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Leaf gas exchange and water relations in two assai cultivars submitted to water-deficit

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Abstract: Assai (*Euterpe oleracea* Mart.) cultivars BRS-Pará (BRS-PA) and BRS-Pai d'Égua (BRS-PDE) were selected for cultivation in upland regions of the Amazon. Given these cultivars were developed from different progenitors, we postulated that they differ regarding water-deficit tolerance. To test this hypothesis, plants of both cultivars were evaluated under well-watered (control) and water-deficit conditions (pre-dawn leaf water potential of – 2.33 MPa). Relative to control, the water-deficit decreased net CO_2 assimilation rate (*A*) and transpiration by 82% and 86% in both cultivars, while the stomatal conductance (g_s) was reduced by 93% and 87% in stressed plants of BRS-PDE and BRS-PA. The water-deficit improved instantaneous water-use efficiency by 43% in both cultivars, while intrinsic water-use efficiency (A/g_s) increased by 193% and 33% in BRS-PDE and BRS-PA. The water-deficit induced 44% increase in foliar proline and 27% decrease in soluble carbohydrates in both cultivars, while foliar sucrose decreased by 53% in BRS-PA and 16% in BRS-PDE in relation to control. The relative water content in stressed plants of both cultivars was decreased by 8.5% in relation to control. In conclusion, the more efficient stomatal opening control and higher A/g_s in BRS-PDE indicate this cultivar better copes with drought than BRS-PA.

Index terms: Instantaneous Water Use Efficiency, Intrinsic Water Use Efficiency, Osmotic Adjustment, Foliar Proline Concentration.

Trocas gasosas e relações hídricas em duas cultivares de açaí submetidas ao déficit hídrico

Resumo - As cultivares de açaí (*Euterpe oleracea* Mart.) BRS-Pará (BRS-PA) e BRS-Pai d'Égua (BRS-PDE) foram selecionadas para cultivo em regiões de terra firme da

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Amazônia. Como essas cultivares foram desenvolvidas a partir de diferentes progenitores, nós postulamos que essas cultivares podem diferir na tolerância ao déficit hídrico. Para testar essa hipótese, plantas de ambas os cultivares foram avaliadas em condições adequadas de irrigação (controle) e déficit hídrico (potencial hídrico foliar na antemanhã de – 2,33 MPa). Em relação ao controle, o déficit hídrico reduziu a taxa de assimilação líquida de CO_2 (A) e a transpiração, em 82%, e 86% em ambas as cultivares, enquanto a condutância estomática (g_s) foi reduzida em 93% e 87%, nas plantas estressadas de BRS-PDE e BRS-PA. O déficit hídrico aumentou a eficiência instantânea do uso da água em 43%, em ambas as cultivares, enquanto a eficiência intrínseca do uso da água (A/g_s) aumentou 193% na BRS-PDE e 33% na BRS-PA. O déficit hídrico induziu o aumento de 44% na prolina foliar e um decréscimo de 27% nos carboidratos solúveis totais, enquanto a sacarose foliar diminuiu 53% na BRS-PA e 16% na BRS-PDE, em relação ao controle. O conteúdo relativo de água nas plantas estressadas de ambas as cultivares diminuiu em 8,5% em relação ao controle. Em conclusão, o controle da abertura estomática mais eficiente e a maior A/g_s, na BRS-PDE, indicam que esta cultivar respondeu melhor ao déficit hídrico que a BRS-PA.

Termos para indexação: Eficiência Instantânea do Uso da Água, Eficiência Intrínseca do Uso da Água, Ajustamento Osmótico, Concentração Foliar de Prolina.

Introduction

Several plant species have been cultivated in the Amazon biome on a large scale, including assai palm (*Euterpe oleracea* Mart.), whose fruit pulp holds good nutritional quality and medicinal properties (BONOMO et al., 2014). Assai palm is, however, highly sensitive to drought (BARBOSA et al., 2017; SANTOS et al., 2022; SILVESTRE et al., 2016; 2017; OLIVEIRA et al., 2019). For instance, the vegetative growth of young assai plants; assessed as plant height, stem diameter, number of leaves and leaflets, and total leaf area, markedly decreased upon irrigation with 45% or 70% of soil field capacity (SILVESTRE et al., 2016). Furthermore, assai plants growing under limited irrigation were more sensitive to pathogens, becoming senescent up to 90 days of cultivation from sowing (SILVESTRE et al., 2016). In addition to the effect of water-deficit on growth, the sensitivity of assai palms to drought is also evidenced by decreases in net CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration (E) over the stress progress (CALBO; MORAES, 2000; SILVESTRE et al., 2016; 2017; OLIVEIRA et al., 2019). At least in part, decreases in A in drought-stressed assai plants are related to impairments in the photochemical reactions and depletion of proteins associated with biochemical yield in photosynthesis, photorespiration, and antioxidant defense system (OLIVEIRA et al., 2019).

