Original Research Article

Deficit Irrigation in *Ricinus communis* L.: Effects on Water Use Efficiency, Carbon Assimilation and Water Relations

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ABSTRACT

Aims: This study evaluated carbon assimilation, water relations, intrinsic and instantaneous water use efficiency, and water consumption of two cultivars of *Ricinus communis* L. cv. BRS 188 Paraguaçu and BRS Energia, subjected to regulated-deficit irrigation.

Study Design: The experiment was arranged in a completely randomized scheme in a factorial arrangement of 5 x 2, with five replicates.

Place and Duration of Study: The experiment was conducted in a greenhouse at the Universidade Estadual de Santa Cruz, Ilhéus, Brazil from December 2008 to February 2009.

Methodology: The growing plants were subjected to different water conditions by predefined quantities of water, so as to maintain the substrate under the following matric potential (Ψm) during the experimental period: -1.6 kPa (near field capacity), -3.0 kPa, -7.3 kPa, -26.7 kPa, and -183.0 kPa.

Results: The cultivars differed significantly ($P = .05$) in predawn leaf water potential and relative water content, showing that the tissues of BRS Energia remained more hydrated compared to BRS 188 Paraguaçu. Under -183.0 kPa, the intrinsic water use efficiency and instantaneous water use efficiency were significantly higher in BRS Energia than in BRS 188 Paraguaçu, suggesting a conservative behavior of the cultivar BRS Energia. Non-stomatal limitations to photosynthesis were observed in BRS 188 Paraguaçu. Under greater water stress, BRS 188 Paraguaçu and BRS Energia plants had the leaf area reduced by 75.58% and 23.13%, respectively compared with the control. The water use efficiency of biomass was significantly higher in BRS Energia than in BRS 188 Paraguaçu.

Conclusion: The cultivar BRS Energia was more promising in relatively drier conditions compared to BRS 188 Paraguaçu. The carbon assimilation decreased in both castor bean cultivars only under severe water stress (-183.0 kPa), suggesting that the use of the deficit irrigation technique may be viable leading to lower water consumption and higher photosynthesis efficiency.

Keywords: castor bean; water stress; gas exchange; biomass; Euphorbiaceae.

1. INTRODUCTION

Castor bean (*Ricinus communis* L.), one of the 7000 species of the family Euphorbiaceae [1]. Castor bean is an important oil-seed crop grown throughout the world [2]. Production is concentrated in India, China, Brazil and Mozambique [3]. In Brazil, small- and medium-scale farmers have been producing castor oil for more than a century, especially in the state of Bahia [4,5]. Cultivation of castor bean is a good alternative for those farmers, because this crop has a low production cost, is drought-tolerance can be easily cultived [6,7], and can grow any where including in infertile soil considered unsuitable for food production [8]. The species shows satisfactory fruit production even in the semi-arid region of northeastern Brazil where rainfall is sparse [9]. Thus, castor bean may be an alternative source of income for farmers in northeastern Brazil [9], especially for family farmers [10,8], allowing them to remain economically viable [11].

Given the global climate changes that are increasing water scarcity, irrigation and rational use of water have become important objects of study [12]. Strategies to reduce irrigation-water consumption and to improve water use efficiency (*WUE*) have become a priority for water conservation in agriculture [13]. In the cultivation of *Pyrus* L., deficit irrigation has reduced water consumption by about 5 to 18%, i.e., this irrigation method has enabled a water saving of 13-25% compared to full irrigation [14]. Regulated Deficit Irrigation (*RDI*) is among the water-saving strategies based on the adaptive and specific responses of plants to drought [15], where supplying less water than the plants require is an important tool in reducing consumption of irrigation water [16,17].Several cases of success using this technique have been reported, with gains in productivity [16] of many species such as *Olea europaea* L. [18], *Dianthus caryophyllus* L. [19], *Capsicum annum* L. [20], *Citrus sinensis* [21], *Prunus armeniaca* [22], *Pistacia vera* L. [23], *Vitis vinifera* L. [24] and *Citrus paradisi* Mac. [25]. Deficit irrigation (50% of evapotranspiration) in *Vitis vinifera* L. cultivation was sufficient to ensure a high yield, water use efficiency - *WUE* (yield/water applied in irrigation) and good fruit quality [26]. *WUE* can be optimized by increasing the productivity of a crop in line with the volume of water applied, or by reducing irrigation without significantly reducing productivity [27].

