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ORIGINAL ARTICLE

Drought tolerance in two oil palm hybrids as related to adjustments in carbon metabolism and vegetative growth

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Abstract Drought tolerance was examined in two oil palm hybrids (BRS Manicoré and BRS C 2501) grown in large pots and subjected to long-term drought (57 days) and rehydration. Regardless of hybrids, predawn water potential (Ψ_{pd}), net photosynthesis rates, and stomatal conductance decreased similarly upon drought imposition, but the absolute values of these variables were lower in BRS C 2501 than in BRS Manicoré. Overall, drought-induced decreases in activities of key enzymes associated with carbon metabolism, including Rubisco, ADP-glucose pyrophosphorylase, and sucrose-phosphate synthase, were stronger in BRS C 2501 than in BRS Manicoré. Our data suggest that synthesis of starch (and possibly sucrose) was fundamentally limited by a lower substrate availability rather than by enzymatic constraints, particularly until day 34 after suspending watering. Drought stress provoked similar decreases in biomass accumulation in either hybrid; however, BRS Manicoré plants displayed higher total leaf area and root length coupled with greater relative decreases in dry matter of above-ground parts than of roots as compared to BRS C 2501, thereby leading to an increased root-to-above ground ratio in the former. Upon resuming irrigation, the slow recovery of Ψ_{pd} preceded the recovery of stomatal conductance and photosynthesis irrespective of hybrid. BRS Manicoré was better able to recover enzyme activities and carbohydrate status than BRS C 2501. In conclusion, both hybrids could tolerate (or survive) the severe drought conditions, but, overall, BRS Manicoré plants were better able to adjust its physiological, morphological, and biochemical traits to cope with drought than did BRS C 2501.

Keywords Drought recovery · Photosynthesis · *Elaeis guineensis* · *Elaeis oleifera* · Carbon metabolism · Water deficit

Introduction

Oil palm is a perennial palm cultivated as monoculture or in agroforestry system (Harun and Salleh 2015) and plantations worldwide are commonly formed using genotypes of African oil palm (*Elaeis guineensis* Jacq.), which are distributed over humid tropical areas, particularly in some equatorial countries of Africa, Asia, and Latin America (Villela et al. 2014; Barcelos et al. 2015). This species produces high annual fruit loads that, coupled with a high efficiency of the extraction and refining processes for obtaining crude oil palm and palm kernel oil from mesocarp and kernel, respectively (Barcelos et al. 2015; Mba et al. 2015), makes it of great economic importance. Indeed, considerable amounts of total vegetable oil and fats demanded for cooking and frying or used in food industry, cosmetics, medicine, lubricants, and biodiesel production are obtained from oil palm fruits (Mba et al. 2015).

In several reports, a marked sensibility of oil palm genotypes to drought has been demonstrated (e.g., Méndez

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et al. 2012; Silva et al. 2016; Sun et al. 2011; Suresh et al. 2012). Under increasing soil water deficiency, net CO_2 assimilation rate (A), stomatal conductance to water vapor (g_s), and transpiration rate (E) were progressively decreased with soil water depletion, all of which reaching values near zero when leaf water potential of drought-stressed palms was approximately −3.6 MPa (Suresh et al. 2010). The decreases in A were accompanied by significant decreases in several chlorophyll (Chl) *a* fluorescence variables, including the maximum quantum efficiency of PSII primary photochemistry and apparent electron transport rate (Suresh et al. 2010). In 3-month-old oil palm seedlings, drought caused significant decreases in Chl *a* and Chl *b* contents and increased activity of catalase and guaiacol peroxidase in addition to up-regulating several genes related to drought in both leaves and roots (Azzeme et al. 2016). In in vitro drought-stressed seedlings (induced using mannitol or polyethylene glycol), significant decreases in A and Chl *a* fluorescence variables and in both Chl *a* and total carotenoids pools have been also observed (Cha-um et al. 2010, 2012). The vegetative growth of drought-stressed oil palm trees was also impaired by drought; these responses differed greatly between plant materials according to the severity and magnitude of drought stress (Sun et al. 2011; Méndez et al. 2012).

There is great genotype variability among wild populations of both African (*E. guineensis*) and American (*E. oleifera* Kunth, Cortés) oil palm and among intraspecific (*E. guineensis* × *E. guineensis*) and interspecific (*E. guineensis* × *E. oleifera*) hybrids. Intrinsic phenotypic traits of particular genotypes have been used in breeding programs to develop shorter and more productive palms as well as to select genotypic plant materials showing improved Fusarium wilt tolerance and improved fatty acid, carotenoid, and vitamin E contents, among other traits (for a review see Barcelos et al. 2015). The oil palm breeding programs focusing on drought tolerance has been also targeted. Indeed, several screening experiments have been carried out aiming at identifying plant materials showing morphological and physiological strategies enabling them to tolerate drought more satisfactorily. Results indicate that tolerance to drought of oil palm hybrids is remarkably associated with (1) improved stomatal control of transpiration (Suresh et al. 2012; Jazayeri et al. 2015), (2) higher A and water use efficiency (Méndez et al. 2012; Jazayeri et al. 2015), and (3) lower respiration rate and higher accumulation of leaf reducing sugars possibly associated with an osmotic adjustment (Méndez et al. 2012). In high-yielding *tenera* hybrid, an ability to adjust seasonal source-sink imbalances using non-structural carbohydrates from stem rather than adjusting net photosynthesis was also suggested under drought stress (Legros et al. 2009).

In 2014, Brazilian oil palm plantations were spread over an area of 126,559 ha, producing 1,393,873 tons of fruits (IBGE 2016). Notably, 85% of the total Brazilian fruit production has been obtained from 72,528 ha of oil palm plantations located on northeast Pará State, specifically in areas where drought spells are uncommon, i.e., annual water deficit below 100 mm (Bastos et al. 2001; Villela et al. 2014). Nonetheless, in regions with moderate (annual water deficiency between 100 and 350 mm) or severe (greater than 350 mm) annual drought seasons, oil palm yields can be remarkably constrained; indeed, drought is believed to be an important environmental factor limiting the expansion of oil palm plantations in the Amazonian region (Bastos et al. 2001). Therefore, the identification of oil palm genotypes with improved physiological performance under drought conditions is crucial for breeding programs focusing on drought tolerance.

