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Upland rice: phenotypic diversity for drought tolerance

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ABSTRACT: Upland rice is cultivated mostly in Latin America and Africa by small farmers and in areas with risk of dry spells. This study evaluated morphophysiological mechanisms of upland rice associated to drought adaptation. A set of 25 upland rice genotypes were grown in a plant phenotyping platform during 2015 and 2017 under regular irrigation and water restriction. We evaluated morphophysiological traits in shoots (vegetative structures growth, gas exchange, water use efficiency, carboxylation efficiency, water status) and roots (length, surface area, volume and diameter), as well as agronomic traits (grain yield and its components). There was a reduction in grain yield by up to 54 % and 58 % in 2015 and 2017, respectively, under water deficit. Five upland rice genotypes with the best yield performances in both water treatments applied were recommended to the upland rice-breeding program: Bico Ganga, BRS Esmeralda, BRSMG Curinga, Guarani, and Rabo de Burro. In this study, morphophysiological traits associated to drought tolerance concerned the plant high capacity to save water in the leaves, low leaf water potential, high ability to reduce vegetative structures, high water use efficiency, high photosynthetic capacity, and improved capacity to absorb water from drying soil, either by osmotic adjustment or additional investment into the root system. Therefore, we concluded that different secondary traits contributed to drought tolerance and should be evaluated along with grain yield to improve efficiency of breeding selection.

Keywords: grain yield, gas exchange, water status, root system, vegetative morphology

Introduction

Rice (*Oryza sativa* L.) is essential for food security for more than half of the world's population (Jumaa et al., 2019). Since rice has an evolutionary peculiarity of semi-aquatic, flooded rice paddies have become the major form of cultivation, growing in irrigated and rainfed lowland conditions, equivalent to 75 % and 19 % of the global production area, respectively (Kikuta et al., 2016). Increasing grain yield of irrigated areas is not enough to supply future demand for rice; furthermore, expansion of production areas is restricted, due to the water scarcity (Parthasarathi et al., 2012). Upland rice represents 4 % of the global rice production and is grown less than 9 % of total rice acreage in Asia, 46 % in Latin America, and 47 % in West Africa (Kikuta et al., 2016). According to Singh et al. (2014), upland rice accounts for 84 % of the total area in Sub-Saharan Africa and it is cultivated mostly by smallholder farms with an average area smaller than 0.5 ha. On the other hand, in Latin America, upland rice is cultivated in large-areas of mechanized harvesting (Bernier et al., 2008).

Drought is one of the most severe abiotic stresses limiting rice yield worldwide and poses a serious threat to rice sustainability in rainfed agriculture (Wu and Cheng, 2014). According to Heinemann et al. (2015), rice yield in upland cultivation (tropical regions mainly) has its yield potential reduced by up to 35 % due to drought-stress conditions.

Reduction in water availability for plants results in a complex response characterized by a decrease in the water potential of its tissues, leading to several changes in different plant processes (Rosales et al., 2012). Some processes reported for upland rice are (a) appropriate phenological patterns that combine crop growth and the amount of water available in the soil (water environment), (b) deep root system, (c) thick stems and reduced number of stomata, (d) osmotic adjustment to maintain cell homeostasis and, consequently, avoid a rapid decrease in leaf-water potential, and (e) senescence delay, also known as stay-green trait, which allows the maintenance of the photosynthetic capacity and the photoassimilate remobilization for a longer time period (Fukai and Cooper, 1995; Boonjung and Fukai, 1996).

Thus, the establishment of sustainable crop systems of upland rice requires better understand of changes in the morphophysiological mechanisms, contributing to drought tolerance and yield effects. This study aimed to (a) identify a series of morphophysiological and agronomic traits related to drought tolerance in upland rice genotypes of Embrapa Core Collection under greenhouse cultivation, and (b) characterize morphophysiological components to be used as indicators for drought tolerance for plant breeding processes.

Materials and Methods

Germplasm

We used 25 accessions of upland rice (*Oryza sativa* L.) with different responses to drought, obtained

through previous field experiments (Bueno et al., 2012). The accessions were represented by 16 landraces, six commercial cultivars from the Embrapa rice-breeding program and three international lines from France and Africa (Table 1). The genotypes were categorized in five phenological groups based on days for the beginning of the reproductive stage (R2 - collar formation on flag leaf/R3 - panicle exsertion) (Counce et al., 2000).

Table 1 – Information on 25 upland rice (*Oryza sativa* L.) genotypes, categorized into five phenological groups, in both years of trials, 2015 and 2017: genotype identification (ID), code, subspecies, R2/R3 and R8/R9 reproductive stages (DAE, days after emergence), germplasm type, origin, and water deficit period.

Year	Group	ID	Code	Sub specie	R2/R3	R8/R9	Germplasm type	Origin	Drought period
2015	I	Arroz Carolino	BGA013061	Tropical Japonica	51	91	Landrace	Brazil	31/03 - 14/04/2015
		Três Meses Branco	BGA011901	Tropical Japonica	51	91	Landrace	Pitangueiras/SP-Brazil	
		BRS Soberana	BGA008711	Tropical Japonica	51	91	Cultivar	Santo Antônio de Goias/GO-Brazil	
		Aimoré	BGA007119	Tropical Japonica	51	91	Landrace	Santo Antônio de Goias/GO-Brazil	
		CIRAD 392	IRGC121727	Tropical Japonica	51	91	Cultivar	França	
		Branquinho 90 Dias	BGA011897	Tropical Japonica	51	91	Landrace	Batatais/SP-Brazil	
		Tangará	BGA005180	Tropical Japonica	51	91	Landrace	Santo Antônio de Goias/GO-Brazil	
	II	IRAT 112	BGA006574	Tropical Japonica	53	94	Cultivar	França	02/04 - 16/04/2015
		Comum	BGA011951	Tropical Japonica	53	94	Landrace	Cajazeiras/PB-Brazil	
		Arroz 4 Meses	BGA013769	Tropical Japonica	53	94	Landrace	Itaguara/MG-Brazil	
		Casca Branca	BGA013771	Tropical Japonica	53	94	Landrace	Piracema/MG-Brazil	
		Rio Doce	BGA004168	Tropical Japonica	53	94	Landrace	Santo Antônio de Goias/GO-Brazil	
		Guarani	BGA004121	Tropical Japonica	53	94	Landrace	Santo Antônio de Goias/GO-Brazil	
		Carajás	BGA006701	Tropical Japonica	53	94	Landrace	Santo Antônio de Goias/GO-Brazil	
	III	BRS Primavera	BGA008070	Tropical Japonica	61	101	Cultivar	Santo Antônio de Goias/GO-Brazil	09/04 - 23/04/2015
		BRS Serra Dourada	BGA014150	Tropical Japonica	61	101	Cultivar	EMBRAPA-UFG-Brazil	
		Amarelão	BGA011242	Tropical Japonica	61	101	Landrace	Bonito/MS-Brazil	
		Bico Ganga	BGA013753	Tropical Japonica	61	101	Landrace	Pontalina/GO-Brazil	
	IV	BRSMG Curinga	BGA008812	Tropical Japonica	67	107	Cultivar	EMBRAPA-EPAMIG/Brazil	16/04 - 30/04/2015
		Agulhão	BGA013020	Tropical Japonica	67	107	Landrace	Caracaraí/RR-Brazil	
		BRS Esmeralda	BGA015465	Tropical Japonica	67	107	Cultivar	Santo Antônio de Goias/GO-Brazil	
	V	Douradão	BGA012711	Tropical Japonica	80	120	Cultivar	Rio Pomba/MG-Brazil	29/04 - 13/05/2015
		Saia Velha	BGA012954	Tropical Japonica	81	121	Landrace	Brejinho/MA-Brazil	
		Rabo de Burro	BGA012426	Tropical Japonica	79	109	Landrace	São João dos Patos/MA-Brazil	
		Moroberekan	BGA002524	Tropical Japonica	85	125	Cultivar	Africa	
2017	I	Arroz Carolino	BGA013061	Tropical Japonica	44	103	Landrace	Brazil	03/10 - 17/10/2017
		Três Meses Branco	BGA011901	Tropical Japonica	44	103	Landrace	Pitangueiras/SP-Brazil	
		Arroz 4 Meses	BGA013769	Tropical Japonica	44	103	Landrace	Itaguara/MG-Brazil	
		Rio Doce	BGA004168	Tropical Japonica	44	103	Landrace	Santo Antônio de Goias/GO-Brazil	
		CIRAD 392	IRGC121727	Tropical Japonica	44	103	Cultivar	França	
		Douradão	BGA005166	Tropical Japonica	44	103	Cultivar	Rio Pomba/MG-Brazil	
		Tangará	BGA005180	Tropical Japonica	44	103	Landrace	Santo Antônio de Goias/GO-Brazil	
	II	IRAT 112	BGA006574	Tropical Japonica	47	110	Cultivar	França	06/10- 20/10/2017
		Aimoré	BGA007119	Tropical Japonica	47	110	Landrace	Santo Antônio de Goias/GO-Brazil	
		Casca Branca	BGA013771	Tropical Japonica	47	110	Landrace	Piracema/MG-Brazil	
		Branquinho 90 Dias	BGA011897	Tropical Japonica	47	110	Landrace	Batatais/SP-Brazil	
		Guarani	BGA004121	Tropical Japonica	47	110	Landrace	Santo Antônio de Goias/GO-Brazil	
	III	BRS Primavera	BGA008070	Tropical Japonica	53	115	Cultivar	Santo Antônio de Goias/GO-Brazil	12/10 - 26/10/2017
		Comum	BGA011951	Tropical Japonica	53	115	Landrace	Cajazeiras/PB-Brazil	
		Carajás	BGA006701	Tropical Japonica	53	115	Landrace	Santo Antônio de Goias/GO-Brazil	
		Amarelão	BGA011242	Tropical Japonica	53	115	Landrace	Bonito/MS-Brazil	
		Bico Ganga	BGA013753	Tropical Japonica	53	115	Landrace	Pontalina/GO-Brazil	
	IV	BRSMG Curinga	BGA008812	Tropical Japonica	60	126	Cultivar	EMBRAPA-EPAMIG/Brazil	19/10 - 02/11/2017
		Agulhão	BGA013020	Tropical Japonica	60	126	Landrace	Caracaraí/RR-Brazil	
		Rabo de Burro	BGA012426	Tropical Japonica	60	126	Landrace	São João dos Patos/MA-Brazil	
		BRS Serra Dourada	BGA014150	Tropical Japonica	60	126	Cultivar	EMBRAPA-UFG-Brazil	
		BRS Esmeralda	BGA015465	Tropical Japonica	60	126	Cultivar	Santo Antônio de Goias/GO-Brazil	
	V	Saia Velha	BGA012954	Tropical Japonica	70	133	Landrace	Brejinho/MA-Brazil	27/10 - 10/11/2017
		BRS Soberana	BGA008711	Tropical Japonica	65	128	cultivar	Santo Antônio de Goias/GO-Brazil	
		Moroberekan	BGA002524	Tropical Japonica	70	133	Cultivar	Africa	

Experimental conditions

The experiments were carried out under a greenhouse condition at the plant phenotyping platform facility the Integrated System for Drought-Induced Treatment (Portuguese acronym SITIS) from Feb to June 2015, and from Aug 2017 to Jan 2018, 16°28'00" S, 49°17'00" W, altitude of 823 m. At the facility, 384 soil columns (diameter: 25 cm; height: 100 cm) were placed on a digital scale to monitor the water amount in each column. The soil, characterized as red latosol (Oxisol), was sieved through 125 mm mesh to remove larger aggregates and it was enriched with minerals, including 1.125 g kg^{-1} of 5-30-15 formulation, and 0.250 g kg^{-1} of ammonium sulfate after germination. Urea was applied at the beginning of tillering (V4-V5 stage; 0.350 g kg^{-1}) and in the panicle differentiation (R1 stage; 0.150 g kg^{-1}), four days before the period of water restriction.