Energy crops such as castor beans have attracted attention for producing biofuels such as biodiesel, in developed as well as developing countries contribuiting to reduce dependency on fossil fuel [8]. Studies on castor bean production systems in the climate conditions of Brazil are especially relevant with regard to irrigation conditions, in order to augment the income of producers [28].

The castor bean cultivar BRS Energia has an earlier cycle in relation to the other cultivars, with 120-150 days between the germination and maturation of recent racemes, and the first raceme appears about 30 days after germination [29]. Thus, the precocity associated with easy cultivation makes a cultivar BRS Energy with great productive potential of great social and economic importance to the semi-arid region of northeastern Brazil. The BRS 188 Paraguaçu has agronomic and technological characteristics superior to those of commercial cultivars [30]. Thus, the comparative study of the physiological characteristics of each cultivar under water restriction conditions can aid in selecting the best cultivar in response to the minimum water availability needed for higher productivity and lower costs.

Growing of drought-tolerant cultivars will contribute to stable castor bean production, while the screening of cultivars or breeding lines to drought stress responses can be a crucial part of breeding programs [2]. In the present study, our main objective was to evaluate carbon assimilation, water relations, intrinsic and instantaneous water use efficiency, and water consumption of two castor bean cultivars, BRS 188 Paraguaçu and BRS Energia, subjected to regulated deficit irrigation.

2. MATERIAL AND METHODS

2.1 Plant material and growing conditions

The experiment was conducted in a greenhouse at the Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil (14°47'00" S, 039°02'00" W) from December 2008 to February 2009. According to the Köppen climate classification, the local climate is the Af type humid tropical climate, with mean annual temperatures ranging from 22 to 25°C [31]. During the experimental period inside the greenhouse the air temperature ranged from 24 °C to 31 °C and relative humidity (RH) from 65% to 98% (Hobo H8 Pro sensors, Onset Computer, Massachusetts, USA), and cumulative photosynthetically active radiation (PAR) from 4.9 to 33 mol photons m^{-2} day^{-1} (S-LIA-M003 quantum sensors coupled to a Hobo Micro Station Data Logger, Onset Computer, Massachusetts, USA).

Two cultivars of *Ricinus communis* L. (BRS 188 Paraguaçu and BRS Energia) with different growing cycle were used in the study. In BRS 188 Paraguaçu, the mean period between seedling emergence and emission of the first raceme (inflorescence) is 54 days and the whole growing cycle last for 250 days. The mean oil content in its seeds is 48%, and the mean yield is 1,500 kg/ha in a longer 250-day cycle under the rain-fed semi-arid conditions of northeastern Brazil [32]. BRS Energia is a shorter cycle cultivar with120 to150 days between the germination and maturation of recent racemes, whereas the first raceme emerges earlier at about 30 days after germination [29].The oil content of seeds is 48% and fruit productivity is 1,500 kg/ha, on average, under rain-fed semi-arid conditions [33].

The seeds were soaked for 2 h and then treated with the systemic fungicide Derosal®. The plants were grown for 66 days in 21L pots filled with a mixture of sand and soil (3:1); textural analysis showed 60 dagkg^{-1} coarse sand, 16 dag kg^{-1} fine sand, 9 dag kg^{-1} silt, and 15 dag kg^{-1} clay. The substrate was prepared based on its chemical composition (Table 1). Pots similar to those used in the experiment were assembled to estimate field capacity of substrate. After correcting the pH with 1.55 g dm^{-3}dolomitic limestone (PRNT 90.87%) and adding 1.37 g dm^{-3} triple superphosphate and 0.60 g dm^{-3} of ready commercial formulation containing (N -16%; K_2O – 16%; S – 7%; B – 0.2%; Cu – 0.2%; MgO – 1%; Zn and Mn – 0,5%.

Top-dressing chemical fertilization was based on 80 mg dm^{-3} urea and 10 mg dm^{-3} potassium chloride. Each pot was filled with a known weight of soil which was irrigated to field capacity and then sown five seeds per pot. When the plantlets were approximately 0.10 to 0.12 m tall, they were thinned by leaving only one plant per pot. The plantlets isolated from thinning were used to collect zero (initial biomass). Each pot was fertilized monthly with 50 mL of nitrogen (urea) and potassium (potassium chloride) solutions at concentrations of 28.4 g L^{-1} and 2.15 g L^{-1}, respectively.