In a previous study, we have demonstrated the occurrence of drought-mediated oxidative stress in two oil palm hybrids (BRS Manicoré and BRS C 2501), which was believed to be triggered by an imbalance between light capture and use, particularly under moderate-to severe drought. The results evidenced that BRS Manicoré presented more robust enzymatic and non-enzymatic strategies involved in reactive oxygen species scavenging and dissipation of excess energy and/or reducing equivalents, particularly under severe drought stress (Silva et al. 2016). Therefore, it is tempting to hypothesize that the photosynthetic apparatus (and carbon metabolism) should be better protected against drought stress in BRS Manicoré than in BRS C 2501; accordingly, it is expected that vegetative growth should be impaired by drought to a lesser extent in BRS Manicoré plants. To test these hypotheses, young BRS oil palms were subjected to a progressive soil water deficit during 57 days and drought-mediated changes in leaf water potential, leaf gas exchange, leaf carbohydrates, growth traits, and enzyme activities related to carbon metabolism were periodically assessed during stress period and after resuming irrigation (rehydration period). This long-term experiment was carried out in large containers to relatively simulate the conditions of long-term dry seasons that often occur in some parts of the Amazon biome (Bastos et al. 2001; Brando et al. 2010; Davidson et al. 2012). Our results provide novel insights in understanding physiological responses to drought in oil palm.

Methods

Plant material and growth conditions

The experiment was set up in a greenhouse at the Federal Rural University of the Amazon, in Belém-PA

(01°28′03″S, 48°29′18″W), north Brazil. Seedlings of two oil palm hybrids [BRS Manicoré, *E. guineensis* Jacq. × *E. oleifera* (Kunth) Cortés, Cunha and Lopes 2010; and BRS C 2501, *E. guineensis* cv. psifera – La Mé × *E. guineensis* cv. dura – Deli, Cunha et al. 2007] were produced from pre-germinated seeds sown in polyethylene trails filled with Yellow Dystrophic Latosol. After emergence, seedlings with similar number of leaves, leaflets, and height were transferred to 50-L pots filled with 40 kg of the same substrate. The pH was adjusted to approximately 6.0 using dolomitic limestone (30 g per pot). Fertilizations were performed by applying 5 g NPK 20-20-20 per plant every 15 days, 2.5 g $MgSO_4 \cdot 7\ H_2O$ per plant every 30 days and 1 g $Na_2B_4O_7 \cdot 10\ H_2O$ per plant at 180 days after planting (Franzini and Silva 2012). All plants were irrigated daily to maintain the soil near to the field capacity; volume of irrigation water was estimated by the gravimetric method (Klar et al. 1966). After cultivation for 12 months, plants were subjected to two watering regimes following a fully randomized design: (1) plants that were irrigated continuously as described above (Control treatment); and (2) plants subjected to water deficit imposed by withholding watering (Water-deficit treatment). Five replicates per each treatment were used and a single plant per pot was considered as a replicate. Two groups of plants were simultaneously subjected to drought stress: in the first group, plants were grown for assessing predawn water potential (Ψ_{pd}), leaflet gas exchange [net CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration rate (E)] measurements, and sampling for biochemical assays during the stress imposition and after resuming irrigation (see details below); in the second group, plants were only assessed at the end of the drought stress period when growth traits were measured.

The drought stress was imposed during 57 days in an attempt to simulate the long-term drought spells that may occur in some areas of north Brazil. Over the course of the experiment, the Ψ_{pd} and leaflet gas exchange variables were monitored every 7 days (starting when irrigation was suspended in the drought treatment). Sampling for biochemical assays were performed at day 0 and when Ψ_{pd} of drought-stressed plants reached approximately −2.0, −3.0, and −4.0 MPa (days 21, 34, and 57, respectively). After measurements and samplings on day 57, the irrigation was resumed to evaluate the ability of plants to recover their tissue hydration and physiological performance. The recovery period was carried out until Ψ_{pd} of stressed plants of at least one hybrid did not differ significantly in relation to their respective control counterparts. During the recovery period, the measurements of Ψ_{pd} and leaflet gas exchange variables were assessed in 4-day intervals, whereas samplings for biochemical assays were performed just at the end of the rehydration period (day 98). Middle leaflets of the third or fourth leaves from the shoot apex were selected for Ψ_{pd} and leaflet gas exchange measurements and sampling for biochemical assays. The collected leaflet samples were flash frozen and kept in liquid nitrogen until analysis. Growth attributes were assessed at the end of stress period (day 57), using intact plants subjected to the same watering treatments as described above. During the experimental period, the mean diurnal air temperature (T_{air}), relative humidity (RH), and light duration and intensity at the experimental site were recorded and registered using a data logger (HOBO U12-012, Onset Computer Corporation, Bourne, EUA). The means for these parameters were 29.2 ± 0.2 °C, 76.8 ± 0.9%, 12.8 ± 0.5 h, and 1512 ± 63 μmol photons $m^{-2}\ s^{-1}$, respectively.

Ψ_{pd} and leaflet gas exchange

The Ψ_{pd} was measured using a Scholander type pressure chamber (mod. PMS Instrument Co., Corvalles, USA) (Pinheiro et al. 2008). A, g_s, and E were determined with a portable open-system infrared gas analyzer (LCpro+, ADC BioScientific Ltd., Hoddesdon, UK) between 7:40 and 8:40 h under ambient CO_2 concentration and photosynthetically active radiation (PAR) set up at 1100 μmol photons $m^{-2}\ s^{-1}$ (Suresh et al. 2012). The instantaneous water use efficiency (WUE) was calculated as A/E. Means of T_{air}, RH, PAR, and vapor pressure deficit inside greenhouse during morning measurements (between 06:00 and 10:00 h) were 28.8 ± 0.1 °C, 81 ± 0.7%, 937 ± 39 μmol photons $m^{-2}\ s^{-1}$ and 0.80 ± 0.03 kPa, respectively.

Enzyme activities

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39), ADP-glucose pyrophosphorylase (AGPase, EC. 2.7.7.27), sucrose-phosphate synthase (SPS, EC 2.4.1.14), sucrose synthase (SuSy, EC 2.4.1.13), and both acid and alkaline invertases (EC 3.2.1.26) were obtained from leaflet samples (25 mg fresh matter) that were previously ground in liquid nitrogen and thoroughly shaken with 800 μL extractor solution according to Geigenberger and Stitt (1993). Samples were centrifuged at 3000×*g* for 5 min at 4 °C and the supernatant was collected for enzymatic assays, which were carried out as described previously: Rubisco (Sulpice et al. 2007), AGPase (Gibon et al. 2004), SPS (Sinha et al. 1997), and SuSy and both acid and alkaline invertases (Dancer et al. 1990).