The treatments consisted of combinations of two water levels including normal watering (control treatment) and restriction water (stress treatment) conditions. In the control treatment, the amount of soil water was equivalent to 80 % – 85 % of field capacity (FC) established and kept throughout the crop cycle. For the stress treatment, irrigation was performed until the plant reached the reproductive stage (R2/R3), followed by suspension of irrigation for five days, with subsequent replacement of only 50 % of evapotranspirated water at the plate placed on the column bottom for 10 days. The amount of evapotranspirated water was estimated based on the water quantity required to keep soil FC at 80 % – 85 % in the control treatment. Water stress was kept until the control plants reached R6 (grain depth expansion) / R7 (grain dry down) stage. After this 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 three plants.

Agronomic and morphophysiological measurements

Grain yield and yield *components*

The agronomic traits evaluated were grain yield (GY - g column^{-1}, which means the total mass of grains, in grams, obtained for three plants per column) and its components, such as the number of filled grains (NFG, filled grains average in six panicle column^{-1}), number of empty grains (NEG, empty grains average in six panicle column^{-1}), and 100-grain mass (100GM, g). The last variable was evaluated in 2015. Spikelet sterility was estimated as SS = (NEG × 100) TG^{-1}, where SS = spikelet sterility, NEG = number of empty grains, and TG = total number of grains.

Shoot growth

The following assessments were made for shoot (vegetative structures) growth and reproductive organs traits: (a) leaf area (LA, cm^2), average of two flag-leaf of two plants in column, using LI-COR leaf area meter; (b) plant height (PH, cm); (c) tiller number (TN, units); (d) panicle length (PL, cm); (e) shoot dry matter biomass (SDMB, g), through drying samples at 65 °C until a constant weight was achieved and (f) panicle number (PN, units). Data on PH, TN, SDMB, and PN were the average of three plants in the column. Additionally, LA and TN were measured on the last day of water restriction. The PH, PL, SDMB, and PN were obtained at harvesting time. LA and PL were measured in 2015.

Root phenotyping

The root system was evaluated according to the methodology described by Lanna et al. (2016). Briefly, to carry out the root system capture, acrylic tubes were installed inside the columns and three rice plants were planted around the tube. The root system growth was assessed by measuring length (cm), surface area (cm^2), volume (cm^3) and diameter (mm) of the roots through images generated by CI – 600 root scanner, with quantification by the WinRhizo software. Root images corresponding to depth 1 (5 to 25 cm) and 2 (25 to 45 cm) were taken on the 1st day after irrigation cut-off (phase I), 5th day after irrigation cut-off (phase II) and 10th day after the plants received 50 % of water at the column base (phase III). These parameters were evaluated in 2017.

Gas exchange

Gas exchange rates were taken on flag leaves of two plants in each column and measurements were made using a portable gas exchange analyzer in the infrared region (LCpro+). The parameters measured were: photosynthetic rate (A, µmol CO_2 m^{-2} s^{-1}), transpiration rate (E, mmol H_2O m^{-2} s^{-1}), stomatal conductance (gs, mol H_2O m^{-2} s^{-1}), and internal CO_2 concentration (Ci, µmol mol^{-1}). The equipment was set to use temperature and concentrations of 370 - 400 mol mol^{-1} CO_2 in the air, the reference condition used in the IRGA phothosynthesis chamber. The photon flux density photosynthetic active (PPFD) used was 1200 µmol [quanta] m^{-2} s^{-1}. The minimum equilibration time set for performing the reading was 2 min. Measurements in both control and stressed plants were carried out at from 07h30 to 11h00 a.m. on three evaluation dates during the water deficit period. These dates included the 1st day after irrigation cut-off (phase I), 5th day after irrigation cut-off (phase II), and 10th day after the plants received 50 % of water at the column base (phase III). Water use efficiency (WUE, µmol CO_2 mol^{-1} H_2O) was calculated as the ratio between A and gs (Rosales et al., 2012). Carboxylation efficiency (CE, (µmol m^{-2} s^{-1}) (µmol mol^{-1})$^{-1}$) was expressed as the ratio between A and Ci (Silva et al., 2013).

Water status

Leaf water potential (Ψw) was evaluated between 05h00 and 06h00 a.m. using a Scholander pressure chamber (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 restriction period. Pressure was applied until exudation from the cut made in the leaf collar. Leaf relative water content (RWC, %), osmotic potential (Ψs, MPa), and osmotic adjustment (OA; MPa) were also determined according to the methodology described by Bajji et al., 2001. These parameters were evaluated in 2015.

Experimental design and statistical analysis

All 25 genotypes were evaluated in a 5 × 5 lattice design with 12 repetitions: six repetitions (columns) were for irrigated conditions, and other six repetitions were used for the water deficit treatment, totaling 300 experimental units (with each column containing three plants). Among the six repetitions per water treatment, three repetitions were used for destructive (LA, Ψw, RWC, Ψs and OA; only in 2015) and three for non-destructive measurements (gas exchange, shoot structure, grain yield and its components). For all measurements of shoot traits, transformation $\sqrt{x} + 1.0$ was applied (where x represents the analyzed variables), which is often used for measurable or count data for normalizing and reducing data skewness (Shapiro and Wilk, 1965, normality test 5 %). The transformed data were subjected to the analysis of variance (ANOVA) based on a fixed linear model and to the joint analysis within each year (2015 and 2017), considering the following: blocks effects, two water levels effects, 25 genotypes, and water level × genotype interaction. The treatment means were compared by the Scott-Knott test ($p < 0.05$), due to a large number of treatments used in this study, which facilitated the ranking of 25 genotypes into homogeneous groups, without ambiguity. These analyses were carried out using the R platform (R Core Team, 2018). For the root traits, the data were analyzed by the GENES statistical analysis software. The joint analysis of variance was performed between the environments (irrigated and stressed) for each depth, and the significant differences were tested by the Tukey test at $p < 0.05$.

Results and Discussion

In crops, such as upland rice, where seeds are the product of interest, the main criteria for selecting agronomical tolerance to drought are the traits that lead to higher grain yield. In this study, the analysis of grain yield showed a significant difference ($p < 0.05$) for all variation sources. For 2015 and 2017, the genotypes accounted for 41 % and 50 % of the total sum of squares, while the environment (water level) accounted for 41 % and 44 % and the genotype *versus* environment

interaction accounted for 18 % and 7 %, respectively. The agronomic performance (grain yield) of genotypes cultivated under two water treatments in 2015 and 2017 is shown in Figures 1A and 1B. In 2015, Bico Ganga, BRS Esmeralda, BRSGO Serra Dourada, BRSMG Curinga, Casca Branca, Guarani, Rabo de Burro, Rio Doce, and Três Meses Branco showed better yield under drought (average grain yield 70.9 g column^{-1}) and irrigated (average grain yield 119.8 g column^{-1}) conditions. In 2017, Agulhão, Bico Ganga, BRS Esmeralda, BRS Primavera, BRS Soberana, BRSMG Curinga, Guarani, and Rabo de Burro were more productive under drought (average grain yield 40.90 g column^{-1}) and irrigated (average grain yield 63.98 g column^{-1}) conditions. Among the upland rice genotypes evaluated, Bico Ganga, BRS Esmeralda, BRSMG Curinga, Guarani, and Rabo de Burro showed better agronomic performance at both water levels in both two years of trials and were then ranked as top genotypes. These genotypes probably
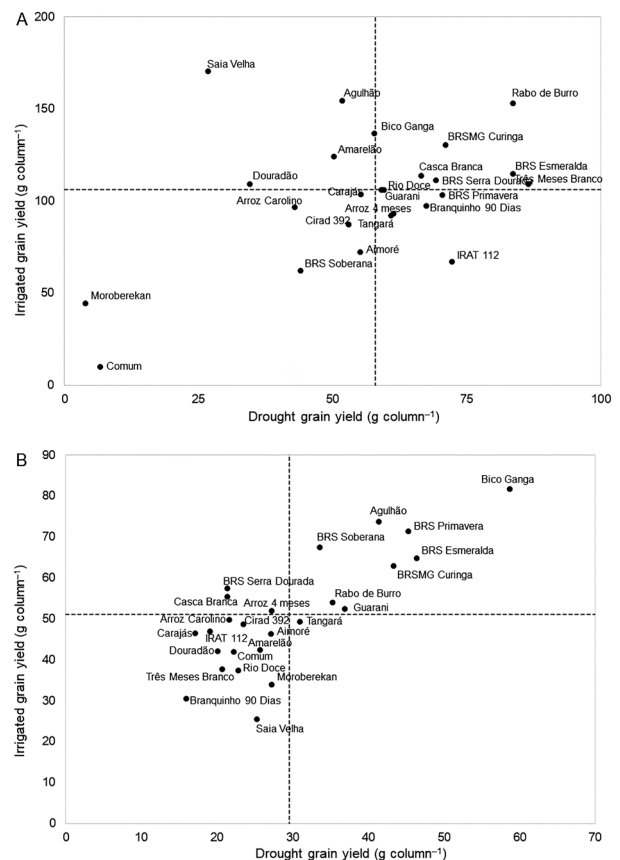
Figure 1 – Grain yield of upland rice (*Oryza sativa* L.) cultivated in SITIS Platform in years 2015 (A) and 2017 (B). The dotted lines define the average value of grain yield under irrigated and drought conditions. Genotypes that showed higher yield under irrigated and drought conditions were identified in the upper right-hand quadrant in Figures A and B. Bico Ganga, BRS Esmeralda, BRSMG Curinga, Guarani, and Rabo de Burro stood out in both years of trials.

present favorable alleles of drought tolerance that may be useful in breeding programs of upland rice. Two of these genotypes are modern cultivars (BRS Esmeralda and BRSMG Curinga), which could be qualified as parents in breeding programs of upland rice. For yield components, the average number of filled-grains and empty-grains was 138 and 46 in 2015, and 266 and 82 in 2017, respectively, in rice cultivated under irrigated condition (Table 2). For plants under drought, the total number of filled-grains and empty-grains were 99 and 37 in 2015, and 184 and 73 in 2017, respectively. The average value of 100-grain weight was 3.03 g under irrigated condition and 2.62 g under stress, determined only in 2015. IRAT 112 (41 %) and Douradão (52 %) presented the highest percentage of spikelet sterility under irrigated condition, and Moroberekan (94 %) and Branquinho 90 Dias (73 %) under drought condition in 2015 and 2017, respectively. In both years of trials, environmental conditions of phenotyping platform SITIS were severe. Particularly in 2017, in addition to artificially imposed water stress, the maximum temperature of 44.7 °C was 6.7 °C higher than the conditions of the 2015 trial, during the water deficit period. In addition, the minimum relative humidity of 26 % was 42 % lower than that of the 2015 trial (Table 3). According to Choudhary et al. (2018), drought commonly occurs combined with other environmental stresses, such as excessive light incidence, heat, and low relative humidity, and characterizes multiplicity of stresses in the tropics. For rice, along with drought, high temperature (up to 33.5 °C) contributed to yield reduction due to the shortening of the vegetative period and high spikelet sterility (Peng et al., 1995; Matsui et al., 1997; Shah et al., 2011).