Table 1. Chemical analysis of the substrate used in the experiment

	cmol$_c$/dm^3							mg/dm^3			
pH	**Al**	**H+Al**	**Ca**	**Mg**	**Ca+Mg**	**P**	**K**	**Fe**	**Zn**	**Cu**	**Mn**
4.47	0.67	4.9	0.19	0.08	0.27	0.4	8	103	1.17	0.5	1.7

Regulated-deficit irrigation (*RDI*) was started at 32 days after sowing (DAS) and the growing plants were then subjected to different water conditions by predefined quantities of water, so as to maintain the substrate under the following matric potential (*Ψm*) during the experimental period: -1.6 kPa (near field capacity), -3.0 kPa, -7.3 kPa, -26.7 kPa, and -183.0 kPa. The substrate *Ψ*) for each treatment was estimated using an equation derived from the soil water-retention curve (Table 2).

Table 2. Mean percentages of water content of substrate (*WCS*) 20, 16, 12, 9 and 7% and their corresponding matric potential (*Ψm*)

Treatments	*WCS* (%)	*Ψm* (-KPa)
20	19.7	1.6
16	15.6	3.0
12	12.1	7.3
9	9.1	26.7
7	6.7	183.0

Before each irrigation, all the pots were weighed and the difference between the current weight and that corresponding to each treatment corresponded to the weight of replacement water (evapotranspiration). Water consumption was considered as the water lost by the plants via transpiration, and the evaporation from the substrate in the pot.

2.2 Water relations

The pre-dawn leaf water potential (Ψ_{PD}) was evaluated 18 days after the RDI application (DAAT), using a Pressure Chamber Instrument Model 1000 (PMS Instrument Company, USA). Pressurization was carried out slowly, and the time between the leaf collection and the measurement was as short as possible [34]. The measurements were performed between 02:00 and 04:00 h, when the mean air temperature was around 23.3°C and the relative humidity was 74%.

2.3 Leaf relative water content

Leaf samples were first weighed (P1) and then placed to hydrate in pots filled with water, for 12 h in the dark, this time was enough to reach the max turgor. After hydration, the leaves were weighed again to obtain the turgid weight (P2) and were then placed in a forced-air oven at 75°C for 72 h to obtain the biomass dry weight (P3). Relative water content was calculated using the following formula: $RWC = [(P1-P3)/(P2-P3)]x100$ [35].

2.4 Leaf gas exchange

Leaf gas exchange was evaluated 18 days after the application of treatments (DAAT), between 08:00and 12:00 h, in the middle part of fully expanded physiologically mature leaves from five randomly selected plants from each treatment. Net photosynthesis rate (*A*), intercellular CO_2 concentration (*Ci*), stomatal conductance to water vapor (*gs*), and transpiration (*E*) per unit of leaf area were measured using the Li-6400 Portable Photosynthesis System (LI-COR Biosciences Inc., Nebraska, USA) with integrated fluorescence camera (LI-6400-40 leaf chamber fluorometer, LI-COR). Photosynthetically active radiation (PAR), atmospheric CO_2 concentration (*Ca*), and block temperature were set at 1200 mol photons m^{-2} s^{-1}, 400 µmol mol^{-1} and 26°C, respectively, using the equipment controls.

2.5 Water use efficiency

Three forms of expressing water use efficiency were used in the analysis and interpretation of experimental data: instantaneous water use efficiency (*A/E*), intrinsic water use efficiency (*A/gs*) and water use efficiency of biomass (kg m^{-3}), calculated as the ratio of biomass produced to water consumed (evapotranspiration). The calculations were performed with data collected at 8 DAAT (1^{st}harvest) and 34 DAAT (2nd harvest).

2.6 Biomass determination

Two destructive measurements at the beginning (8 DAAT) and the end (34 DAAT) of the experimental period were performed. The harvests were treated independently, since the plants collected 8 DAAT were different from those collected 34 DAAT. Leaf area was estimated, both non-destructively and destructively, using allometric coefficients (width and length of a mature leaf) previously generated for this purpose as described by [36], and a LI-COR 3100 (Biosciences Inc., Nebraska, USA) automatic leaf area meter. The dry mass of plant organs (root, stem and leaves) was used to estimate the variables for growth, such as relative growth rate (*RGR*) according to Hunt (1990). Each plant was placed in paper bags and oven-dried in a forced-air oven at 75°C until constant weight.