Leaflet carbohydrates

Lyophilized leaflet samples (25 mg fresh matter) were subjected to ethanolic extraction (Trethewey et al. 1998) and the supernatant was used for glucose, fructose, and sucrose determinations. The resulting pellet was frozen for starch determination. Leaf concentrations of glucose, fructose, and sucrose were determined according Stitt et al. (1989), with some modifications. The reaction mixture contained 100 mM imidazole/5 mM $MgCl_2$ buffer (pH 6.9), 2 mM NAD^+, 1 mM ATP, 1 Unit (U) glucose-6-phosphate dehydrogenase (EC 1.1.1.49), and 7.5 µL leaflet ethanolic extract. Glucose, fructose, and sucrose determinations were assayed by adding 1 U hexokinase (EC 2.7.1.1), 1 U glucose-6-phosphate isomerase (EC 5.3.1.9), and 1 U invertase (EC 3.2.1.26), respectively. After each enzyme addition, the NADH production was accompanied at 340 nm in a microplate reader (mod. VersaMaxTM, Molecular Devices, Sunnyvale, USA). For starch determination, the frozen pellets obtained from the ethanolic extraction were vigorously shaken in 1 mL absolute ethanol and incubated for 20 min at 80 °C. After centrifugation at 12,000×*g* for 5 min at 4 °C, the supernatant was discarded and the pellet was incubated in 1 mL 0.2 M KOH for 60 min at 90 °C. The supernatants obtained after centrifugation at 12,000×*g* for 5 min at 4 °C were neutralized with acetic acid before starch determination (Trethewey et al. 1998). Then, an aliquot (20 µL) of the neutralized extract was incubated for 60 min at 55 °C in a reaction mixture containing 30 µL 0.3 M sodium citrate/0.3 M citric acid buffer (pH 4.6), 10 µL (or 1 U) amyloglucosidase (EC 3.2.1.3), and 240 µL distilled water. After hydrolysis, the resulting glucose content was assayed as previously described and used to calculate starch concentration. Standard curves of glucose, fructose, sucrose, and starch were performed for each assay.

Growth variables

Plant height was determined from the soil surface until the apex of the highest leaf using a ruler. The number of arrow leaves, leaves, and leaflets were directly counted in each plant. At the end of the stress period, leaflets were detached and digitalized with a scanner for total leaflet area (TLA) determination using Image J (Wayne Rasband no National Institute of Mental Health, USA, 2010). The root length was directly measured using a ruler, taking into consideration the root of greater size. Plant parts (arrow leaves, leaflets, petioles and rachis, bulb, and root system) were separated to each other and roots were gently washed with tap water under a fine mesh sieve to remove residual substrate. Plant parts were individually oven dried at 72 °C until constant mass and their dry matters were obtained accordingly. The following variables were calculated: leaf dry matter, as the sum of leaflets, petioles and rachis dry matters; root-to-above ground ratio (R/AG ratio), as the ratio between root system dry matter and dry matter of above-ground parts (arrow leaf + leaflet + petiole + rachis + bulb); total plant dry matter, by summing dry matters of all plant parts; and specific leaflet area (SLA) as the ratio between TLA and leaflet dry matter.

Statistics

Data of physiological and biochemical variables collected in different time points were subjected to ANOVA (repeated-measures procedure) tested for significance by *F'* test at $P \leq 0.05$ (Lima et al. 2010). Data of growth variables obtained at the end of the stress period (day 57) were subjected to ANOVA (*F'* test, $P \leq 0.05$) considering the randomized design with four treatment combinations, forming a 2 × 2 factorial scheme (two hybrids and two watering regimes) with five replicates. Statistical significances of mean differences were tested by Tukey's test ($P \leq 0.05$). Regression analysis was performed to examine the relationship between $g_s \times \Psi_{pd}$ and its significance was tested using the *F*'s test ($P \leq 0.05$). The statistical procedures were carried out using the statistical software Systat (v. 12.0.0.1, 2012, Systat Software Inc., Paris, France).

Results

Ψ_{pd} and leaflet gas exchange

The well-watered plants of both hybrids showed similar values of Ψ_{pd}, *A*, and g_s throughout the experimental days (Fig. 1). The Ψ_{pd} was nearly constant over the entire experiment, averaging on -0.11 MPa (Fig. 1a). The *A* values varied similarly in both hybrids from approximately 8 µmol m^{-2} s^{-1} on day 0 to 11 µmol m^{-2} s^{-1} on day 57 (Fig. 1b), while g_s changed from approximately 100 mmol m^{-2} s^{-1} on day 0 to 56 mmol m^{-2} s^{-1} on day 57 (Fig. 1c).

The water deficit caused progressive decreases in Ψ_{pd} in both hybrids upon suspending watering. Although the overall pattern of changes in Ψ_{pd} did not differ significantly between BRS hybrids, the Ψ_{pd} values in stressed plants of BRS Manicoré tended to be slightly higher than those in BRS C 2501 between days 21 and 57 (Fig. 1a). At the end of stress period, Ψ_{pd} was −4.0 MPa in BRS Manicoré and −4.4 MPa in BRS C 2501 (Fig. 1a).

Regardless of hybrids, the decreases in Ψ_{pd} in the stressed plants caused sharp decreases in *A* and g_s, particularly during the two initial weeks of stress period, in which both variables were decreased by about 87% in relation to their respective control plants (Fig. 1b, c). Further decreases in *A* were observed with the progress of stress period, reaching negative values earlier in BRS C 2501 (on day 34) than in BRS Manicoré (on day 50) (Fig. 1b) in parallel with a complete stomata closure

