (Lemoine et al., 2013; Xu et al., 2015; Zhang et al., 2016). The *R:S* of an individual plant is modulated by environmental factors and its plasticity has major implications for our understanding of the contribution of vegetation to the global carbon cycle and responses to climatic change (Poorter et al., 2012; Ledo et al., 2018).

The use of Si in combination with *BRM63523+BRM32114* consortium also promoted greater yield stability in stressed *Samambaia Branco* plants (reduction of 14.6% in GY compared to pretreated *WW* plants) and higher *A* (50.0%), *gs* (14.4%), *LWP* (61.0%) and *WUE* (49.1%) than non-pre-treated plants (Figs. 3 and 4). These results together show that the performance of the use of Si in combination with *BRM63523+BRM32114* is the best among the treatments evaluated in this study.

Verma et al. (2020) reported that the use of Si delays leaf abscission, increasing *WUE* and cell wall extensibility, synergistically prolonging water and nutrient absorption, thus optimizing drought mitigation. While the study of Nascente et al. (2017) showed that, the use of bioagents improve the upland rice physiological traits such as gas exchange, nutrient uptake and biomass production. Therefore, it is the strategy for enhancing and conserving soil water act to maintain leaf gas exchange and substantially contribute to biomass, the capacity for grain filling and ultimately, the grain yield (Xue et al., 2006; Lan-Ping et al., 2011).

In summary, upland soils are constantly aerated with moisture levels below saturation, thus management strategies improving the root system robustness (deep and thick roots coupled with the plasticity in branching) are essential for avoiding dehydration as a mechanism of tolerance in upland rice crop. It should be noted that studies similar to this one must be conducted in the field since abiotic and biotic conditions can be very different between the greenhouse and the field (Heinze et al., 2016; Schittko et al., 2016).

5. Conclusion

Si and bioagents, highlighting the consortium *BRM63523+BRM32114*, mediated the morphological plasticity of the root of *Samambaia Branco* plants under water stress by stimulating the increase in surface area, diameter, volume and length density. In addition to the number of fine and thick roots mainly at 45 cm soil depth. Upland rice plants with greater strength of the root system showed improved shoot performance such as photosynthesis, stomatal conductance, leaf water potential, water use efficiency and grain yield. Thus, such inputs can play an important role in upland rice sustainability and key root traits can be used as a crucial criterion in crop management practice.

Author contributions

ACL, APC, MCCF and RB conceived the study and supervised the project. ACL, MCCF and APC designed and performed the experiments. ACL, NBC, MGM, APC and R.B. wrote the manuscript. ACL, NBC, DRF and SMM assisted in performing the experiments. All authors read and approved the final manuscript.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2023.100142.

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