In general, plants adjust morphological, physiological, biochemical, and molecular mechanisms to cope with drought. It is worth noting that the magnitude of such adjustments and subsequent responses to drought differ both among plant species and genotypes within the same species. Then, this inherent genetic variability allows the identification of sensitive- and drought-tolerant genotypes, as observed in *Elaeis guineensis* (BAYONA-RODRIGUEZ; ROMERO, 2019; SURESH et al., 2012), *Vitis vinifera* (BOTA et al., 2016), and *Zea mays* (PIRES et al., 2020; SHAFIQ et al., 2019).

Among mechanisms that likely contribute to a higher tolerance to water-deficit, it has been reported that plants improve water-use efficiency and water status through osmotic adjustment in roots and/or leaves. The water-use efficiency can be assessed by the quotient between A and E, as instantaneous water use efficiency (A/E); or by the quotient between A and g_s, namely intrinsic water use efficiency (A/g_s) (LIU et al., 2019; SILVA et al, 2022). Therefore, the adjustments in A/E and A/g_s directly depend on the mechanisms of regulation of A, g_s, and

E during the progress of soil water deprivation, and, in general, both instantaneous and intrinsic water-use efficiency is higher in drought-tolerant genotypes than in sensitive ones (BOTA et al., 2016; ALVES et al., 2021; MESQUITA et al., 2020; TEZARA et al., 2021).

On the other hand, the osmotic adjustment is estimated as the difference between the osmotic potential of the drought-stressed and well-watered plants, being thus pointed out as an important mechanism of drought tolerance in plants. Given the osmotic potential is dependent on cellular concentration of ions (e.g., Na^+ and $Cl^–$) and osmotically active solutes (e.g., proline, glycine betaine, mannitol, trehalose, and galactinol) (VALLIYODAN; NGUYEN, 2006; GOMES et al., 2010; MACÊDO et al., 2019; LI et al., 2020; OZTURK et al., 2020; TRAVERSARI et al., 2020), the osmotic potential decreases in response to increases in concentration of both ions and osmotically active solutes. Decreases in both osmotic potential and leaf water potential sustain water uptake by roots and its transport to leaves, thereby leading to cell turgor maintenance during drought conditions. In this context, an osmotic adjustment mediated by leaf accumulation of proline, glycine betaine, sucrose, and mannitol has been observed in drought-tolerant genotypes of several crops and tree species (GOMES et al., 2010; TOUNEKTI et al., 2018; GHARBI et al., 2019; MACÊDO et al., 2019; SHAFIQ et al., 2019).

In assai, the water-deficit imposed by daily irrigation with 40% soil field capacity induced negligible changes in *A/E* (SILVESTRE et al., 2016). In contrast, the adjustments in *A* and *E* led to an increased *A/E* when the irrigation was completely withheld and the water-deficit became severe (SANTOS et al., 2022). On the other hand, the osmotic adjustment in assai was first reported in young palms submitted to water-deficit marked by leaf water potential around – 2.5 MPa; however, the solutes involved in such responses were not identified (CALBO; MORAES 2000). In drought-stressed plants from two assai materials (BRS-PA cv. and Hideo ecotype), the foliar concentration of total soluble carbohydrates, glycine betaine, and proline were differentially increased in assai plants grown under limited irrigation for 45 days (SILVESTRE et al., 2017). Taken together, these results indicate that *A/E* and osmotic adjustment likely play an important role in the drought responses in assai and may be pivotal for differential tolerance to drought among cultivars of this species.

In this work, we examined drought responses in the two commercial cultivars of assai, named BRS-Pará (BRS-PA) and BRS-Pai d'Égua (BRS-PDE). These cultivars were genetically selected for cultivation in upland areas of the Amazon, where edaphoclimatic conditions lead to more significant drought periods between July and November (OLIVEIRA; FARIAS NETO, 2004; ALVARES et al., 2013; FARIAS NETO, 2019). Under water-deficit conditions, we previously demonstrated that plants of the BRS-PA cultivar performed physiologically better than Hideo ecotype (SILVESTRE et al., 2016; 2017). On the other hand, the physiological responses of the new commercial cultivar of assai (BRS-PDE) were not deeply evaluated. Considering BRS-PA and BRS-PDE assai cultivars were selected from different progenitors, then we hypothesized that these cultivars may differ in terms of drought tolerance. To test this hypothesis, we compared the physiological performance of assai cultivars BRS-PA and BRS-PDE under full irrigation and water-deficit conditions. Then, comparisons between cultivars were accomplished by assessing parameters related to plant water status, leaf gas exchange, instantaneous and intrinsic water use efficiencies (*A/E* and A/g_s, respectively), and foliar concentration of osmotically active solutes linked to osmotic adjustment. The present work is the first investigation on the physiological performance of BRS-PDE assai cultivar either under well-watered or under water-deficit conditions and the reported data may support further experiments focusing on assai palm at a field scale cultivation.