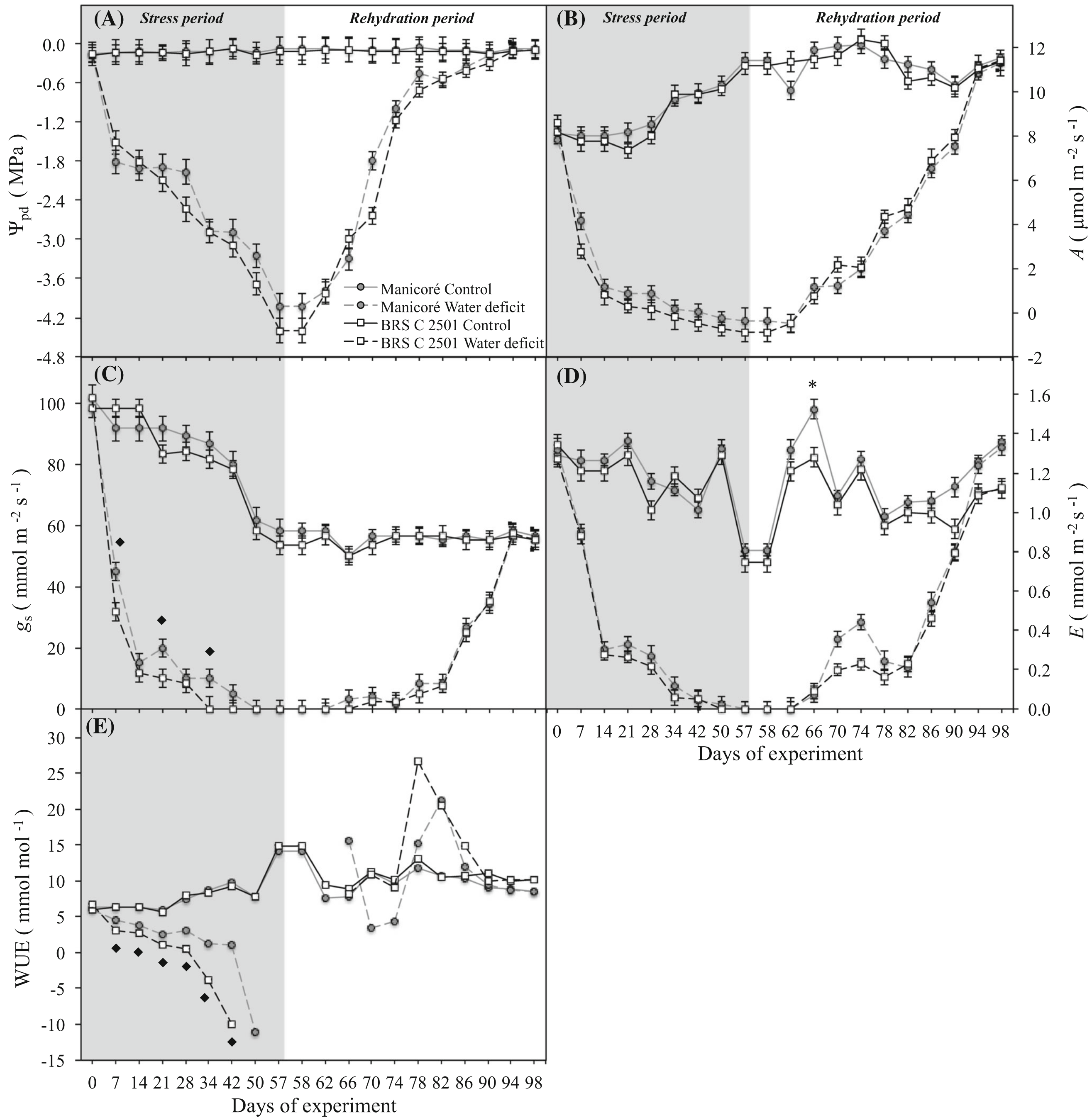

Fig. 1 Predawn water potential (Ψ_{pd}) and leaflet gas exchange (net CO_2 assimilation rate, A; stomatal conductance to water vapor, g_s; transpiration rate, E; and water use efficiency, WUE) in two oil palm hybrids (BRS Manicoré and BRS C 2501) subjected to progressive drought and rehydration. *Asterisks* denote statistical differences between well-watered plants of BRS hybrids within each time point. *Diamonds* denote statistical differences between stressed plants of BRS hybrids within each time point. Mean comparisons were tested for significance by Tukey's test ($P \leq 0.05$). $n = 5 \pm$ SD

(g_s = zero) (Fig. 1c). The interactions between $g_s \times \Psi_{pd}$ were highly significant for stressed plants of both hybrids, with a curvilinear decrease of g_s with decreasing Ψ_{pd} with no threshold Ψ_{pd} value determining g_s decreases (Fig. 2). When irrigation was resumed, Ψ_{pd}, A, and g_s were recovered slowly in both hybrids until reaching values that were similar to those of control plants only at 36 days latter (i.e., on day 94, Fig. 1a). In any case, resumption of Ψ_{pd} preceded resumption of both g_s and A.

The E in stressed plants of both hybrids was decreased at the same magnitude in all time points, being completely suppressed ($E = 0$ mmol m^{-2} s^{-1}) on day 50 (BRS C

2501) and on day 57 (BRS Manicoré) (Fig. 1d). The magnitude of changes in A and E during the stress period influenced WUE, particularly in BRS C 2501 in which decreases in WUE were stronger than in BRS Manicoré (Fig. 1e). In the former, WUE was decreased by 51% on day 7 and by 208% on day 42, with negative averages registered on days 34 (-3.74 mmol mol^{-1}) and 42 (-9.94 mmol mol^{-1}). In the latter, WUE was decreased by 27% on day 7 and by 90% on day 42 and 242% on day 50, with negative mean value registered only on day 50 (-11 mmol mol^{-1}) (Fig. 1e). The WUE was not calculated on days 50 (BRS C 2501) and 57 (both hybrids), because E was zero in both hybrids (Fig. 1f). After resuming irrigation, both E and WUE were also recovered to control levels in both hybrids.

Enzyme activities

The progressive water-deficit conditions caused significant ($P \leq 0.05$) decreases in both initial and final Rubisco activities in both hybrids, but to a greater extent in BRS C 2501 than in BRS Manicoré in all time points during the stress period (Fig. 3). Under more severe water-deficit condition (day 57), the initial and final Rubisco activities were decreased by approximately 55% in BRS Manicoré and 64% in BRS C 2501 as compared to their respective control plants (Fig. 3). After resuming irrigation, Rubisco activity was recovered to a greater extent in BRS Manicoré than in BRS C 2501 (Fig. 3). Although the Rubisco activities have been negatively affected by drought, it is interesting to note that the Rubisco activation state (averaged on 83%) did not vary significantly ($P > 0.05$) regardless of treatments (data not shown).

The AGPase activity was significantly ($P \leq 0.05$) decreased in stressed plants of both hybrids from day 34 onwards (Fig. 4a). On day 57, AGPase activity was decreased by 45 and 60% in stressed plants of BRS Manicoré and BRS C 2501 as compared to their control counterparts, respectively (Fig. 4a). The AGPase activity was fully recovered in rehydrated plants of both hybrids BRS (Fig. 4a).