According to Bernier et al. (2008), practices based on the assessment of agronomic performance of crop species require a long procedure, which limits breeding efficiency. Thus, a better understand of mechanisms of drought tolerance is necessary, since the association between main (grain yield and its components) and secondary (morphophysiology) traits could provide greater selection efficiency. For this, identifying morphophysiological traits related to drought tolerance is relevant to assist in the identification of mechanisms underlying these adaptation processes and thus in the selection of tolerant genotypes. In this study, upland rice plants reacted to drought stress by slowing down their growth (Table 4). In 2015, most genotypes (Agulhão, Aimoré, Amarelão, Arroz 4 meses, Bico Ganga, BRS Esmeralda, Primavera, BRSMG Curinga, Carajás, Casca Branca, Cirad 392, Douradão, Guarani, Moroberekan, Rabo de Burro, Rio Doce, Tangará, and Três Meses Branco) showed reduced PH (14 % on average) under drought condition. While, in 2017, only six genotypes (Agulhão, Bico Ganga, BRS Serra Dourada, Carajás, Rabo de Burro, and Rio Doce) presented an average reduction of 12 %. Overall, there was no difference between plants grown under both water levels for SDMB, TN, and PN, in both years of trials. Parameters

LA and PL, taken in 2015, showed reductions of 13 % and 3 %. LA and PH were the main morphological traits affected by drought stress in top genotypes Bico Ganga, BRS Esmeralda, BRSMG Curinga, Guarani, and Rabo de Burro, in both years of trials. According to Fischer et al. (2003) and Chaves et al. (2009), reduction of leaf growth and stem elongation in rice plants are the first processes affected by drought and could be considered as a tolerance mechanism, since they reduce the transpiration capacity, and consequently, plant demand for water. Furthermore, slowed growth (due to reduction of stomatal conductance, CO_2 assimilation and, consequently, photoassimilates production and accumulation) has been suggested as an adaptive trait for plant survival under stress. This trait allows plants to divert assimilates and energy into protective molecules to deal with stress (Zhu, 2002) and/or keep root growth by increasing water acquisition (Chaves et al., 2003; Pandey and Shukla, 2015).

The effect of the drought treatment was also evaluated by characterization of the root system, an important organ to increase rice yield under water stress (Pandey and Shukla, 2015; Kundur et al., 2015). According to Kato et al. (2006), rice root is complex, combining various root morphologies and showing considerable genotypic variation, also subjected to environmental effects. Thereby, a deep root system could improve adaptation of upland rice during drought by increasing capacity of extraction water, keeping high leaf water status with better crop performance under drought conditions (Kamoshita et al., 2004; Mishra and Salokhe, 2011). In this study, the analysis of the root system of upland rice showed a significant difference ($p < 0.05$) for most variation sources. At depth 1 (5 - 25 cm), the genotypes accounted for 14 % of the total sum of squares, the environment (water level) accounted for 54 %, and the double interaction, genotype *versus* water lever, accounted for 32 %. At depth 2 (25 - 45 cm), the genotypes accounted for 62 % of the total sum of the square, the environment (water level) accounted for 20 %, and the double interaction, genotype *versus* water level, accounted for 17 %.

The root system properties (length, surface area, volume, and diameter) of upland rice plants during the drought period are shown in Figure 2. Under irrigated condition, the genotypes that stood out mostly in terms of length, area, volume, and root diameter were IRAT 112, Agulhão, BRSMG Curinga (top genotype), Comum, Rabo de Burro (top genotype), and Saia Velha, at both depths. Under drought condition, the highlight was BRSMG Curinga followed by Agulhão, Comum, Rabo de Burro, and Saia Velha. Therefore, among top genotypes, BRSMG Curinga, and Rabo de Burro presented greater robustness of the root system, mainly at depth 2 (25 - 45 cm), irrespective of the water level applied. This is in accordance with Pandey and Shukla (2015), which describe that under water deficit, root growth is usually kept, while shoot growth is inhibited. Conversely, Ji et

Table 2 – Grain yield (GY, g column⁻¹) and yield components: number of filled grains (NFG), number of empty grains (NEG; average of six panicles column⁻¹), 100-grain mass (100GM; g), and spikelet sterility (SS; %) of upland rice (*Oryza sativa* L.) cultivated under irrigated and drought conditions. Trials in 2015 and 2017.

Genotypes	Irrigated					Stressed				
	Yield componentes					Yield components				
	GY	NFG	NEG	100GM	SS	GY	NFG	NEG	100GM	SS
Agulhão	153.92Aa / 73.47Da	158Aa / 257Da	63Aa / 21Db	3.20Aa / -	13.3Bb / 7.7Cb	51.88Ab / 41.48Cb	60Cb / 185Db	25Bb / 64Ca	2.85Aa / -	53.0Ba / 29.3Ca
Aimoré	72.01Da / 46.10Ca	133Ba / 234Da	38Ba / 88Ba	3.14Aa / -	19.7Aa / 27.3Aa	55.27Aa / 27.21Db	123Ba / 100Eb	32Ba / 20Db	2.91Aa / -	24.0Ca / 17.0Ca
Amarelão	123.70Ba / 42.20Ca	128Ba / 238Da	49Aa / 58Ca	3.19Aa / -	16.7Bb / 19.0Ba	50.31Ab / 25.77Db	78Cb / 214Ca	25Ba / 60Ca	3.00Aa / -	38.3Ca / 22.0Ca
Arroz 4 meses	92.77Ca / 51.74Ba	166Aa / 215Da	46Ba / 128Bb	2.89Ba / -	21.7Aa / 37.7Ab	61.44Ab / 27.31Db	115Bb / 87Eb	42Ba / 214Aa	2.72Aa / -	26.7Ca / 71.7Aa
Arroz Carolino	96.11Ca / 49.60Ca	138Ba / 276Da	47Aa / 112Ba	3.13Aa / -	24.0Aa / 29.7Aa	43.10Bb / 21.70Db	108Ba / 259Ca	44Ba / 68Da	2.69Aa / -	29.7Ca / 21.3Ca
Bico Ganga	136.46Ba / 81.57Aa	125Ba / 320Ca	38Ba / 8Da	2.91Ba / -	14.0Ba / 2.7Ca	57.93Ab / 58.78Ab	89Ca / 292Ba	21Ba / 20Ca	2.04Bb / -	30.3 Ca / 6.3Da
Branquinho 90 Dias	96.81Ca / 30.34Da	124Ba / 116Ea	49Aa / 107Bb	3.52Aa / -	30.3Aa / 47.3Ab	67.57Aa / 15.96Db	112Ba / 66Eb	24Ba / 185Aa	2.69Ab / -	16.3Ca / 72.7Aa
BRS Esmeralda	114.47Ca / 64.69Aa	177Aa / 448Ba	55Aa / 68Ca	2.40Ba / -	19.3Ab / 13.3Ba	83.71Ab / 46.45Bb	156Aa / 311Bb	43Ba / 59Ca	2.33Ba / -	26.3Ca / 15.7Da
BRS Primavera	103.04Ca / 71.17Aa	177Aa / 549Aa	67Aa / 71Ca	2.28Ba / -	28.3 Aa/11.0Ba	70.60Ab / 45.33Bb	176Aa / 428Ab	58Ba / 109Ba	2.21Ba / -	24.7Ca / 20.3Ca
BRS Serra Dourada	110.98Ca / 57.29Ba	228Aa / 432Ba	31Ba / 74Bb	2.17Ba / -	11.3Bb / 14.7Ba	69.44Ab / 21.42Db	174Ab / 212Cb	62Bb / 134Ba	2.03Ba / -	27.0Ca / 39.0Ba
BRS Soberana	61.81Da / 67.23Aa	118Ba / 332Ca	61Aa / 49Ca	2.46Ba / -	34.0Aa / 12.7Ba	44.13Ba / 33.61Cb	118Ba / 202Cb	43Ba / 32Da	2.39Ba / -	26.7Ca / 13.7Da
BRSMG Curinga	129.98Ba / 62.71Aa	145Ba / 295Ca	47Ba / 17Da	2.61Aa / -	9.0Ba / 5.3Cb	72.17Ab / 43.37Bb	120Ba / 219Cb	14Bb / 35Da	2.15Ba / -	31.3Ca / 13.3Da
Carajás	103.16Ca / 46.37Ca	165Aa / 236Da	48Aa / 90Ba	3.19Aa / -	11.3Bb / 27.7Ab	55.43Ab / 17.19Db	93Cb / 107Eb	22Ba / 114Ba	2.79Aa / -	37.0Ca / 52.0Ba
Casca Branca	113.45Ca / 55.23Ba	157Aa / 244Da	51Aa / 118Ba	3.52Aa / -	21.3Aa / 34.0Aa	66.65Ab / 21.45Db	135Ba / 159Db	42Ba / 51Cb	2.96Aa / -	28.0Ca / 23.7Ca
Cirad 392	87.02Ca / 48.56Ca	124Ba / 222Da	46Ba / 101Ba	2.87Ba / -	12.7Bb / 31.0Aa	53.07Ab / 23.54Db	106Ba / 136Db	17Bb / 70Ca	2.83Aa / -	30.7Ca / 34.0Ba
Comum	9.53Da / 41.72Ca	56Ca / 255Da	13Ba / 36Da	3.45Aa / -	6.3Ba / 11.7Ba	6.85Ca / 22.31Db	- / 176Db	- / 43Db	-/-	- / 19.7Ca
Douradão	108.77Ca / 1.86Ca	120Ba / 132Ea	46Ba / 156Aa	2.76Ba / -	11.0Bb / 52.3Aa	34.68Bb / 20.14Db	50Cb / 102Ea	15Bb / 129Ba	2.07Bb / -	48.0Ba / 52.7Ba
Guarani	105.75Ca / 37.18Da	109Ba / 146Ea	43Ba / 84Ba	3.74Aa / -	14.0Bb / 36.7Aa	59.65Ab / 22.88Db	81Ca / 138Da	18Ba / 64Ca	3.23Aa / -	34.7Ca / 32.0Ca
IRAT 112	72.37Da / 46.70Ca	91Ba / 185Ea	56Aa / 125Ba	3.80Ba / -	41.0Aa / 40.3Aa	66.80Aa / 19.12Db	82Ca / 143Da	35Ba / 45Cb	3.37Aa / -	27.7Ca / 26.3Cb
Moroberekan	44.18Da / 33.79Da	111Ba / 263Da	47Aa / 26Da	2.89Ba / -	30.0Ab / 9.3Cb	4.08Cb / 27.32Da	7Db / 169Db	117Ab / 54Ca	2.14Bb / -	94.0Aa / 24.0Ca
Rabo de Burro	152.69Aa / 53.78Ba	173Aa / 367Ca	58Ba / 66Ca	3.21Aa / -	8.3Bb / 14.7Ba	83.79Ab / 35.35Cb	104Bb / 373Aa	16Bb / 60Ca	2.86Aa / -	38.0Ca / 13.7Da
Rio Doce	105.75Ca / 52.29Ba	139Ba / 297Ca	49Aa / 214Aa	3.33Aa / -	25.0Aa / 42.0Aa	59.25Ab / 36.94Cb	125Ba / 214Cb	46Ba / 46Cb	2.61Ab / -	28.0Ca / 17.3Db
Saia Velha	170.02Aa / 25.30Da	119Ba / 155Ea	26Ba / 63Ca	2.35Ba / -	17.7Aa / 28.7Aa	26.93Bb / 25.30Da	19Db / 105Ea	92Ab / 60Ca	2.34 Ba / -	83.0Ab / 35.7Ba
Tangará	91.70Ca / 49.08Ca	123Ba / 219Da	33Ba / 59Ca	3.77Aa / -	21.7Aa / 21.0Aa	60.96Ab / 30.98Db	104Ba / 122Db	30Ba / 35Da	2.73Ab / -	23.0Ca / 22.3Ca
Três Meses Branco	108.79Ca / 37.60Da	145Ba / 205Da	40Aa / 100Ba	3.48Aa / -	22.0Aa / 32.7Aa	86.67Aa / 20.79Db	144Ba / 86Eb	32Ba / 60Ca	3.0Aa / -	18.3Ca / 42.7Ba

Capital letters compare the genotypes within each water regime and small letters the water levels within each genotype. Means followed by the same capital letter in the column and means followed by the same letter on the lines not differ by the Scott-Knott test 5% error probability. Transformed data in square root of Y + 1.0 – SQRT (Y + 1.0) to statistical analysis.