Materials and Methods

Plant material and growth conditions

Pre-germinated seeds of two commercial assai (*Euterpe oleracea* Mart.) cultivars (BRS-Pará, BRS-PA; and BRS-Pai d'Égua, BRS-PDE) were sowed in 25 × 15 cm (height × diameter) polyethylene bags filled with a mixture of soil (Yellow Latosol) and poultry bad (3:2 v/v) as substrate. The initial growth of seedlings was carried out in a nursery at the Federal Rural University of the Amazon, in Belém, Brazil (01°27'19" S and 48°26'19" W), under daily irrigation to keep water moisture in the soil near field capacity (SILVESTRE et al., 2016). Fertilization of seedlings was carried out in 15-day intervals by providing 11.1 mL per plant of a 4 g L^{-1} Complex 151 solution (Nutriplant S.A., São Paulo, Brazil). For experimental setup, 180-day-old plants of both cultivars were transferred to polyethylene pots (24 × 22 cm, height × diameter) filled with 10 L of the same substrate used for initial seedling growth. The substrate pH was adjusted to around 5.5 by adding 27.4 g dolomitic limestone per pot 30 days before transplanting. All plants were cultivated in a nursery under daily irrigation set up to full field capacity until the experimental arrangement. During this period, additional fertilization with 2.7 g 18-18-18 NPK per pot was carried out at 15, 30, and 45 days after transplanting.

Experimental setup

The experiment was set up when plants were about 60 cm high and presented seven fronds. These above-ground traits were observed when the plants were around 330 days old. The selected plants of each cultivar were randomly distributed into two treatments: Control, in which the plants were daily irrigated to full field capacity; and water-deficit, in which irrigation was withheld to induce soil water deprivation. Five replicates per treatment were prepared, with a single plant per pot as an experimental unit.

Treatment evaluation

Treatment comparisons were performed when predawn leaf water potential (Ψ_{pd}) in drought-stressed plants reached about – 2.5 MPa, since this magnitude induces significant reductions in leaf gas exchange parameters as previously reported for the reference cultivar BRS-PA (OLIVEIRA et al., 2019). For both cultivars, the average time to reach this Ψ_{pd} was 20 days. Physiological assessments and sampling were accomplished in leaflets from the second frond from the apex. Sampling for Ψ_{pd} and relative water content (RWC) was performed at predawn (between 4:00 and 5:00 h), while leaf gas exchange determination and sampling for biochemical assays were carried out between 9 am and 11 am. During leaf gas exchange measurements, averages of air temperature, relative air humidity, photosynthetically active radiation, and vapor pressure deficit in the nursery were respectively 27.7 ± 0.12 °C, 81.5 ± 0.75%, 342 ± 53 µmol photons mol m^{-2} s^{-1}, and 0.78 ± 0.03 kPa.

Predawn leaf water potential and relative water content

Predawn leaf water potential (Ψ_{pd}) was determined with a Scholander type pressure chamber (m 670, Pms Instrument Co., Albany, USA) as described in Pinheiro et al. (2008). The relative water content (RWC) was determined from leaf samples consisting of 15 leaf discs (4 mm diameter each) per plant according to González and González-Vilar (2001).

Leaf gas exchange

Leaf gas exchange parameters (net CO_2 assimilation rate, *A*; stomatal conductance to water vapor, g_s; and transpiration rate, *E*) were assessed using an infrared gas analyzer (LI-6400 XT; LICOR Biosci. Inc., Nebraska, USA). Measurements were carried out under a CO_2 concentration of 400 µmol mol^{-1} and PAR of 1000 µmol m^{-2} s^{-1} (OLIVEIRA et al. 2019). From the data, both instantaneous (A/E) and intrinsic (A/g_s) water-use efficiency were estimated (LIU et al. 2019; SILVA et al. 2022).

Proline, glycine betaine, and total soluble carbohydrates

All assays were conducted from fresh samples (100 mg) collected from the same leaflet used for leaf gas exchange measurements. Samples were fast-frozen in liquid nitrogen and kept at – 20 °C until assays.

Foliar proline concentration was determined according to Bates et al. (1973). The extraction was carried out in distilled water at 100 °C for 30 min and reaction was performed using acid ninhydrin solution and acetic acid. The mixture was incubated for 1 h at 100 °C, and the reaction was interrupted under an ice bath. Then, a volume of toluene (99.5% grade) was added to each sample, followed by a vortex cycle. The toluene phase was aspired for new tubes and absorbances were determined at 520 nm. Proline concentration was calculated based on a proline standard curve.

Foliar glycine betaine was determined according to Grieve and Grattan (1983). Extraction was conducted in distilled water at 25 °C, under shaking, for 4 h. After centrifugation, an aliquot of the supernatant was acidified with the same volume of 2 N H_2SO_4 for 1 h under ice bath before reaction with KI-I_2 solution. The mixture was shaken and incubated at 0 °C for 16 h. After centrifugation, the pellet was twice-washed using 1 N H_2SO_4 at 8 °C. After centrifugation, the pellet was dissolved in 1,2-dichloroethane and samples remained at 25 °C for 2 h before reading the absorbances at 365 nm. Glycine betaine concentration was calculated based on a glycine betaine standard curve.