Drought stress provoked a 16% decrease in the initial SPS activity in both hybrids on day 34 (Fig. 4b). On day 57, these decreases were 17 and 34% in BRS Manicoré and BRS C 2501, respectively (Fig. 4b). The final activity of SPS did not vary significantly ($P > 0.05$) in stressed plants of BRS Manicoré, but it was decreased by 47% in stressed plants of BRS C 2501, as assessed on day 57 (Fig. 4b). The SPS activation state averaged on 75% for both hybrids, with only minor, if at all, variations during the stress period

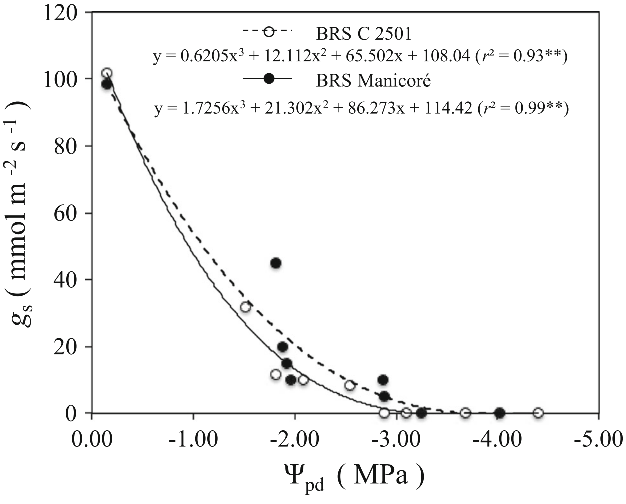

Fig. 2 Changes in stomatal conductance to water vapor (g_s) as a function of decreasing predawn water potential (Ψ_{pd}) in drought-stressed plants of two oil palm hybrids (BRS Manicoré and BRS C 2501). Data are the mean of five replicates. *Asterisk* means statistical significance of the regression analysis tested by F's test ($P \leq 0.01$)

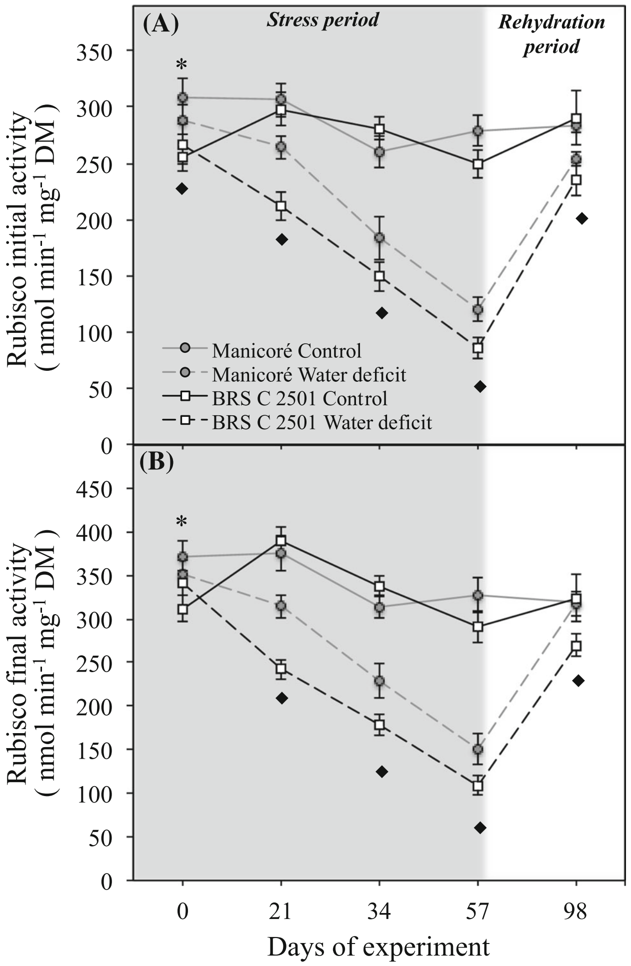

Fig. 3 Initial and final Rubisco activities in two oil palm hybrids (BRS Manicoré and BRS C 2501) subjected to progressive drought and rehydration. Statistic as in Fig. 1

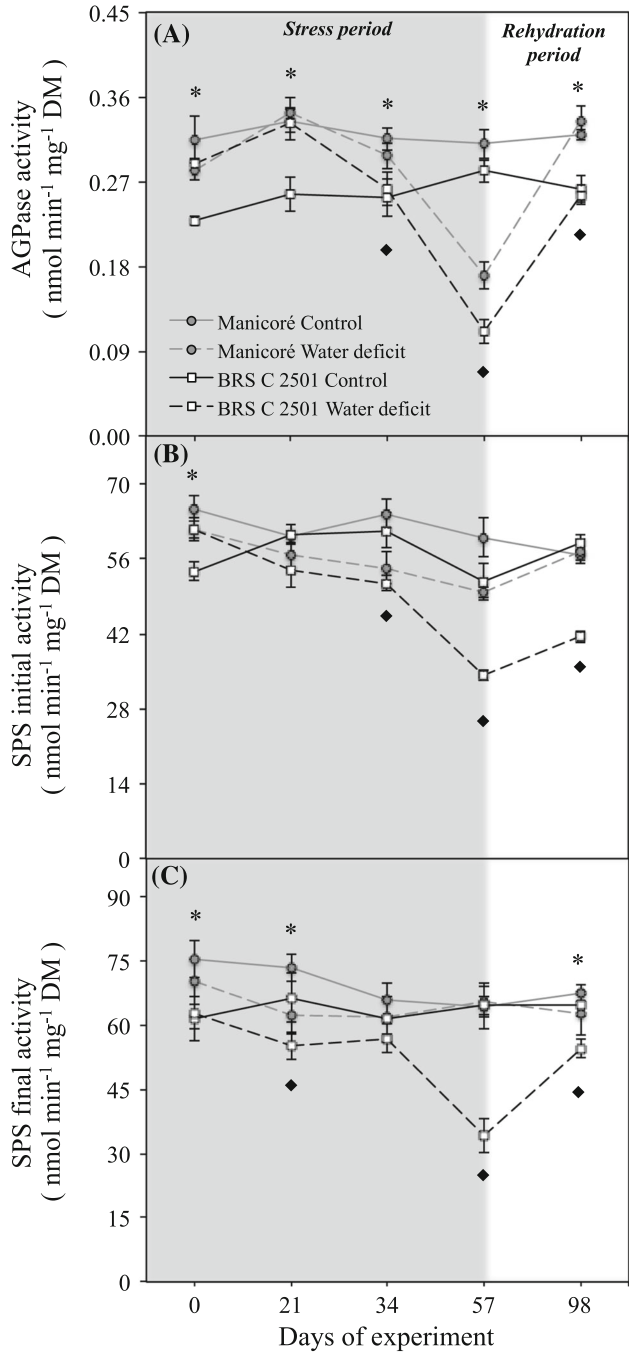

Fig. 4 Changes in ADP-glucose pyrophosphorylase (AGPase) and initial and final sucrose-phosphate synthase (SPS) activities in two oil palm hybrids (BRS Manicoré and BRS C 2501) subjected to progressive drought and rehydration. Statistic as in Fig. 1

(data not shown). During rehydration, both the initial and final SPS activities were only fully recovered in BRS Manicoré plants (Fig. 4b, c).