Table 3 – Climatic variables on the phenotyping platform SITIS on growth of upland rice (*Oryza sativa* L.), including temperature and relative humidity, maximum and minimum values. Upland rice (A and C) and drought period (B and D), in 2015 and 2017.

Climatic condition	T max	T min	RH max	RH min
	———— °C ————		———— % ————	
2015				
Upland rice cycle[A]	37.5	21.5	81.3	40.9
Drought period[B]	38.0	22.4	84.3	44.6
2017				
Upland rice cycle[C]	43.4	22.1	66.9	27.6
Drought period[D]	44.7	23.3	62.7	26.0

[A]02 Feb to 15 June, 2015; [B]31 Mar to 13 May, 2015; [C]21 Aug, 2017 to 19 Jan, 2018; [D]03 Oct to 10 Nov, 2017.

al. (2012) found a more extensive deeper root growth in a tolerant rice cultivar, IRAT109, after 20 days of irrigation cut-off. The findings of our study indicate a mechanism at the molecular level underlying a constitutive root growth for the root traits evaluated. Water deficit is an important environmental constraint and influences all physiological processes in plant growth, affecting gas exchange mechanisms (Ma et al., 2018).

The stress effects on *A*, *E*, *gs*, *Ci*, *WUE*, and *CE* in upland rice plants are shown in Table 5. During phase I, where control and stress columns were in similar conditions of soil water availability, there was genetic variability among rice accessions, implying a contrast for the gas exchange traits evaluated, in both years of
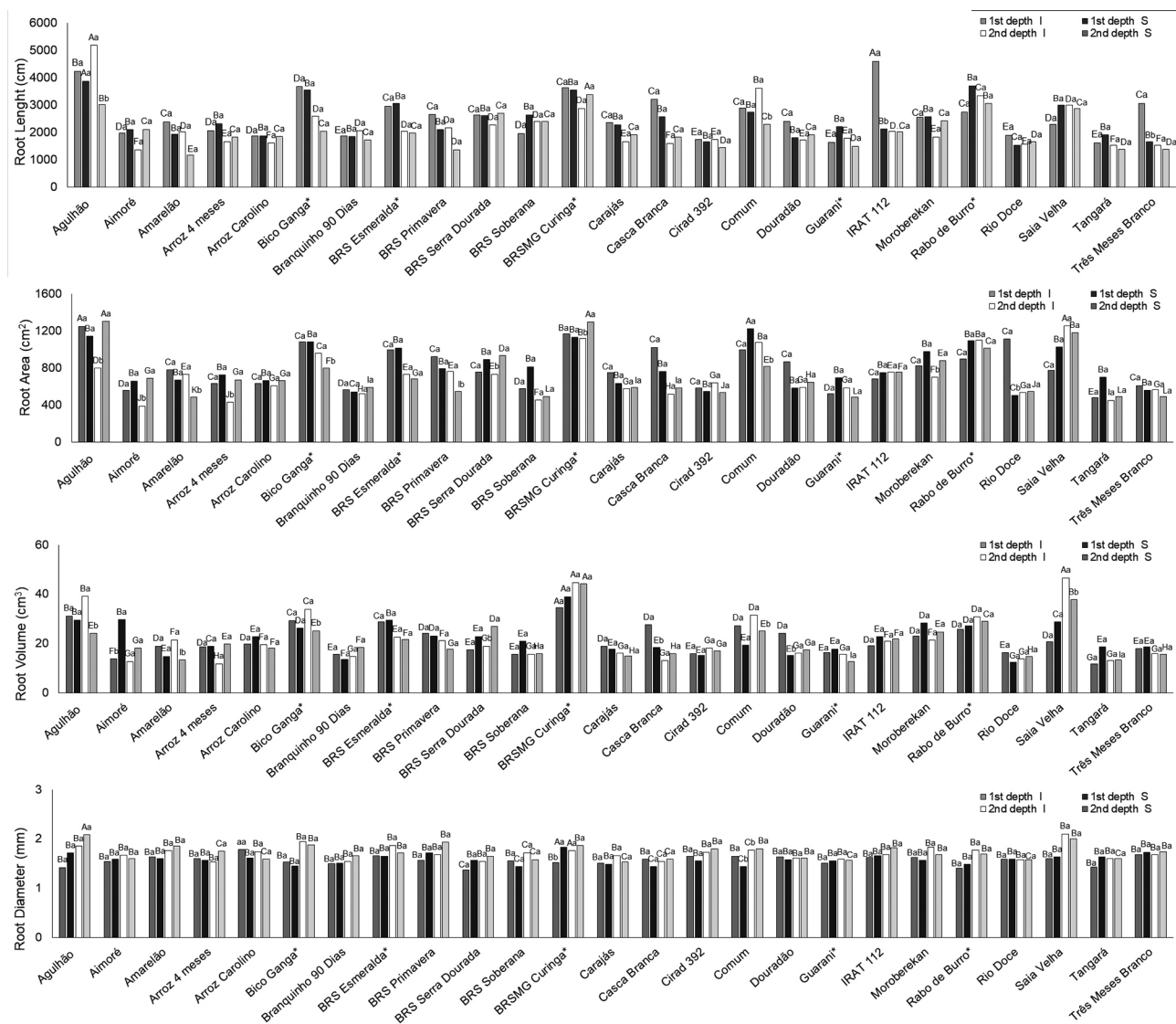
Figure 2 – Root length (cm), Root area (cm²), Root volume (cm³), and Root diameter (mm), at first (soil layer of 5 - 25 cm) and second (soil layer of 25 - 45 cm) depths of the soil cultivated with upland rice (*Oryza sativa* L.). Plants were grown under irrigated and drought conditions. Capital letters compare genotypes within each water regime and small letters compare water regimes within each genotype. Means followed by the same letter do not differ by the Tukey test 5 % error probability. Parameters were evaluated in 2017.

Table 4 – Shoot dry matter biomass (SDBM, g), leaf area (LA, cm²), plant height (PH, cm), tiller number (TN, unit), panicle number (PN, unit), and panicle length (PL, cm) of upland rice (*Orysa sativa* L.) grown under irrigated and drought conditions. Trials in 2015 and 2017.