Foliar total soluble carbohydrates were determined according to Dubois et al. (1956). The extraction was performed by incubating the samples in 80% (v/v) ethanol at 75 °C, under shaking, for 60 min. After centrifugation, an aliquot of the supernatant was mixed with 5% phenol and H_2SO_4 (concentrated). After mixing, the samples were incubated at 25 °C for 20 min before the determination of absorbances at 490 nm. The foliar concentration of total soluble carbohydrates was determined using a glucose standard curve.

Statistical analysis

The independent effects of assai cultivars (BRS-PA and BRS-PDE) and watering regimes (control and water-deficit) and their interactions (cultivar × watering regime) for each variable were examined using a two-way ANOVA procedure, performed with software R (v. 3.4.1; R Core Team 2016).

Results

Predawn leaf water potential and leaf gas exchange

The Ψ_{pd} was significantly affected by watering regimes, with no effect concerning cultivar and their interaction (Table 1). Therefore, the mean of Ψ_{pd} in control plants was – 0.10 MPa, while – 2.33 MPa in stressed plants (Figure 1). This result highlights that stressed plants of the two assai cultivars were compared under the same level of stress condition.

Table 1. F-test coefficients and significance levels for the effects of cultivar (cv; BRS-PA and BRS-PDE), watering regime (WR; control and water-deficit), and cv x WR interaction on plant water status, leaf gas exchange, and biochemical variables.

Variable	Factor		
	cv	WR	cv x WR
Ψ_{pd}	0.80 ^{ns}	3150.88 ***	0.38 ^{ns}
A	0.06 ^{ns}	1230.74 ***	0.21 ^{ns}
g_s	0.05 ^{ns}	3079.44 ***	9.91 **
E	15.0 ^{ns}	41.30 ***	18.0 ***
A/E	1.89 ^{ns}	108.08 ***	0.67 ^{ns}
A/g_s	18.26 ***	84.86 ***	26.75 ***
Proline	0.85 ^{ns}	9.43 **	0.49 ^{ns}
Total soluble carbohydrates	2.83 ^{ns}	29.52 ***	0.10 ^{ns}
Sucrose	1.13 ^{ns}	33.69 ***	11.36 **
Glycine betaine	0.39 ^{ns}	0.09 ^{ns}	0.28 ^{ns}
RWC	0.02 ^{ns}	10.89 **	3.45 ^{ns}

^{ns} non-significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$

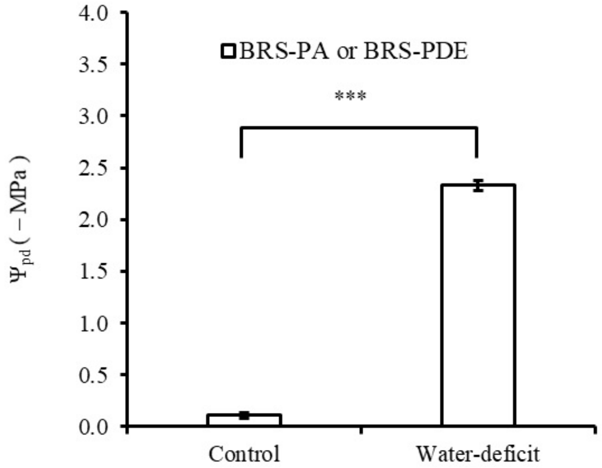

Figure 1. Predawn leaf water potential (Ψ_{pd}) in two assai cultivars (BRS-PA and BRS-PDE) submitted to well-watered (Control) and water-deficit (Water-deficit) conditions. Data are the mean ± S.E. (n = 5). Asterisks indicate mean difference between control and stressed plants (F-test, $P < 0.001$).

As shown in Table 1, A was only significantly affected by the watering regimes while significant effects of the interaction between cultivar and water regimes were observed for g_s and E. Then, both assai cultivars showed similar A under well-watered (9.66 μmol m^{-2} s^{-1}) and under water-deficit (1.74 μmol m^{-2} s^{-1}) conditions. This accounts for a decrease of 82% in A for both cultivars under stress as compared with their respective control (Figure 2A). In control plants, g_s was 5% higher in BRS-PDE than in BRS-PA, with 68.0 mmol m^{-2} s^{-1} and 64.9 mmol m^{-2} s^{-1} , respectively (Figure 2B). In stressed plants, g_s was 58% lower in BRS-PDE than in BRS-PA (4.97 mmol m^{-2} s^{-1} and 8.98 mmol m^{-2} s^{-1}, respectively) (Figure 2B). Therefore, relative to their respective control, the water-deficit induced a more expressive reduction in g_s in BRS-PDE (93%) than in BRS-PA (87%) (Figure 2B). E was significantly lower (3.2%) in control plants of BRS-PA than in BRS-PDE, while significantly lower (4.5%) in BRS-PA than in BRS-PDE concerning stressed plants (Figure 2C). Although these differences between cultivars compared within the same watering regime were statistically significant, the magnitude of such differences in E was subtle and, for this reason, the water-deficit induced similar decreases in E (86%) in both plant materials as compared with their respective control plants (Figure 2C).