The water deficit did not cause any significant changes in SuSy activities in BRS Manicoré over the entire experiment (Fig. 5a). By contrast, SuSy activities were significantly ($P \leq 0.05$) decreased by 16 and 44% in stressed plants of BRS C 2501, as assessed on days 34 and 57, and partially recovered after resuming irrigation (Fig. 5a). The activity of acid invertase was decreased by 18% in stressed plants of BRS Manicoré, as assessed on days 34 and 57, while in BRS C 2501, it was unaffected by drought (Fig. 5b). On days 34 and 57, drought stress caused decreases in alkaline invertase activities in both BRS Manicoré (16 and 32%, respectively) and BRS C 2501 (23 and 44%, respectively) (Fig. 5c). The acid and alkaline invertase activities were fully recovered in rehydrated plants of both hybrids (Fig. 5b, c).

Leaf carbohydrates

The starch and glucose concentrations were similarly affected by water deficit in both hybrids (Fig. 6a, b). In BRS Manicoré, drought stress caused 53, 72, and 86% decreases in starch concentration on days 21, 34, and 57, respectively, whereas in BRS C 2501, these decreases were 72% on day 21 and 86% on days 34 and 57 (Fig. 6a). The decreases in glucose pools caused by drought averaged on 58% in both BRS hybrids on days 21 and 34 (Fig. 6b). On day 57, glucose concentrations tended to increase in both hybrids in relation to values observed on day 34; nevertheless, these values still remained 30 and 52% lower in stressed plants of both BRS Manicoré and BRS C 2501 plants than in their respective control plants (Fig. 6b).

Water deficit affected fructose concentrations in varying ways in either hybrid. Compared with controls, water deficit caused a 41% increase (day 21) and a 34% decrease (day 57) in fructose pools in BRS Manicoré, and decreases (32% on day 21, and 16% on days 34 and 57) in BRS C 2501 (Fig. 6c). Sucrose was not detected in this study regardless of treatments.

After resuming irrigation, starch concentrations in BRS Manicoré and BRS C 2501 plants were, respectively, recovered by 84 and 68% as compared with their respective control counterparts at the end of rehydration period (Fig. 6a). At this time, both glucose and fructose concentrations were fully recovered in stressed plants of BRS Manicoré, but it remained approximately 31% lower in BRS C 2501 plants subjected to rehydration (Fig. 6b, c).

Growth variables

Overall, growth variables were similarly affected by the imposed treatments with only minor differences between hybrids (Table 1). The stressed plants were approximately 17% shorter than their respective control plants. The number of arrow leaves was similar regardless of hybrids and watering regimes, although the number of definitive leaves was 11% lower in stressed plants. The number of leaflets and TLA in stressed plants decreased by 52 and

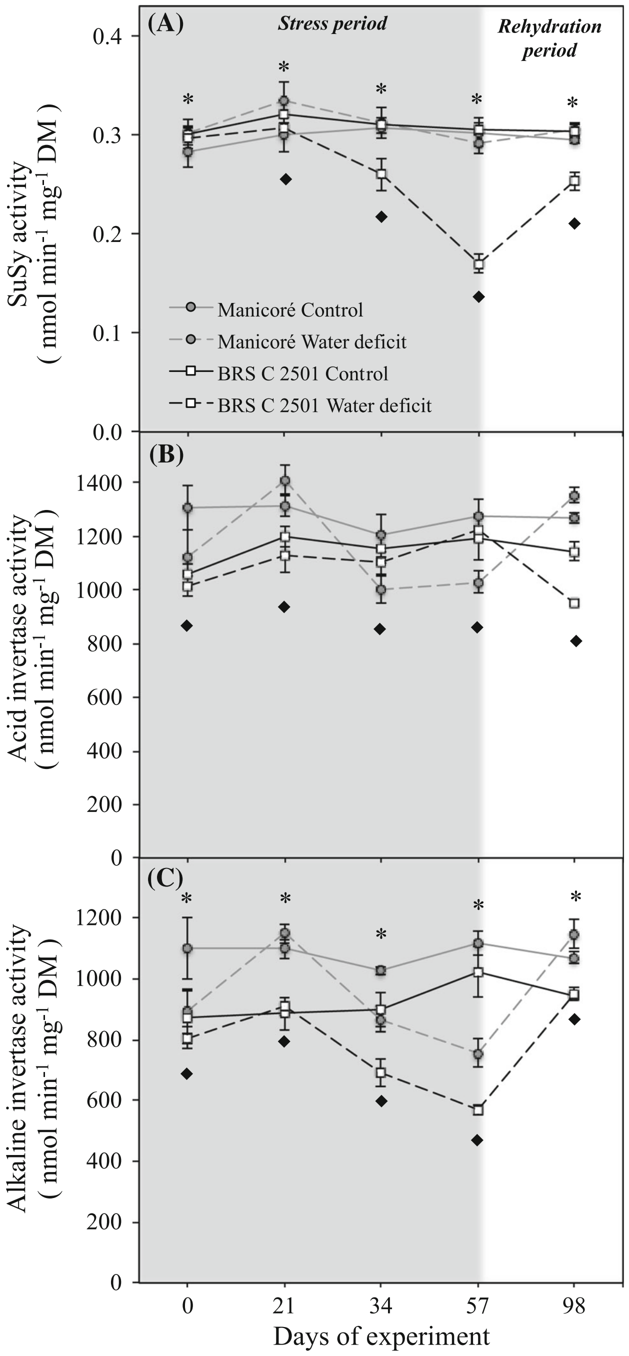

Fig. 5 Changes in sucrose synthase (SuSy) and in both acid and alkaline invertases in two oil palm hybrids (BRS Manicoré and BRS C 2501) subjected to progressive drought and rehydration. Statistic as in Fig. 1

37%, in BRS Manicoré, respectively, and by approximately 45% in BRS C 2501. The SLA was unaffected by the watering regime treatments in BRS Mancioré, but SLA was 28% higher in stressed plants of BRS C 2501 in relation to their respective control plants. Regardless of hybrids, differences in leaf and leaflet number were unrelated to leaf and leaflet abscission.