Genotypes	Water level 2015 / 2017											
	Irrigated						Stressed					
	SDBM	LA	PH	TN	PN	PL	SDBM	LA	PH	TN	PN	PL
Agulhão	140.24 Ba/112.24 Ba	85.7127 Aa/-	136.9 Ba/129.3 Aa	14.1 Aa/13.2 Aa	12.3 Aa/11.3 Aa	29.6 Aa/-	135.33 Ba/112.60 Ba	70.8553 Aa/-	109.8 Bb/108.2 Bb	14.3 Ba/14.8 Ca	13.1 Ba/11.0 Aa	24.8 Bb/-
Aimoré	59.33 Ca/41.48 Da	54.3373 Ca/-	120.9 Ca/80.5 Ea	8.4 Ba/7.8 Cb	8.3 Ba/7.7 Ba	25.0 Ba/-	54.72 Ca/31.07 Da	51.7803 Aa/-	104.1 Bb/81.7 Da	8.6 Ca/9.7 Ca	8.1 Da/8.7 Ba	26.4 Aa/-
Amarelão	127.69 Ca/54.94 Da	86.5447 Aa/-	145.8 Aa/127.1 Aa	10.7 Ba/7.3 Ca	9.7 Ba/7.3 Ba	27.7 Aa/-	115.44 Ba/52.36 Ca	48.3237 Bb/-	132.7 Ab/117.7 Aa	9.3 Ca/5.5 Eb	9.3 Ca/5.3 Db	25.3 Ba/-
Arroz 4 meses	79.02 Ca/62.50 Ca	87.4770 Aa/-	153.3 Aa/112.4 Ba	6.8 Ba/7.7 Ba	6.7 Ba/7.3 Ba	30.6 Aa/-	70.36 Ca/49.01 Ca	76.4233 Aa/-	123.9 Ab/103.4 Ba	7.6 Ca/7.6 Da	7.55 Da/7.0 Ca	26.4 Aa/-
Arroz Carolino	72.59 Ca/55.03 Da	66.6093 Ba/-	140.0 Ba/105.7 Ca	9.2 Ba/7.5 Cb	9.2 Ba/6.3 Ba	29.4 Aa/-	71.64 Ca/49.97 Ca	60.5197 Aa/-	129.6 Aa/98.2 Ca	9.5 Ca/9.7 Ca	9.1 Ca/6.3 Ca	30.3 Aa/-
Bico Ganga	138.56 Ba/154.84 Ba	81.5693 Aa/-	156.9 Aa/139.1 Aa	13.1 Aa/12.9 Aa	13.1 Aa/12.3 Aa	26.3 Ba/-	135.03 Ba/117.87 Ba	60.2790 Ab/-	133.4 Ab/121.8 Ab	14.4 Ba/11.5 Ba	15.6 Aa/10.3 Aa	26.1 Ba/-
Branquinho 90 Dias	74.85 Ca/56.14 Da	54.5883 Ca/-	136.7 Ba/90.6 Da	9.6 Ba/7.0 Cb	9.6 Ba/7.0 Ba	25.8 Ba/-	64.71 Ca/38.97 Da	53.9200 Aa/-	122.3 Aa/82.3 Da	9.0 Ca/8.8 Da	8.9 Ca/8.3 Ba	23.7 Ba/-
BRS Esmeralda	85.50 Ca/65.00 Ca	54.1700 Ca/-	121.7 Ca/101.6 Ca	9.9 Ba/9.1 Ca	9.7 Ba/8.7 Ba	29.4 Aa/-	80.91 Ca/63.25 Ca	38.8567 Ba/-	106.6 Bb/95.4 Ca	9.9 Ca/9.3 Ca	9.4 Ca/8.7 Ba	25.9 Ab/-
BRS Primavera	97.86 Ca/72.87 Ca	82.6263 Aa/-	135.9 Aa/120.0 Ba	9.6 Ba/7.4 Ca	9.2 Ba/7.3 Ba	29.3 Aa/-	92.33 Ca/58.78 Ca	63.8400 Ab/-	121.1 Ab/111.2 Ba	10.1 Ca/7.3 Da	9.8 Ca/5.7 Da	28.1 Aa/-
BRS Serra Dourada	93.29 Ca/61.87 Ca	71.7250 Ba/-	113.7 Ca/104.9 Ca	9.8 Ba/8.6 Ca	9.8 Ba/8.3 Ba	29.5 Aa/-	89.99 Ca/47.81 Ca	61.6593 Aa/-	111.0 Ba/91.4 Cb	9.2 Ca/9.6 Ca	9.8 Ca/8.0 Ba	27.8 Aa/-
BRS Soberana	64.71 Ca/73.11 Ca	55.8537 Ca/-	138.8 Ba/86.8 Da	8.1 Ba/12.6 Aa	8.1 Ba/12.0 Aa	27.5 Aa/-	63.63 Ca/59.34 Ca	50.1880 Aa/-	130.1 Aa/79.7 Da	7.9 Da/11.4 Da	7.7 Da/9.3 Bb	28.3 Aa/-
BRSMG Curinga	120.3 Ba/78.91 Ca	76.4703 Ba/-	114.2 Da/98.7 Ca	15.5 Aa/13.1 Aa	12.6 Aa/12.7 Aa	25.7 Ba/-	119.13 Ba/70.13 Ca	49.2980 Bb/-	95.0 Cb/89.7 Ca	17.7 Aa/11.6 Ab	16.4 Ab/11.3 Aa	24.5 Ba/-
Carajás	77.11 Ca/45.39 Da	71.8847 Ba/-	138.0 Ba/89.9 Da	9.1 Ba/8.3 Ca	9.0 Ba/8.0 Ba	27.8 Aa/-	74.67 Ca/42.32 Da	70.6663 Aa/-	120.2 Ab/79.8 Db	8.0 Ca/10.1 Ca	7.8 Da/8.7 Ba	22.9 Bb/-
Casca Branca	86.07 Ca/50.48 Da	74.6667 Ba/-	143.6 Aa/99.8 Ca	8.6 Ba/7.1 Ca	8.3 Ba/7.0 Ba	27.7 Aa/-	69.55 Ca/44.07 Da	64.3147 Aa/-	123.0 Ab/92.3 Ca	7.6 Ca/6.8 Ea	7.2 Ca/6.7 Ca	25.1 Ba/-
Cirad 392	76.86 Ca/38.84 Da	55.0230 Ca/-	127.3 Ca/93.3 Da	14.8 Aa/10.5 Ba	14.4 Aa/10.0 Aa	26.8 Ba/-	62.83 Ca/34.09 Da	48.3480 Ba/-	114.9 Bb/91.5 Ca	11.3 Cb/12.6 Ba	10.6 Cb/11.3 Aa	26.2 Aa/-
Comum	36.88 Da/124.57 Ba	150.0533 Aa/-	98.0 Da/118.4 Ba	4.7 Ca/7.8 Ca	1.7 Ca/7.3 Ba	9.5 Ca/-	34.51 Da/101.30 Ba	96.2612 Ab/-	64.43 Ca/119.6 Aa	9.0 Ca/7.3 Da	1.0 Ea/7.0 Ca	9.6 Ca/-
Douradão	206.06Aa/49.13 Da	54.5177 Ca/-	145.7 Aa/92.2 Da	13.8 Aa/7.6 Ca	10.2 Ba/7.3 Ba	24.1 Ba/-	198.27 Aa/39.26 Da	48.6343 Ba/-	121.0 Ab/86.6 Ca	14.4 Ba/8.4 Da	12.3 Ba/8.3 Ba	20.3 Bb/-
Guarani	78.22 Ca/53.08 Da	68.3230 Ba/-	132.8 Ba/91.1 Da	10.0 Ba/7.7 Cb	10.0 Ba/7.7 Ba	28.4 Aa/-	68.41 Ca/42.99 Da	57.8473 Aa/-	110.6 Bb/90.0 Ca	9.0 Ca/9.8 Ca	9.0 Ca/9.3 Ba	25.1 Ba/-
IRAT 112	54.42 Ca/42.13 Da	66.3190 Da/-	113.3 Da/81.9 Ea	8.4 Ba/8.2 Ca	8.2 Ba/8.7 Ba	26.0 Ba/-	52.19 Ca/34.49 Da	64.4373 Aa/-	112.1 Ba/76.7 Da	7.2 Ca/9.2 Ca	7.2 Ca/8.7 Ba	24.5 Ba/-
Moroberekan	223.75Aa/122.30 Ba	86.1173 Aa/-	135.6 Ba/119.1 Ba	7.9 Ba/5.8 Ca	6.8 Ba/5.7 Ba	27.6 Aa/-	169.66 Ab/109.47 Ba	70.3757 Aa/-	108.2 Bb/115.7 Aa	7.1 Ca/5.9 Ea	3.9 Ea/4.3 Da	26.0 Aa/-
Rabo de Burro	131.65 Ba/137.37 Ba	58.7113 Ca/-	149.7 Aa/131.6 Aa	11.3 Ba/7.5 Ca	10.8 Aa/7.0 Ba	28.8 Aa/-	130.65 Ba/89.34 Ba	38.0407 Bb/-	126.2 Ab/118.0 Ab	12.6 Ba/5.9 Eb	9.8 Ca/5.3 Da	26.5 Aa/-
Rio Doce	78.82 Ca/46.67 Da	7.3593 Da/-	146.3 Aa/106.7 Ca	9.2 Ba/7.8 Ca	9.1 Ba/8.0 Ba	29.0 Aa/-	70.86 Ca/47.54 Ca	60.2577 Aa/-	130.0 Aa/95.7 Cb	8.1 Ca/8.4 Da	7.9 Da/8.3 Ba	26.4 Aa/-
Saia Velha	212.43Aa/300.01 Aa	36.9460 Ca/-	115.2 Da/135.2 Aa	14.6 Aa/13.2 Aa	11.1 Aa/12.3 Aa	24.1 Ba/-	209.54 Aa/205.27 Ab	27.1570 Ca/-	109.1 Ba/123.4 Aa	17.2 Aa/12.2 Ba	15.6 Ab/11.0 Aa	22.9 Ba/-
Tangará	70.73 Ca/45.98 Da	56.2763 Ca/-	108.4 Da/75.9 Ea	11.0 Ba/8.1 Ca	10.9 Aa/8.0 Ba	26.6 Ba/-	69.28 Ca/34.66 Da	55.2497 Aa/-	98.8 Cb/70.1 Da	10.6 Ca/9.7 Ca	10.3 Ca/9.0 Ba	23.6 Ba/-
Três Meses Branco	76.83 Ca/40.43 Da	60.4217 Da/-	130.9 Ba/95.9 Ca	9.2 Ba/6.7 Cb	9.2 Ba/6.7 Ba	28.0 Aa/-	71.68 Ca/40.05 Da	59.9543 Aa/-	118.9 Ab/80.8 Ca	9.2 Ca/8.4 Da	8.9 Ca/7.0 Ca	27.5 Aa/-

Capital letters compare genotypes within each water regime and small letters compare water levels within each genotype. Means followed by the same capital letter in the column and means followed by the same letter on the rows do not differ by the Scott-Knott test 5 % error probability. Transformed data in square root of Y + 1.0 – SQRT (Y + 1.0) for the statistical analysis.

Table 5 – Photosynthetic rate (A, μmol CO_2 m⁻² s⁻¹), transpiratory rate (E, mmol H_2O m⁻² s⁻¹), stomatal conductance (g_s, mol H_2O m⁻² s⁻¹), internal CO_2 concentration (C_i, μmol mol⁻¹), water use efficiency (WUE, μmol CO_2 mol⁻¹ H_2O), and carboxylation efficiency (CE; (μmol m⁻² s⁻¹) (μmol mol⁻¹) ⁻¹) of upland rice (*Oryza sativa* L.). The evaluation during three periods: Phase I - the first day after irrigation cut-off, Phase II - the fifth day after irrigation cut-off, and Phase III - the tenth day after plants received 50 % of water at the column base. Trials in 2015 and 2017.

Phase I — 2015 / 2017 — Irrigated

Genotypes	A	E	g_s	WUE	CE
Agulhão	16.35 B / 9.73 C	5.18 D / 4.80 C	0.34 C / 0.17 D	48.1 A / 57.2 B	0.067 A / 0.72 B
Aimoré	21.09 A / 19.71 A	7.97 B / 9.54 B	0.42 B / 0.21 C	50.2 A / 93.3 A	0.080 A / 0.113 A
Amarelão	22.12 A / 18.37 B	5.00 D / 9.34 B	0.60 A / 0.23 C	36.9 A / 79.9 A	0.067 A / 0.090 A
Arroz 4 meses	23.62 A / 21.74 A	6.64 D / 4.71 C	0.47 B / 0.43 A	50.3 A / 50.6 B	0.081 A / 0.087 B
Arroz Carolino	21.19 A / 22.73 A	7.36 C / 6.48 C	0.35 C / 0.42 A	60.5 A / 54.1 B	0.089 A / 0.095 A
Bico Ganga	21.44 A / 11.87 B	5.92 D / 6.79 B	0.52 A / 0.21 D	41.2 A / 56.5 B	0.068 A / 0.069 B
Branquinho 90 Dias	20.74 A / 16.05 B	6.69 D / 5.36 C	0.39 B / 0.26 C	53.2 A / 61.7 B	0.078 A / 0.089 A
BRS Esmeralda	19.21 A / 16.20 B	6.51 D / 7.18 B	0.42 B / 0.20 C	45.7 A / 81.0 A	0.079 A / 0.082 B
BRS Primavera	20.89 A / 12.37 B	6.39 D / 5.86 C	0.50 A / 0.22 D	41.8 A / 56.2 B	0.070 A / 0.069 B
BRS Serra Dourada	25.25 A / 18.90 B	6.43 D / 7.54 B	0.52 A / 0.28 C	48.6 A / 67.5 B	0.089 A / 0.099 A
BRS Soberana	25.31 A / 20.29 A	9.17 A / 11.65 A	0.45 B / 0.26 C	56.2 A / 78.0 B	0.107 A / 0.101 A
BRSMG Curinga	15.26 D / 12.70 B	6.15 D / 4.87 C	0.36 C / 0.14 D	42.4 A / 90.7 A	0.059 B / 0.064 B
Carajás	20.46 A / 16.66 B	6.81 D / 8.44 B	0.42 B / 0.20 C	48.7 A / 83.3 A	0.072 A / 0.087 B
Casca Branca	21.98 A / 16.64 B	6.92 C / 8.17 B	0.40 B / 0.20 C	55.0 A / 93.2 A	0.083 A / 0.104 A
Cirad 392	24.62 A / 25.91 A	9.34 A / 7.65 B	0.45 B / 0.45 A	54.7 A / 57.6 B	0.101 A / 0.108 A
Comum	17.13 B / 16.99 B	6.11 B / 6.99 B	0.39 B / 0.22 C	43.9 A / 77.2 B	0.058 B / 0.078 B
Douradão	13.61 B / 20.26 A	3.61 E / 5.38 C	0.27 D / 0.32 B	50.4 A / 63.3 B	0.048 B / 0.087 A
Guarani	23.12 A / 20.87 A	7.86 B / 8.33 C	0.40 B / 0.23 C	57.8 A / 90.7 A	0.088 A / 0.117 A
IRAT 112	22.46 A / 19.09 B	7.55 C / 6.50 C	0.52 A / 0.26 C	43.2 A / 73.4 B	0.074 A / 0.087 B
Moroberekan	15.82 B / 10.41 C	5.64 D / 6.11 C	0.28 D / 0.13 D	56.5 A / 80.1 A	0.060 B / 0.050 C
Rabo de Burro	16.36 B / 7.95 C	3.93 E / 4.16 C	0.26 D / 0.08 D	62.9 A / 99.4 A	0.067 A / 0.047 C
Rio Doce	19.99 A / 21.85 A	6.98 C / 6.31 C	0.33 C / 0.43 A	60.6 A / 50.8 B	0.079 A / 0.087 B
Saia Velha	8.34 C / 11.60 B	2.60 E / 6.45 C	0.16 D / 0.13 D	52.1 A / 89.2 A	0.028 B / 0.057 C
Tangará	19.69 A / 22.92 A	7.47 C / 6.21 C	0.37 C / 0.47 A	53.2 A / 48.8 B	0.080 A / 0.093 A
Três Meses Branco	22.47 A / 21.07 A	7.46 C / 6.10 C	0.41 B / 0.38 B	54.8 A / 55.4 B	0.088 A / 0.088 B