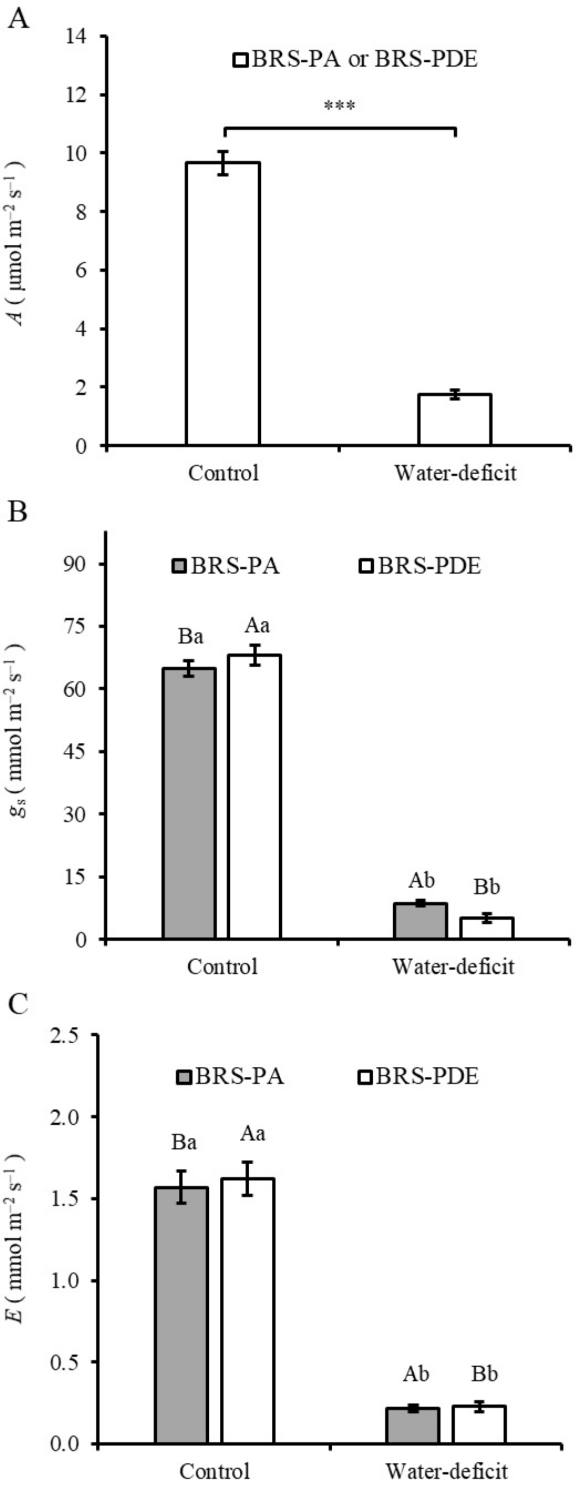

Figure 2. Net CO_2 assimilation rate (A, Figure 2A), stomatal conductance to water vapor (g_s, Figure 2B), and transpiration rate (E, Figure 2C) in two assai cultivars (BRS-PA and BRS-PDE) submitted to well-watered (Control) and water-deficit (Water-deficit) conditions. Data are the mean ± S.E. (n = 5).

In Fig. 2a, asterisks indicate mean difference between control and stressed plants (F-test, $P < 0.001$). In Figures 2B and 2C, the uppercase letters compare different cultivars within the same watering regime (cultivar effect) and lowercase letters compare each cultivar separately upon different watering regimes (watering regime effect). Means followed by different uppercase and lowercase are statistically different by Tukey's test ($P < 0.05$).

Instantaneous and intrinsic water use efficiency

The differential responses of A, g_s, and E between cultivars and watering regimes led to different responses in A/E and A/g_s. While A/E was significantly affected by the watering regimes only, A/g_s was significantly influenced by the interaction between cultivars and watering regimes (Table 1). Thus, relative to control plants, the water-deficit induced 42.7% increases in A/E in both assai cultivars (Figure 3A). On the other hand, A/g_s was similar (0.15 mmol mol^{-1}) between control plants of the two assai cultivars, while A/g_s were statistically different between stressed plants of BRS-PA (0.20 mmol mol^{-1}) and BRS-PDE (0.41 mmol mol^{-1}) (Figure 3B). Therefore, the water-deficit induced increased A/g_s in 33% and 193% in both stressed plants (BRS-PA and BRS-PDE) as compared to their respective control (Figure 3B).