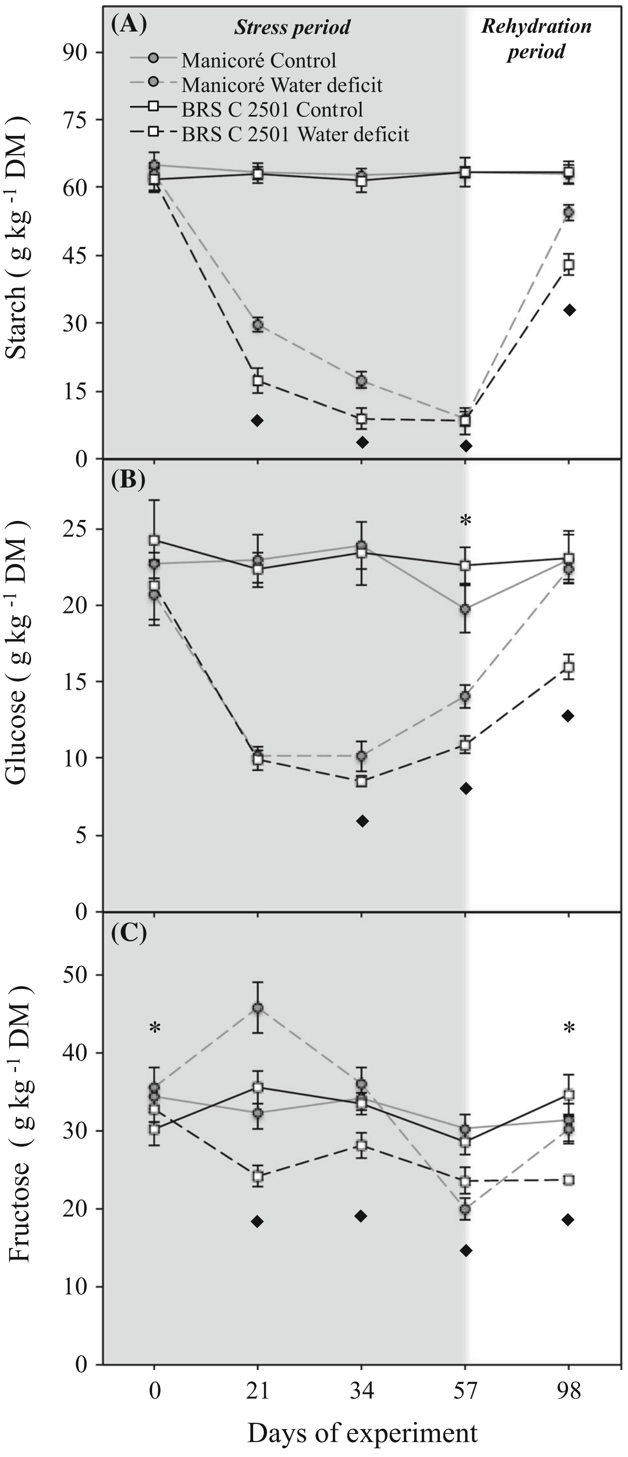

Fig. 6 Changes in leaflet contents of starch, glucose, and fructose in two oil palm hybrids (BRS Manicoré and BRS C 2501) subjected to progressive drought and rehydration. Statistic as in Fig. 1

Drought stress caused different effects in dry matter accumulation of individual plant parts of either hybrid. In BRS Manicoré, water deficit caused greater decreases in dry matters of petioles and bulb (∼54%) than in dry matters of arrow leaves, leaflets, and roots (∼42%). In

Table 1 Growth variables in two oil palm hybrids (BRS Manicoré and BRS C 2501) subjected to long-term drought (57 days)

Variables	BRS Manicoré		BRS C 2501	
	Control	Water deficit	Control	Water deficit
Plant height (m)	1.64 ± 0.05 Aa	1.36 ± 0.05 Ba	1.79 ± 0.03 Ab	1.49 ± 0.04 Bb
Arrow leaf number (unit)	2.4 ± 0.6 ns	2.8 ± 0.4 ns	2.4 ± 0.5 ns	2.4 ± 0.5 ns
Leaf number (unit)	17.2 ± 0.7 Aa	15.2 ± 0.6 Aa	16.6 ± 0.4 Aa	14.8 ± 1.2 Aa
Leaflet number (unit)	284 ± 2 Aa	137 ± 1 Ba	338 ± 2 Ab	193 ± 1 Ab
TL_A (m^2)	2.47 ± 0.37 Aa	1.56 ± 0.22 Ba	2.14 ± 0.27 Ab	1.11 ± 0.30 Bb
SL_A ($m^2\ kg^{-1}$)	65.7 ± 0.1 Aa	64.0 ± 0.2 Aa	84.3 ± 0.2 Ab	107.9 ± 0.2 Bb
Total plant dry matter (g)	695.9 ± 1.6 Aa	357.2 ± 2.6 Ba	617 ± 2.4 Ab	303.5 ± 3.5 Bb
Arrow leaf dry matter (g)	32.7 ± 1.0 Aa	19.2 ± 0.7 Ba	22.6 ± 0.8 Ab	15.3 ± 0.5 Bb
Leaf dry matter (g)	293.6 ± 2.0 Aa	154.5 ± 1.7 Ba	270.2 ± 1.3 Ab	129.9 ± 1.8 Bb
Leaflet dry matter (g)	172.6 ± 1.7 Aa	96 ± 0.8 Ba	171.5 ± 0.9 Aa	73.9 ± 1.2 Bb
Petiole + rachis dry matter (g)	121.0 ± 1.0 Aa	58.5 ± 1.0 Ba	98.7 ± 0.6 Ab	56.0 ± 1.7 Bb
Bulb dry matter (g)	220.11 ± 0.6 Aa	96.45 ± 1.3 Ba	183.2 ± 1.4 Ab	100.1 ± 1.6 Bb
Root dry matter (g)	149.4 ± 1.2 Aa	87.1 ± 1.3 Ba	141.0 ± 0.8 Ab	58.2 ± 1.0 Bb
Root length (cm)	68.2 ± 1.9 Aa	76.6 ± 1.7 Ba	71.1 ± 1.2 Aa	68 ± 1.4 Ba
R/AG ratio	0.27 ± 0.02 Aa	0.32 ± 0.05 Ba	0.30 ± 0.01 Ab	0.24 ± 0.03 Bb

BRS C 2501, drought stress caused greater decreases in dry matters of leaflets and roots (∼58%) than in dry matters of petioles and bulb (∼44%) and in arrow leaves (32%). Drought caused 12% increase in root length of BRS Manicoré plants, with non-significant effect in BRS C 2501. Taken together, these differences caused similar decreases (∼50%) in total plant dry matter accumulation in both hybrids; notably, however, biomass partitioning was differently affected by drought, as denoted by the significant ($P \leq 0.05$) increases (19% in BRS Manicoré) and decreases (19% in BRS C 2501) in the R/AG ratio.

Discussion

In oil palm, water deficit can differentially affect growth traits according to the genotype and drought stress severity (Cha-um et al. 2010; Sun et al. 2011; Cha-um et al. 2012; Méndez et al. 2012, 2013). In this study, although drought caused minimal differences in leaf water status and gas exchanges between genotypes, the drought-stressed BRS Manicoré plants displayed larger reductions in shoot dry matter concomitantly with longer roots and higher root dry matter accumulation (thus resulting in greater R/AG ratio) than BRS C 2501 plants. This strategy could allow the BRS Manicoré plants to gain greater access to water towards the bottom of the pots and, therefore, to postpone to a certain extent the development of internal water deficits; this advantage is expected to be more evident in the field where the development of the root system is much less restricted (Pinheiro et al. 2005). An increased R/AG ratio was also observed in oil palm seedlings grown for 90 days under irrigation with 50% of volume water required to maintain the soil at the field capacity (Sun et al. 2011).