Phase II — 2015 / 2017

Genotypes	Irrigated A	E	g_s	WUE	CE	Stressed g_s	A	WUE	CE
Agulhão	18.88 Aa / 16.06 Ba	4.62 Ca / 4.80 Ba	0.50 Aa / 0.21 Ca	37.8 Aa / 76.5 Ba	0.070 Ba / 0.068 Ba	0.10 Bb / 0.05 Cb	4.02 Bb / 2.95 Db	40.2 Aa / 59.0 Ca	0.013 Bb / 0.010 Cb
Aimoré	24.96 Aa / 20.83 Aa	6.78 Ba / 9.72 Aa	0.56 Aa / 0.22 Ca	44.6 Aa / 94.7 Aa	0.098 Aa / 0.125 Cb	0.25 Ab / 0.08 Cb	14.46 Ab / 8.13 Cb	57.8 Aa / 101.6 Aa	0.055 Ab / 0.037 Bb
Amarelão	19.24 Aa / 17.27 Ba	6.40 Ca / 8.00 Aa	0.43 Aa / 0.17 Ca	44.7 Aa / 101.6 Aa	0.074 Aa / 0.096 Cb	0.06 Bb / 0.05 Cb	1.56 Bb / 3.14 Ab	36.8 Aa / 108.0 Aa	0.004 Bb / 0.026 Cb
Arroz 4 meses	21.17 Aa / 18.19 Aa	4.60 Ca / 8.74 Aa	0.51 Aa / 0.17 Ca	41.5 Aa / 107.0 Aa	0.080 Aa / 0.118 Aa	0.11 Bb / 0.06 Cb	1.35 Bb / 3.61 Ab	49.1 Aa / 92.3 Ba	0.019 Bb / 0.044 Bb
Arroz Carolino	25.68 Aa / 22.25 Aa	7.75 Aa / 6.53 Ba	0.46 Aa / 0.28 Ba	55.8 Aa / 79.5 Aa	0.111 Aa / 0.103 Aa	0.05 Bb / 0.23 Aa	1.77 Bb / 19.21 Aa	25.4 Aa / 83.5 Ba	0.004 Bb / 0.094 Aa
Bico Ganga	18.64 Ba / 10.13 Ba	7.39 Ba / 4.94 Ba	0.39 Aa / 0.17 Da	47.8 Aa / 59.6 Aa	0.073 Ba / 0.064 Ba	0.05 Bb / 0.02 Ca	1.73 Bb / 1.65 Bb	26.4 Aa / 31.0 Db	0.004 Db / 0.002 Cb

Table 5 – Continuation.

Genotypes	Irrigated A	E	g_s	WUE	CE	Stressed A	E	g_s	WUE	CE
Branquinho 90 Dias	21.64 Aa / 16.19 Ba	5.62 Ca / 6.98 Ba	0.49 Aa / 0.16 Ca	44.2 Aa / 101.2 Aa	0.079 Aa / 0.094 Aa	6.89 Bb / 6.56 Cb	1.99 Bb / 2.91 Bb	0.10 Bb / 0.05 Cb	68.9 Aa / 131.2 Aa	0.024 Bb / 0.036 Cb
BRS Esmeralda	20.54 Aa / 14.58 Ba	5.50 Ca / 5.09 Ba	0.58 Aa / 0.16 Ca	35.4 Ba / 91.1 Aa	0.076 Ba / 0.065 Ba	4.45 Bb / 3.28 Db	1.73 Bb / 1.07 Bb	0.09 Bb / 0.02 Cb	49.4 Aa / 164.0 Aa	0.015 Bb / 0.011 Cb
BRS Primavera	20.89 Aa / 12.72 Ba	8.14 Aa / 7.96 Aa	0.39 Aa / 0.13 Da	53.6 Aa / 97.9 Aa	0.091 Aa / 0.069 Ba	1.60 Bb / 0.82 Db	1.48 Bb / 2.03 Bb	0.04 Bb / 0.07 Cb	40.0 Aa / 11.7 Db	0.005 Ab / 0.003 Cb
BRS Serra Dourada	23.23 Aa / 18.34 Aa	8.04 Aa / 6.51 Ba	0.41 Aa / 0.31 Ba	56.7 Aa / 59.2 Ba	0.112 Aa / 0.077 Ba	12.04 Ab / 6.18 Cb	4.14 Ab / 2.18 Bb	0.16 Bb / 0.07 Cb	75.3 Aa / 8.8 Ba	0.054 Ab / 0.026 Cb
BRS Soberana	24.76 Aa / 23.51 Aa	9.28 Aa / 9.55 Aa	0.45 Aa / 0.38 Aa	55.0 Aa / 61.9 Ba	0.121 Aa / 0.097 Aa	9.86 Ab / 9.50 Cb	3.75 Ab / 3.78 Ab	0.12 Bb / 0.10 Cb	82.2 Aa / 95.0 Ba	0.044 Ab / 0.042 Bb
BRSMG Curinga	18.79 Aa / 14.70 Ba	6.28 Ba / 6.99 Ba	0.53 Aa / 0.34 Aa	35.5 Aa / 43.2 Ba	0.068 Ba / 0.053 Ba	3.07 Bb / 1.08 Db	1.93 Bb / 2.19 Bb	0.09 Bb / 0.07 Cb	34.1 Aa / 15.4 Db	0.009 Bb / 0.003 Cb
Carajás	21.90 Aa / 18.63 Aa	5.32 Ca / 8.37 Aa	0.50 Aa / 0.19 Ca	43.8 Aa / 98.1 Aa	0.084 Aa / 0.104 Aa	5.92 Bb / 3.56 Db	1.73 Bb / 2.47 Bb	0.08 Bb / 0.04 Cb	74.0 Aa / 89.0 Ba	0.021 Bb / 0.013 Cb
Casca Branca	21.85 Aa / 19.09 Aa	5.28 Ca / 11.97 Aa	0.50 Aa / 0.25 Ca	43.7 Aa / 76.4 Ba	0.086 Aa / 0.116 Aa	4.91 Bb / 9.02 Cb	1.41 Bb / 5.46 Ab	0.09 Bb / 0.09 Cb	54.6 Aa / 100.2 Ba	0.017 Bb / 0.047 Bb
Cirad 392	24.92 Aa / 21.12 Aa	8.82 Aa / 11.02 Aa	0.47 Aa / 0.18 Ca	53.0 Aa / 117.3 Aa	0.104 Aa / 0.117 Aa	6.01 Bb / 10.22 Bb	2.72 Bb / 5.44 Ab	0.09 Bb / 0.08 Cb	66.8 Aa / 127.8 Aa	0.023 Bb / 0.075 Ab
Comum	17.64 Aa / 14.70 Ba	5.28 Ca / 6.44 Ba	0.46 Aa / 0.19 Ca	38.4 Aa / 77.4 Ba	0.067 Ba / 0.064 Ba	2.39 Bb / 2.52 Db	1.63 Bb / 1.48 Bb	0.07 Bb / 0.03 Cb	34.1 Aa / 84.0 Ba	0.007 Bb / 0.010 Cb
Douradão	14.48 Aa / 16.18 Ba	2.54 Da / 6.63 Ba	0.23 Ba / 0.22 Da	63.0 Aa / 73.6 Aa	0.052 Ba / 0.100 Aa	1.56 Bb / 9.82 Ba	0.97 Ba / 4.36 Aa	0.04 Bb / 0.14 Bb	39.0 Aa / 70.1 Cb	0.004 Bb / 0.073 Aa
Guarani	22.24 Aa / 22.16 Aa	5.90 Ca / 11.08 Aa	0.53 Aa / 0.21 Ca	42.0 Aa / 105.5 Aa	0.085 Aa / 0.151 Aa	8.76 Ab / 1.49 Db	2.50 Bb / 1.72 Bb	0.21 Ab / 0.04 Cb	41.7 Aa / 37.3 Db	0.028 Bb / 0.007 Cb
IRAT 112	20.07 Aa / 23.52 Aa	5.60 Ca / 9.40 Aa	0.69 Aa / 0.40 Aa	29.1 Aa / 58.8 Ba	0.072 Ba / 0.102 Aa	15.67 Ab / 7.85 Cb	3.83 Ab / 2.63 Bb	0.47 Aa / 0.05 Cb	33.3 Aa / 157.0 Aa	0.053 Aa / 0.033 Cb
Moroberekan	11.25 Ba / 13.77 Ba	3.37 Da / 5.50 Ba	0.16 Ba / 0.20 Ca	70.3 Aa / 68.9 Ba	0.046 Ba / 0.061 Ba	1.66 Bb / 4.27 Db	1.26 Bb / 1.63 Bb	0.05 Ba / 0.04 Cb	33.2 Aa / 106.7 Ba	0.004 Bb / 0.018 Cb
Rabo de Burro	16.34 Ba / 13.87 Ba	3.78 Da / 5.57 Ba	0.25 Ba / 0.22 Ca	65.4 Aa / 63.1 Ba	0.061 Ba / 0.058 Ba	1.72 Bb / 3.50 Db	1.21 Bb / 1.44 Bb	0.04 Ba / 0.04 Cb	43.0 Aa / 87.5 Ba	0.005 Bb / 0.013 Cb
Rio Doce	21.18 Aa / 16.79 Ba	5.27 Ca / 8.47 Aa	0.40 Aa / 0.23 Da	53.0 Aa / 73.0 Aa	0.093 Aa / 0.113 Aa	2.38 Bb / 10.60 Ba	1.28 Bb / 5.34 Ab	0.05 Bb / 0.08 Ca	47.6 Aa / 132.5 Aa	0.008 Bb / 0.075 Ab
Saia Velha	11.62 Ba / 15.00 Ba	2.66 Da / 6.29 Ba	0.12 Ba / 0.29 Ba	96.8 Aa / 52.8 Ba	0.041 Ba / 0.053 Ba	1.36 Bb / 1.59 Db	1.21 Bb / 1.44 Bb	0.05 Bb / 0.04 Cb	27.2 Aa / 39.8 Da	0.004 Bb / 0.005 Cb
Tangará	21.81 Aa / 17.89 Aa	7.27 Ba / 7.07 Ba	0.44 Aa / 0.17 Ca	49.6 Aa / 105.2 Aa	0.091 Aa / 0.105 Aa	3.52 Bb / 12.23 Ba	1.92 Bb / 4.86 Aa	0.06 Bb / 0.10 Cb	58.7 Aa / 122.3 Aa	0.009 Bb / 0.082 Aa
Três Meses Branco	23.26 Aa / 23.40 Aa	6.56 Ba / 8.35 Aa	0.49 Aa / 0.31 Ba	47.5 Aa / 75.5 Ba	0.093 Aa / 0.110 Aa	4.39 Ab / 5.02 Ab	1.92 Bb / 4.86 Aa	0.29 Aa / 0.14 Bb	58.0 Aa / 96.0 Ba	0.064 Aa / 0.071 Ab