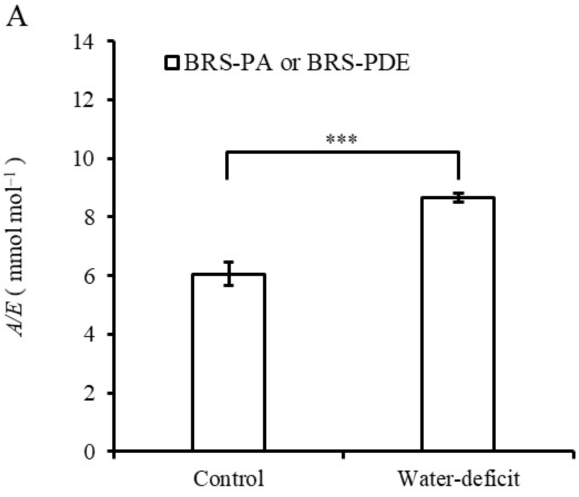

Figure 3A. Instantaneous (A/E, Figure 3A) water use efficiency in two assai cultivars (BRS-PA and BRS-PDE) submitted to well-watered (Control) and water-deficit (Water-deficit) conditions. Data are the mean ± S.E. ($n = 5$).

In Figure 3A, asterisks indicate mean difference between control and stressed plants (F-test, $P < 0.001$).

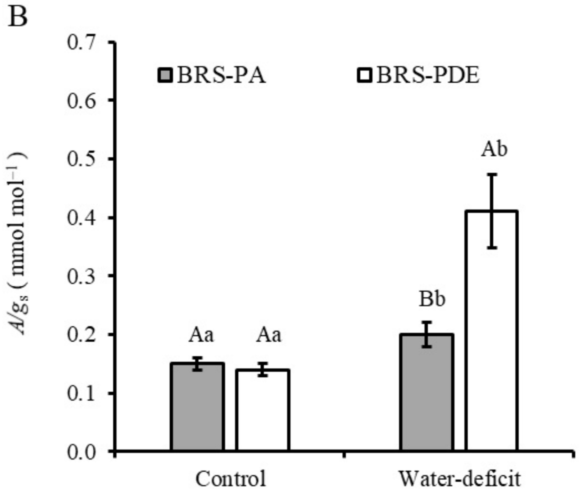

Figure 3B. Intrinsic (A/g_s, Figure 3B) water use efficiency in two assai cultivars (BRS-PA and BRS-PDE) submitted to well-watered (Control) and water-deficit (Water-deficit) conditions. Data are the mean ± S.E. ($n = 5$).

In Figure 3B, the uppercase letters compare different cultivars within the same watering regime (cultivar effect) and lowercase letters compare each cultivar separately upon different watering regimes (watering regime effect). Means followed by different uppercase and lowercase are statistically different by Tukey's test ($P < 0.05$).

Proline, glycine betaine and total soluble carbohydrates

Foliar proline and total soluble carbohydrates were significantly influenced only by watering regimes, while interaction between cultivars and watering regimes was significant for sucrose concentration (Table 1). Thus, regardless of cultivar, the water-deficit increased proline concentration by 44.3% and decreased total soluble carbohydrates by 27% when compared to control (Figure 4 A and B). Foliar sucrose did not differ between control plants of both assai cultivars, with an average of 36.4 mg sucrose g^{-1} dry matter (DM). Under water-deficit conditions, sucrose significantly decreased in both assai cultivars as compared with respective control plants; however, the observed decreases were more expressive in BRS-PA (53.2%) than in BRS-PDE (16.3%) (Figure 4C). Foliar glycine betaine was also determined, however, the independent effect of cultivar and watering regime as well as the effect of cultivar and watering regime interaction were non-significant (Table 1). Thus, an average of foliar glycine betaine of 29.5 ± 6.6 mg g^{-1} DM was observed in all examined plants.