The high sensibility of g_s to drought was evidenced by the curvilinear $g_s \times \Psi_{pd}$ relationship in both BRS hybrids, with no threshold values of Ψ_{pd} to induce sharp stomatal closure. This suggests that decreases in g_s were likely to be mediated by hydraulic feedback mechanism (Jones 1998), i.e., drought is sensed by roots triggering and abscisic acid (ABA)-mediated signal transduction cascade which culminates in stomatal closure (Zhang et al. 2006; Chaves et al. 2009; Cutler et al. 2010). The slope of the curves suggests, however, that g_s is slowly decreased with decreasing Ψ_{pd}, so that reductions of 50% in g_s were observed when Ψ_{pd} reached approximately −1.0 MPa (mean data for both hybrids, as deduced from regression equations). The decreases in E mediated by stomatal closure that were accompanied by marked decreases in A limited WUE accordingly under drought. In any case, WUE was higher in stressed plants of BRS Mancioré than in BRS C 2501, thereby suggesting an improved gas exchange performance. Indeed, higher WUE has been associated with superior tolerance to drought, as observed in conilon coffee (*Coffea canephora*; Pinheiro et al. 2005) and cocoa (*Theobroma cacao*; Almeida et al. 2016).

Regardless of BRS hybrids, the overall limitation in plant growth under drought conditions was not only associated with remarkable decreases in A per unit leaf area but also with decreases in whole plant photosynthesis given that the total leaf area was severely constrained by the imposed drought stress. Our results suggest that the photosynthetic apparatus of both hybrids is very sensitive to slight decreases in Ψ_{pd}, in good agreement with results obtained under drought conditions that were previously reported for other oil palm hybrids (Suresh et al. 2010, 2012; Méndez et al. 2012, 2013; Jazayeri et al. 2015) and other tropical palms, such as açaí (*Euterpe oleraceae*; Calbo and Moraes 2000; Silvestre et al. 2016), peach palm (*Bactris gasipaes*; Oliveira et al. 2002; Tucci et al. 2010), and coconut palm (*Cocos nucifera*; Gomes et al. 2008).

The sharp decreases in A, as particularly noted during the first 21 days upon withholding watering, strongly accompanied the decreases in g_s, suggesting that CO_2 diffusion into leaves largely accounted for the decreases in A. Notably, biochemical limitations to photosynthesis, at least until day 21, should have been negligible, as denoted by the slight (if at all) decreases in Rubisco activity with maintenance of Rubisco activation state. It should be emphasized that, from day 21 to day 57, when A was virtually suppressed, some relevant Rubisco activity was maintained, which might have contributed to a certain extent to support photorespiration in both oil palm hybrids. We have previously demonstrated that these hybrids displayed high activities of key enzymes associated with the photorespiratory pathway (glycolate oxidase and catalase) under severe, long-term drought (Silva et al. 2016), thus circumstantially evidencing increased photorespiration rates that might ultimately contribute to protect plants under drought stress (Voss et al. 2013).

The activities of AGPase and SPS (the key enzymes in the starch and sucrose biosynthetic pathways, respectively) were assessed in this study. Noticeably, drought-induced decreases in leaflet starch content on day 21 preceded any effect of drought on AGPase, whose activity was decreased significantly only on day 34 onwards in both BRS hybrids. Until day 34, the ability for sucrose synthesis through SPS tended to be similarly decreased by drought in both BRS hybrids, but afterwards, such an ability was supposed to be higher in BRS Manicoré (as denoted by the higher initial and final SPS activities) than in BRS C 2501. In any case, given that A was negligible from day 21 onwards, we expect that triose-P production should be strongly constrained and, therefore, we contend that synthesis of both starch and sucrose was fundamentally limited by a lower substrate availability rather than by enzymatic constraints, at least until 34 days after suspending watering.

The activities of SuSy and invertases in both BRS hybrids under moderate drought (until day 21) and the activities of SuSy (BRS Manicoré) and acid invertase (BRS C 2501) under severe drought (from day 34 onwards) remained unchanged in relation to those of control plants, suggesting that ability for sucrose utilization was, overall, maintained over the course of the experiment. Taken all of the information together, despite not having detected sucrose in this current study, our results suggest that oil palm plants display enzymatic machinery for sucrose synthesis and utilization. Therefore, inability for detecting sucrose in this study (provided that substrate for sucrose synthesis is available as under ample irrigation) is suggestive that sucrose does not accumulate in oil palm leaflets, probably because it is translocated rapidly to the growing tissues and reserve organs, as previously reported in adult oil palm trees (Legros et al. 2009; Lamade et al. 2016).

An integrative analysis of all variables upon resuming irrigation demonstrates the ability of physiological and biochemical traits to be recovered in both BRS hybrids. Due possibly to the severity of drought, recovery of both leaf water status and leaf gas exchanges was very slow upon resuming irrigation. Notably, the slow recovery of Ψ_{pd} denotes occurrence of remarkable xylem embolisms that were not promptly reversed (Brodribb 2009; Cochard and Delzon 2013). Nonetheless, recovery of Ψ_{pd} preceded the recovery of g_s, suggesting that non-hydraulic factors possibly mediated by ABA should have played a decisive role in constraining resumption of gas exchanges (Lovisolo et al. 2008). Taken together, this information indicates a poor ability of oil palm plants to recover from drought stress. Irrespective, we contend via physiological, morphological, and biochemical analyses that both hybrids were able to relatively tolerate, or most properly survive, the severe drought conditions imposed in this experiment. Nevertheless, by comparing the performance of the two BRS hybrids during the stress and recovery period, we suggest that BRS Manicoré was able to adjust its physiological and morphological traits to cope with drought more satisfactorily than BRS C 2501, since the former presented positive A values for longer during the stress period coupled to higher Rubisco activities (and, overall, greater activities of carbon metabolism enzymes), as well as it presented higher WUE, deeper and denser root system (with higher R/AG ratio) and higher TLA than BRS C 2501. These traits may be of relevance for plant breeders aiming to develop oil palm cultivars more tolerant to drought stress.

Author contribution statement PAS, VSC, KCBR, and RLC—carried out the seedlings cultivation, the experiment setup and all morphological and physiological measurements and sampling for biochemical assays. PAS and KSCD—carried out the biochemical assays. PAS and FML—carried out all statistic analysis. RAFB, FMD, and HAP—wrote the manuscript; the latter also coordinated the project and advised PAS (PhD Student) and VSC and KCBR (Undergraduate students).

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