Phase III

2015 / 2017

Genotypes	Irrigated A	E	g_s	WUE	CE	Stressed A	E	g_s	WUE	CE
Agulhão	19.14 Aa / 19.18 Ba	5.82 Aa / 5.65 Ca	0.42 Aa / 0.37 Ca	45.6 Aa / 51.8 Ea	0.066 Ba / 0.067 Ca	8.26 Bb / 11.68 Ab	2.53 Bb / 4.64 Aa	0.11 Ab / 0.23 Ab	75.1 Aa / 50.8 Ea	0.031 Bb / 0.039 Cb
Aimoré	21.90 Aa / 18.78 Ba	7.25 Aa / 7.27 Ba	0.50 Aa / 0.19 Da	43.8 Aa / 98.8 Ba	0.085 Aa / 0.115 Ba	14.07 Ab / 8.94 Bb	3.93 Ab / 3.41 Ab	0.21 Ab / 0.07 Cb	67.0 Aa / 127.7 Ab	0.061 Aa / 0.058 Bb
Amarelão	21.05 Aa / 13.74 Ca	6.86 Aa / 10.65 Aa	0.25 Ca / 0.14 Ea	84.2 Aa / 98.1 Ba	0.090 Aa / 0.075 Ca	7.04 Bb / 5.05 Cb	2.68 Bb / 5.03 Ab	0.07 Ab / 0.07 Cb	100.6 Aa / 72.3 Cb	0.029 Bb / 0.024 Cb
Arroz 4 meses	20.10 Aa / 23.49 Aa	5.89 Aa / 7.49 Ba	0.44 Aa / 0.32 Ca	45.7 Aa / 73.4 Ca	0.081 Aa / 0.106 Ba	8.68 Bb / 10.39 Bb	2.62 Bb / 3.44 Bb	0.12 Ab / 0.10 Cb	72.3 Aa / 103.9 Ab	0.038 Bb / 0.058 Bb
Arroz Carolino	22.48 Aa / 18.76 Ba	6.91 Aa / 7.47 Ba	0.46 Aa / 0.23 Da	48.9 Aa / 81.6 Ca	0.089 Aa / 0.093 Ba	9.65 Bb / 13.91 Ab	3.23 Ab / 4.70 Ab	0.14 Ab / 0.11 Cb	74.9 Aa / 126.5 Ab	0.041 Bb / 0.091 Aa
Bico Ganga	19.23 Aa / 15.79 Ca	7.28 Aa / 8.16 Ba	0.29 Ba / 0.23 Da	66.3 Aa / 68.7 Da	0.074 Aa / 0.069 Ca	5.94 Bb / 9.30 Bb	2.77 Bb / 3.91 Bb	0.07 Ab / 0.09 Cb	84.9 Aa / 103.3 Ab	0.022 Bb / 0.047 Ca
Branquinho 90 Dias	17.46 Aa / 16.18 Ca	5.47 Aa / 5.40 Ca	0.49 Aa / 0.15 Ea	35.6 Aa / 107.9 Aa	0.060 Ba / 0.090 Ba	13.80 Ab / 12.67 Aa	3.55 Ab / 3.66 Bb	0.24 Ab / 0.11 Ca	57.5 Aa / 115.2 Aa	0.056 Aa / 0.072 Aa
BRS Esmeralda	20.40 Aa / 16.09 Ca	6.76 Aa / 5.89 Ca	0.44 Aa / 0.33 Ca	46.4 Aa / 48.9 Ea	0.073 Aa / 0.060 Da	8.46 Bb / 9.16 Bb	3.25 Ab / 4.54 Aa	0.13 Ab / 0.14 Db	65.1 Aa / 65.4 Db	0.030 Bb / 0.037 Cb
BRS Primavera	21.65 Aa / 23.55 Ca	8.15 Aa / 10.82 Aa	0.34 Ba / 0.31 Ca	63.7 Aa / 76.0 Ca	0.085 Aa / 0.112 Ba	6.84 Bb / 9.63 Bb	2.89 Bb / 5.69 Ab	0.08 Ab / 0.08 Cb	85.5 Aa / 120.4 Ab	0.027 Bb / 0.044 Cb
BRS Serra Dourada	21.22 Aa / 21.41 Ba	8.28 Aa / 7.45 Ba	0.34 Ba / 0.35 Ca	62.4 Aa / 61.2 Da	0.082 Aa / 0.093 Ba	9.27 Bb / 12.52 Ab	3.39 Ab / 4.39 Ab	0.09 Ab / 0.16 Bb	103.0 Aa / 78.3 Cb	0.040 Bb / 0.060 Bb
BRS Soberana	24.50 Aa / 26.51 Ca	8.09 Aa / 8.49 Aa	0.52 Aa / 0.58 Aa	47.1 Aa / 45.7 Ea	0.100 Aa / 0.090 Ba	16.46 Ab / 16.71 Ab	5.01 Ab / 5.52 Ab	0.24 Ab / 0.27 Ab	68.6 Aa / 61.9 Db	0.074 Aa / 0.061 Bb
BRSMG Curinga	16.94 Aa / 24.10 Ca	6.68 Aa / 10.04 Aa	0.36 Ba / 0.43 Ba	47.1 Aa / 56.1 Ea	0.060 Ba / 0.102 Ba	5.19 Bb / 7.53 Bb	2.32 Bb / 3.46 Bb	0.08 Ab / 0.10 Cb	64.9 Aa / 75.3 Cb	0.018 Bb / 0.032 Cb
Carajás	21.07 Aa / 19.95 Ba	6.78 Aa / 7.43 Ba	0.41 Aa / 0.29 Ca	51.4 Aa / 68.8 Da	0.091 Aa / 0.084 Ca	7.37 Bb / 11.73 Ab	2.46 Bb / 4.76 Ab	0.09 Ab / 0.14 Cb	81.9 Aa / 83.8 Ca	0.034 Bb / 0.053 Cb
Casca Branca	18.03 Aa / 21.42 Ba	6.10 Aa / 9.33 Aa	0.36 Ba / 0.28 Ca	50.1 Aa / 76.5 Cb	0.075 Aa / 0.106 Ba	10.47 Bb / 10.29 Bb	3.51 Ab / 4.15 Ab	0.14 Ab / 0.09 Cb	74.8 Aa / 114.3 Aa	0.048 Ab / 0.064 Bb
Cirad 392	21.40 Aa / 26.83 Ca	7.27 Aa / 9.99 Aa	0.46 Aa / 0.34 Ca	46.5 Aa / 78.9 Ca	0.084 Aa / 0.141 Aa	10.71 Bb / 14.63 Ab	3.48 Aa / 6.00 Aa	0.15 Ab / 0.17 Bb	71.4 Aa / 86.1 Ca	0.047 Ab / 0.082 Ab

Table 5 – Continuation.

Comum	19.45 Aa / 12.64 Ca	7.28 Aa / 6.90 Ba	0.46 Aa / 0.14 Ea	42.3 Aa / 90.3 Ba	0.081 Aa / 0.067 Ca	9.33 Bb / 6.72 Cb	3.11 Bb / 4.75 Ab	0.09 Bb / 0.07 Cb	103.7 Aa / 96.0 Ba	0.042 Bb / 0.036 Cb
Douradão	22.37 Aa / 18.30 Ba	3.07 Ba / 7.34 Ba	0.41 Da / 0.21 Da	54.6 Aa / 87.1 Ba	0.064 Ba / 0.093 Ba	12.67 Ab / 10.25 Bb	2.85 Ba / 4.17 Bb	0.13 Ab / 0.11 Cb	97.5 Aa / 93.2 Ba	0.042 Ba / 0.058 Bb
Guarani	20.76 Aa / 19.00 Ba	7.02 Aa / 8.20 Ba	0.41 Aa / 0.16 Ea	50.6 Aa / 118.8 Aa	0.087 Aa / 0.123 Aa	11.61 Ab / 3.25 Cb	3.74 Ab / 2.25 Cb	0.15 Ab / 0.03 Cb	77.4 Aa / 108.3 Aa	0.054 Ab / 0.016 Ca
IRAT 112	24.93 Aa / 19.59 Ba	6.90 Aa / 6.86 Ba	0.60 Aa / 0.29 Ca	41.6 Aa / 67.6 Db	0.097 Aa / 0.081 Ca	14.29 Ab / 18.02 Ab	3.76 Ab / 5.58 Aa	0.22 Ab / 0.21 Ab	65.0 Aa / 85.8 Ca	0.064 Ab / 0.086 Aa
Moroberekan	11.73 Aa / 12.81 Ca	3.13 Ba / 4.63 Ca	0.13 Ca / 0.25 Da	90.2 Aa / 51.2 Eb	0.043 Ba / 0.046 Da	6.14 Bb / 7.77 Bb	1.86 Bb / 2.87 Bb	0.11 Aa / 0.11 Cb	55.8 Aa / 70.6 Ca	0.021 Ba / 0.032 Ca
Rabo de Burro	18.68 Aa / 13.07 Ca	4.99 Ba / 5.42 Ca	0.32 Ba / 0.33 Ca	58.4 Aa / 39.6 Ea	0.058 Ba / 0.044 Da	6.88 Bb / 12.99 Aa	1.99 Ba / 4.77 Aa	0.12 Ab / 0.26 Aa	57.3 Aa / 50.0 Ea	0.020 Bb / 0.047 Ca
Rio Doce	21.50 Aa / 23.47 Aa	6.78 Aa / 9.90 Aa	0.42 Aa / 0.29 Ca	51.2 Aa / 80.9 Cb	0.045 Aa / 0.133 Aa	6.04 Bb / 14.43 Ab	2.29 Bb / 5.57 Ab	0.08 Ab / 0.12 Cb	75.5 Aa / 120.2 Aa	0.027 Bb / 0.102 Ab
Saia Velha	15.82 Aa / 13.16 Ca	3.49 Ba / 6.81 Ba	0.22 Ca / 0.29 Ca	71.9 Aa / 45.4 Eb	0.054 Ba / 0.046 Da	5.90 Bb / 5.43 Cb	1.65 Bb / 2.72 Bb	0.07 Ab / 0.09 Cb	84.3 Aa / 60.3 Da	0.017 Bb / 0.019 Ca
Tangará	21.27 Aa / 18.98 Ba	6.88 Aa / 8.02 Ba	0.47 Aa / 0.23 Da	45.3 Aa / 82.5 Cb	0.061 Aa / 0.100 Ba	10.10 Bb / 9.19 Bb	3.64 Ab / 3.52 Bb	0.18 Ab / 0.09 Cb	56.1 Aa / 102.1 Aa	0.038 Bb / 0.050 Cb
Três Meses Branco	22.42 Aa / 25.18 Aa	6.81 Aa / 9.74 Aa	0.56 Aa / 0.34 Ca	40.0 Aa / 74.1 Ca	0.083 Aa / 0.125 Aa	15.98 Aa / 15.14 Ab	4.25 Ab / 5.54 Ab	0.25 Ab / 0.16 Bb	61.6 Aa / 94.6 Bb	0.066 Aa / 0.080 Ab

Phase I: Means followed by the same capital letter in the column do not differ by the Scott-Knott test at 5 % error probability. Transformed data in square root of Y + 1.0 SQRT (Y + 1.0) for the statistical analysis; Phase II and Phase III: capital letters compare genotypes within each water regime and small letters compare water regimes within each genotype. Means followed by the same capital letter in the column and means followed by the same letter on the rows do not differ by the Scott-Knott test at 5 % error probability. Transformed data in square root of Y + 1.0 – SQRT (Y + 1.0) for the statistical analysis.

trials. In 2015, A ranged from 8.34 to 25.31 μmol CO_2 m^{-2} s^{-1}, E ranged from 2.60 to 9.34 mmol H_2O m^{-2} s^{-1}, and gs (number and activity of stomata) ranged from 0.16 to 0.52 mol H_2O m^{-2} s^{-1}. In 2017, 7.95 to 25.91 μmol CO_2 m^{-2} s^{-1}, 4.16 to 11.65 mmol H_2O m^{-2} s^{-1}, and 0.13 to 0.47 mol H_2O m^{-2} s^{-1}, respectively. In phase II, 5th day after irrigation cut-off, we observed mechanisms, such as leaf-rolling and stomatal closure. These events soften the solar radiation incidence and transpiration rate, respectively, increasing water conservation and delaying water deficit. Low values of A, E and gs were observed in both years of trials. In 2015, A ranged from 1.27 to 15.67 μmol CO_2 m^{-2} s^{-1}, E ranged from 0.97 to 4.14 mmol H_2O m^{-2} s^{-1}, and gs ranged from 0.04 to 0.47 mol H_2O m^{-2} s^{-1}. In 2017, A ranged from 0.82 to 19.21 μmol CO_2 m^{-2} s^{-1}, E ranged from 1.07 to 6.27 mmol H_2O m^{-2} s^{-1}, and gs ranged from 0.02 to 0.14 mol H_2O m^{-2} s^{-1}. Four out of five top genotypes (Bico Ganga, BRS Esmeralda, BRSMG Curinga, and Rabo de Burro) showed average reduction of 84 %, 72 %, and 81 % in A, E, and gs, respectively, in plants cultivated under drought. In phase III, after plants under stress received 50 % of water at the column base for 10 days, only three genotypes, Três Meses Branco (2015), Branquinho 90 Dias, and Rabo de Burro (2017) restored the functioning of the photosynthetic machinery, since stressed plants showed values of photosynthetic rate similar to those of irrigated plants. Conversely, for the other genotypes including Bico Ganga, BRS Esmeralda, BRSMG Curinga, and Guarani (top genotypes), recovery of A, E, and g_s was 40 %, 46 %, and 30 %, respectively, in stressed plants.