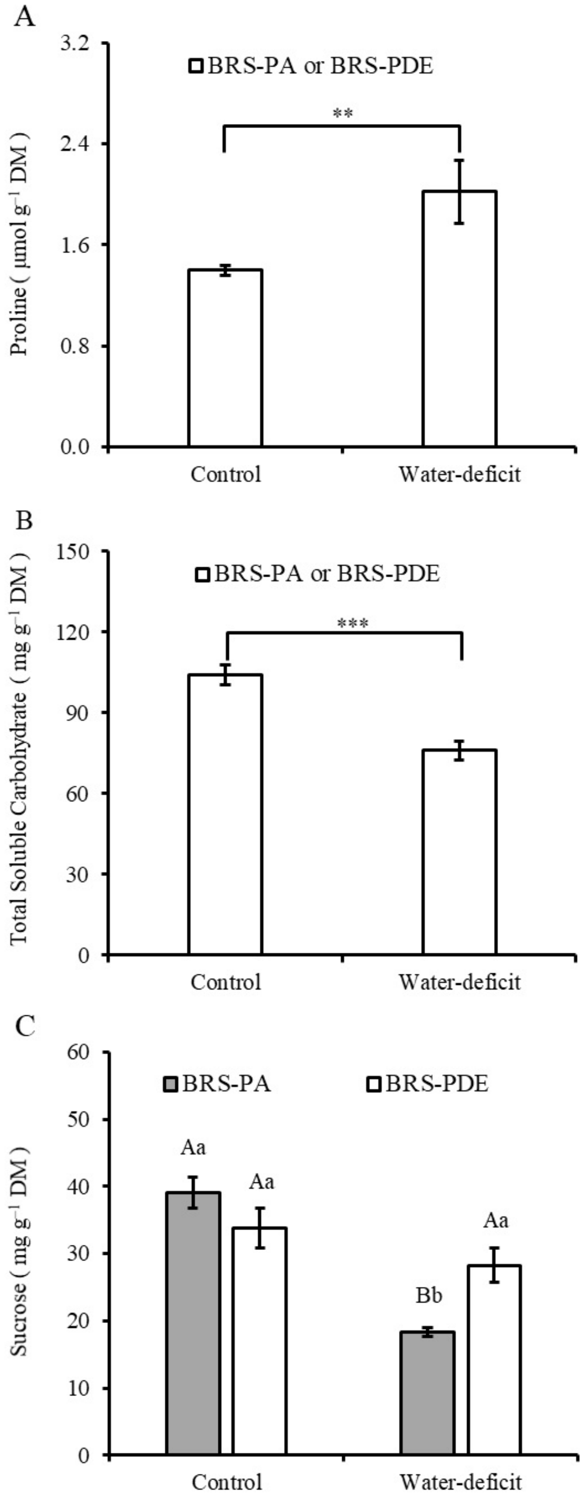

Figure 4. The foliar concentration of proline (A), total soluble carbohydrates (B), and sucrose (C) in two assai cultivars (BRS-PA and BRS-PDE) submitted to well-watered (Control) and water-deficit (Water-deficit) conditions. Data are the mean ± S.E. (*n* = 5). In Figures 4A and 4B, asterisks indicate mean difference between control and stressed plants (F-test, $^{**}P < 0.01$ and $^{***}P < 0.001$). In Figure 4C, the uppercase letters compare different cultivars within the same watering regime (cultivar effect) and lowercase letters compare each cultivar separately upon different watering regimes (watering regime effect). Means followed by different uppercase and lowercase are statistically different by Tukey's test ($P < 0.05$).

Relative water content

The RWC was significantly influenced by the watering regimes, while no interaction was observed between the cultivar and watering regime (Table 1). Therefore, the water-deficit similarly decreased RWC (8.55%) in both cultivars as compared with control counterparts (Figure 5).

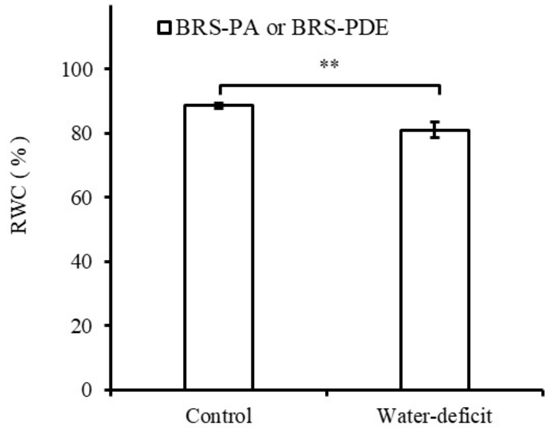

Figure 5. Relative water content (RWC) in two assai cultivars (BRS-PA and BRS-PDE) submitted to well-watered (Control) and water-deficit (Water-deficit) conditions. Data are the mean ± S.E. (*n* = 5). Asterisks indicate mean difference between control and stressed plants (F-test, $^{**}P < 0.01$).

Discussion

Under full irrigation, our results reveal similarities between BRS-PA and BRS-PDE cultivars in most of the evaluated variables. Moreover, A/E and A/g_s did not differ between control plants; even though g_s and E averages were slightly higher in BRS-PDE than in BRS-PA. Comparatively, little differences in growth and leaf gas exchange variables were reported for different assai plant materials grown under full irrigation for up to 180 days of cultivation in the nursery (SILVESTRE et al. 2016). Taken together, our results indicate that the physiological performances of BRS-PA and BRS-PDE plants must be similar under full-irrigation conditions.

Under water-deficit, expressive decreases in A, g_s, and E in both cultivars were observed. In BRS-PA, the present results corroborate with our previous works, in which the high sensitivity of BRS-PA plants to water-deficit was associated to both stomatal and biochemical limitations in net photosynthesis (OLIVEIRA et al. 2019; SANTOS et al. 2022). On the other hand, previous information about the effects of water-deficit in BRS-PDE physiology is unknown, as this cultivar was recently selected for cultivation at field conditions. Despite the similarities between cultivars regarding water-deficit responses, it is important to note that averages of g_s in stressed plants of BRS-PDE (4.97 mmol m^{-2} s^{-1}) were significantly lower than observed in BRS-PA (8.98 mmol m^{-2} s^{-1}), which indicates a more expressive stomatal closure. Considering that all plants in this experiment were grown and evaluated upon similar environmental conditions, the stomatal closure in both assai cultivars must have been chiefly governed by changes in Ψ_{pd}, possibly in a mechanism involving root-to-shoot hydraulic signaling that culminates in enhanced foliar biosynthesis of abscisic acid (CHRISTMANN et al., 2007; IKEGAMI et al., 2009; MCADAM; BRODRIBB, 2018). Differential stomatal closure between plant materials was also observed in other dicotyledons and monocotyledons, in which a lower g_s and E have been claimed as a drought-tolerance mechanism (PINHEIRO et al., 2005; SILVA et al., 2016; SURESH et al., 2012; DAYER et al., 2020). Therefore, drought-tolerant genotypes can present more efficient stomatal closure under drought conditions in relation to stress-sensitive genotypes (COHEN et al., 2021; LOURKISTI et al., 2021).

Although A, g_s, and E data are acceptable indicators to discriminate genotypes regarding their response to abiotic stresses, A/E and A/g_s seem to be more appropriate parameters to assess differential responses of plants to drought (BOTA et al., 2016; HATFIELD; DOLD, 2019; LIU et al., 2019). A/E and A/g_s generally reach the highest values in water-stressed than in non-stressed plants and the magnitude of such increases is expected to be more significant in drought-tolerant genotypes than in sensitive ones (DAMATTA et al., 2003; SURESH et al., 2012; BOTA et al., 2016; ALMEIDA et al., 2016). In assai, it was earlier reported that plants submitted to long-term water-deficit under incipient daily irrigation did not induce significant adjustments in A/E (SILVESTRE et al., 2016). By contrast, in this study, the water-deficit markedly decreased A, g_s, and E, leading to increases in A/E and A/g_s. Increases in A/E did not differ significantly between BRS-PA and BRS-PDE stressed plants, which was likely related to similar decreases in both A and E. On the other hand, our results indicated a clear distinction between assai cultivars in terms of A/g_s, which was significantly higher in BRS-PDE than in BRS-PA. This response is likely related to a more expressive decrease in g_s in the reference cultivar, suggesting thus a higher stomatal sensitivity to abscisic acid. In other plant species, higher A/g_s is commonly observed in drought-tolerant genotypes as compared with sensitive ones (MASHILO et al., 2017; LIU et al., 2019; SILVA et al., 2022), then the higher A/g_s in BRS-PDE may be an advantageous mechanism to cope with drought in this cultivar as compared with BRS-PA.

Besides water-use efficiency, foliar concentrations of osmotically active solutes (proline, glycine betaine, sucrose, and total soluble carbohydrates) and RWC were assessed in this experiment to indirectly examine possible occurrence of osmotic adjustment in stressed assai plants (VALLIYODAN; NGUYEN, 2006; GOMES et al., 2010; MACÊDO et al., 2019; LI et al., 2020; OZTURK et al. 2020; TRAVERSARI et al., 2020). Our results showed similar increases in proline content between stressed plants of both cultivars as compared with respective control plants. This increase in proline concentration was likely linked to *de novo* synthesis of this compound in the cytosol (KOENIGSHOFER; LOEPPERT, 2019; FURLAN et al., 2020). By contrast, foliar glycine betaine under stress conditions did not differ from control plants, confirming our previous findings for two assai plant materials (Hideo ecotype and BRS-PA cultivar; SILVESTRE et al., 2017) and indicating that this compound is unrelated to water-deficit responses in assai cultivars, including in BRS-PDE cultivar. On the other hand, the significant decreases in total soluble carbohydrates and sucrose in stressed plants of both cultivars may be related to a lower triose-P synthesis by the Calvin cycle, since A was sharply decreased in these plants in relation to their counterparts. Since increases in the foliar concentration of proline were counterbalanced by the decreases in foliar concentrations of sucrose and total soluble carbohydrates, thus the foliar pool of osmotically active solutes must have been decreased to some extent. The osmotic potential was not determined in this experiment, then it is not possible to infer the occurrence of osmotic potential. However, relative to control, the slight decrease in RWC (only 8.55%) and the increases in foliar proline in stressed plants of both cultivars strongly evidence the occurrence of osmotic adjustment in this species, as firstly evidenced by Calbo and Moraes (2000). On the other hand, because assai plants are sensitive to photooxidative damages under water-deficit conditions (OLIVEIRA et al., 2019), thus part of the total proline synthesized in water-stressed plants may have played an important role in cell protection against oxidative stress (SZABADOS; SAVOURÉ, 2010). This antioxidant role should be assessed in further experiments.

Conclusions

We have shown that the effects of water-deficit on leaf gas exchange parameters have been close between assai BRS-PDE and BRS-PA cultivars. Likewise, the similar magnitude of both increases in foliar proline and decrease in RWC observed in stressed plants, as compared to their respective control, suggest an occurrence of osmotic adjustment at the same extent in the studied assai cultivars. Finally, our data pointed out specific behaviors in A, g_s, and E between well-watered and stressed plants, which reflected in a higher A/g_s in BRS-PDE when compared to BRS-PA.

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