When water deficits start to increase, leaf stomatal conductance usually decreases faster than carbon assimilation, leading to increased *WUE*. The *WUE* reflects the multiple environmental stimuli perceived and the capacity of a particular genotype to sense the onset of changes in moisture availability and therefore to fine-tune its water status in response to the environment (Wilkinson, 2004; Blankenagel et al., 2018).

However, despite the negative impact of water deficit on gas exchange, in both years of trials, Bico Ganga, BRS Esmeralda, BRSMG Curinga, and Guarani (top genotypes) improved their *WUE* (44 %) when compared with optimal irrigation conditions. This was most probably due to higher stomatal control efficiency, keeping approximately 40 % of the photosynthetic process and drastically reducing stomatal conductance (70 %) by closing the stomata process. Although Rabo de Burro did not show increase in *WUE*, it presented a recovery of the gas exchange apparatus compared to irrigated plants, which can be justified partly by its vigorous root system.

In addition to increased relative stomatal limitation, drought stress is responsible for reducing maximum Rubisco carboxylation activity and electron transport and therefore ribulose bisphosphate (RuBP) regeneration (Perdomo et al., 2017). The carboxylation efficiency could be considered an estimate of the Rubisco activity, illustrating its limitations under stress conditions

(Niinemets et al., 2009). In our study, all upland rice genotypes showed a poor capacity to overcome limitation in CO_2 diffusion by stomata and mesophyll and effective CO_2 fixation (70 % of CE reduction) during phase II for both years of trials. After replenishing 50 % of water at the column base for 10 days, recovery of 55 % and 64 % in the carboxylation efficiency was observed in 2015 and 2017, respectively. Considerable loss of Rubisco activity during stress conditions were also reported for sugarcane subjected to water deficit (Saliendra et al., 1996; Vu and Allen Jr., 2009). Overall, a response pattern was not observed among genotypes with greater yield performance under water deficit, since they showed divergent physiological responses of gas exchange.

Furthermore, remobilization of photoassimilates from vegetative into reproductive structures may have a significant effect on grain yield, although this component was not evaluated in our study. As demonstrated for cereals (Blum et al., 1994) and legumes (Chaves et al., 2002), nutrient pre-anthesis reserves are used for grain filling in addition to current assimilates. In rice, drought-induced leaf senescence also promotes assimilate allocation to grains under development, shortening grain

filling and increasing the grain filling rate (Sehgal et al., 2018). Moreover, senescence and reserve mobilization are integral components of plant development and basic strategies in stress mitigation (Lemoine et al., 2013).

Water stress effects on Ψw, RWC, Ψs, and OA, evaluated only in the 2015 trial, are shown in Table 6. Among top genotypes, BRS Esmeralda, BRSMG Curinga, Guarani, and Rabo de Burro showed a more pronounced gradient of ψ_w and probably enhanced water absorption capacity. Besides, advance of the most severe internal damage may have reduced in the reproductive organs under the drought period. Conversely, Bico Ganga kept high water potential during the water deficit period, which may be associated to a more robust root system in the second soil layer and thus higher panicle water potential, which probably contributes to increased grain yield. According to Guimarães et al. (2016), plants that prevent dehydration presented higher water potential and earliness in flowering, lower height, lower leaf area or lower tillering. Regarding the trait RWC, which is directly related to the plant water status, values ranged from ~ 82 % in leaves under irrigated condition to 75 % for stressed plants. On the other hand, BRSMG Curinga

Table 6 – Water potential (Ψw, MPa), osmotic potential (Ψs, MPa), relative water content (RWC, %), and osmotic adjustment (OA; MPa) of upland rice (*Oryza sativa* L.) grown under irrigated and drought conditions. Trial in 2015.

Genotypes	Water level							
	Irrigated				Stressed			
	Ψ_w	Ψ_s	RWC	OA	Ψ_w	Ψ_s	RWC	OA
Agulhão	−0.39 Aa	−1.235 Ba	81.73 Ba	0.000 Aa	−0.95 Ab	−1.272 Ca	70.09 Bb	0.037 Ea
Aimoré	−0.16 Ba	−0.939 Ea	80.65 Ba	0.000 Aa	−0.53 Ba	−1.062 Da	76.64 Aa	0.122 Db
Amarelão	−0.28 Aa	−1.080 Da	79.67 Ba	0.000 Aa	−0.36 Ba	−1.210 Cb	68.55 Bb	0.130 Db
Arroz 4 meses	−0.03 Ba	−1.079 Da	81.19 Ba	0.000 Aa	−0.90 Ab	−1.132 Aa	70.03 Bb	0.050 Ea
Arroz Carolino	−0.02 Ba	−0.987 Ea	79.34 Ba	0.000 Aa	−0.55 Bb	−1.205 Cb	75.62 Aa	0.217 Bb
Bico Ganga	−0.20 Ba	−1.053 Da	76.19 Ba	0.000 Aa	−0.38 Ba	−1.255 Cb	73.98 Ba	0.202 Bb
Branquinho 90 Dias	−0.03 Ba	−0.940 Ea	84.57 Ba	0.000 Aa	−0.39 Ba	−1.206 Cb	76.99 Ab	0.266 Ab
BRS Esmeralda	−0.02 Ba	−1.250 Ba	83.21 Ba	0.000 Aa	−1.12 Ab	−1.495 Ab	79.36 Aa	0.245 Ab
BRS Primavera	−0.24 Aa	−1.141 Ca	86.35 Ba	0.000 Aa	−0.48 Ba	−1.399 Ab	83.78 Aa	0.258 Ab
BRS Serra Dourada	−0.33 Aa	−1.138 Ca	79.42 Ba	0.000 Aa	−0.38 Ba	−1.267 Cb	77.56 Aa	0.129 Db
BRS Soberana	−0.35 Aa	−1.115 Ca	76.12 Ba	0.000 Aa	−0.36 Ba	−1.165 Ca	66.89 Bb	0.116 Db
BRSMG Curinga	−0.12 Ba	−1.218 Ba	83.04 Ba	0.000 Aa	−0.93 Ab	−1.235 Ca	73.81 Bb	0.022 Ea
Carajás	−0.03 Ba	−0.995 Da	79.01 Ba	0.000 Aa	−0.40 Ba	−1.216 Cb	72.64 Ba	0.221 Bb
Casca Branca	−0.03 Ba	−1.403 Aa	96.72 Aa	0.000 Aa	−0.49 Bb	−1.446 Aa	76.48 Ab	0.043 Eb
Cirad 392	−0.02 Ba	−1.057 Da	76.17 Ba	0.000 Aa	−0.39 Ba	−1.172 Ca	72.22 Ba	0.114 Db
Comum	−0.04 Ba	−1.522 Ab	77.94 Ba	0.000 Aa	−0.51 CB	−1.783 Aa	69.88 Bb	0.051 Ea
Douradão	−0.45 Aa	−1.130 Ca	83.08 Ba	0.000 Aa	−0.71 Ba	−1.142 Da	78.11 Aa	0.012 Eb
Guarani	−0.03 Ba	−1.163 Ca	81.59 Ba	0.000 Aa	−0.43 Bb	−1.318 Bb	79.39 Aa	0.155 Cb
IRAT 112	−0.04 Ba	−0.916 Ea	80.78 Ba	0.000 Aa	−0.50 Bb	−1.017 Da	71.00 Bb	0.101 Db
Moroberekan	−0.12 Ba	−1.259 Ba	83.83 Ba	0.000 Aa	−1.44 Ab	−1.325 Ba	75.88 Ab	0.035 Ea
Rabo de Burro	−0.46 Aa	−1.212 Ba	82.30 Ba	0.000 Aa	−1.33 Ab	−1.228 Ca	81.19 Aa	0.016 Ea
Rio Doce	−0.04 Ba	−1.080 Da	79.49 Ba	0.000 Aa	−0.63 Bb	−1.321 Bb	74.35 Ba	0.241 Ab
Saia Velha	−0.51 Aa	−1.065 Da	79.35 Ba	0.000 Aa	−1.23 Ab	−1.178 Ca	70.34 Bb	0.113 Db
Tangará	−0.40 Aa	−0.988 Ea	70.98 Ba	0.000 Aa	−0.42 Ba	−1.146 Db	70.69 Ba	0.160 Cb
Três Meses Branco	−0.28 Aa	−0.918 Ea	79.71 Ba	0.000 Aa	−0.73 Bb	−1.115 Cb	73.69 Ba	0.316 Ab

Capital letters compare genotypes within each water regime and small letters compare water regimes within each genotype. Means followed by the same capital letter in the column and means followed by the same letter on the rows do not differ by the Scott-Knott test 5 % error probability. Transformed data in square root of Y + 1.0 – SQRT (Y + 1.0) for the statistical analysis.

presented significant RWC reduction due to the stress imposed. This divergent responses regarding leaf water status suggest greater capacity of top genotypes to save water during drought and stimulate an adjustment of the photosynthetic capacity to tolerate changes in water availability (Silva et al., 2007; Rodrigues et al., 2009; Graça et al., 2010). The mechanism of osmotic adjustment (OA), usually accomplished by accumulation of compatible solutes (ψs) and maintenance of RWC, although significant for all genotypes, was numerically higher for BRS Esmeralda, followed by Bico Ganga and Guarani, compared to BRSMG Curinga and Rabo de Burro (top genotypes). This mechanism in upland rice plants during the reproductive phase allows maintenance of adequate physiological state, in which the leaves remain green and cool for a longer time, besides allowing the establishment and retention of spikelet and, consequently, grain yield sustenance (Fischer et al., 2003).

This study describes important aspects of drought-induced effect on upland rice, providing a better understanding of morphophysiological changes under water deficit. Top genotypes showed distinct strategies by activating different physiological responses: higher ability to save water on leaves (Bico Ganga, BRS Esmeralda, BRSMG Curinga and Rabo de Burro), lower leaf water potential (Bico Ganga, BRS Esmeralda, BRSMG Curinga and Guarani), higher ability to reduce vegetative structures (Bico Ganga, BRSMG Curinga and Rabo de Burro), higher efficiency in the use of water (Bico Ganga, BRS Esmeralda, BRSMG Curinga and Guarani), higher photosynthetic capacity (Guarani), and improved ability to absorb water from drying soil, either by osmotic adjustment (Bico Ganga, BRS Esmeralda and Guarani) or additional investment in the root system (BRSMG Curinga and Rabo de Burro). Therefore, different mechanisms, such as vegetative morphology, gas exchange, water status, and root system could be explored simultaneously to support the development of drought-tolerant rice cultivars by breeding programs.

Authors' Contributions

Conceptualization: Vianello, R.P.; Lanna, A.C.; Brondani, C. **Data analysis**: Lanna, A.C.; Coelho, G.R.C.; Moreira, A.S.; Terra, T.G.R. **Data acquisition**: Lanna, A.C.; Coelho, G.R.C.; Saraiva, G.R.; Lemos, F.S. **Design of methodology**: Lanna, A.C.; Guimarães, P.H.R.; Morais Júnior, O.P. **Writing and editing**: Lanna, A.C.; Moreira, A.S.; Brondani, C.; Vianello, R.P.

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