Statistical analysis

The experiment was arranged in a completely randomized scheme in a factorial arrangement of 5 x 2, wherein the factors were: five water regimes and two cultivars of *R. communis,* with five replicates. Differences between the cultivars were assessed using a t-test at 5% probability.

3. RESULTS AND DISCUSSION

3.1 Leaf water relations

The effects of deficit irrigation on Ψ_{PD} and *RWC* differed between the two cultivars (Fig.1 A, B). *RWC* was significantly higher in BRS Energia, with mean values of 89, 85 and 76% at-3.0; -7.3 and -183.0 kPa soil matric potential, respectively (Fig.1 A); whereas the corresponding values for BRS 188 Paraguaçu were 83, 79 and 64% (Fig.1A). These data showed that although both species consumed the same amount of water (Fig. 4 C, D), the short-cycle cultivar BRS Energia was able to maintain more-hydrated tissues compared to the longer-cycle BRS 188 Paraguaçu, especially at higher water deficits. One can therefore infer that BRS Energia is the more promising cultivar in relatively dry locations due to its ability to maintain higher *RWC* and Ψw.

The *RWC* is probably the most appropriate measure of plant water status in terms of the physiological consequences of cellular water deficit. According to [37], the restriction in leaf water status resulting from a reduction in *RWC* affects plant growth and development as observed in BRS 188 Paraguaçu.

As observed for the *RWC*, the Ψ_{PD} of BRS Energia was significantly higher than that of BRS 188 Paraguaçu, with values of -0.49 and -0.89 MPa □PD in the former in contrast to -0.6 and -1.4 MPa □PD in the latter at-7.3 and -183.0 kPa, respectively (Fig.1 B).The non-significant difference between the cultivars for *RWC* and the significant difference for Ψ_{PD} in -26.7 kPa (Fig.1 A, B) may suggest some degree of osmotic adjustment, which enabled the plants to maintain turgor in a relatively low water potential.

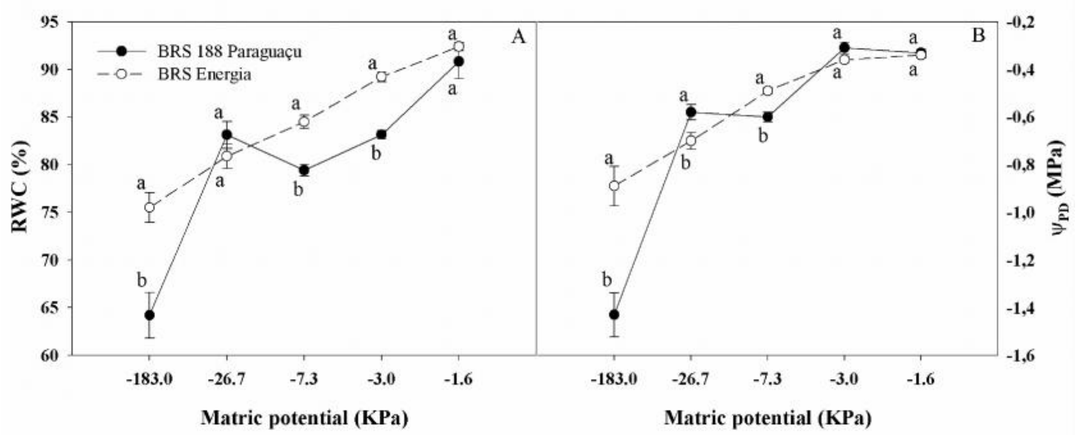

Fig. 1. (A) Relative Water Content (*RWC*) and (B) pre-dawn leaf water potential (Ψ_{PD}) in plants of *Ricinus communis* cv. BRS 188 Paraguaçu and cv. BRS Energia subjected to different water conditions: -1.6; -3.0; -7.3; -26.7 and -183.0 kPa after 18 days of treatment application (DAAT). Points are mean (n=5), error bars are the standard error of the mean, and letters indicate significant differences between cultivars with the same water level, by *t*-test (*P* = .05)

Studies with different hybrids of *R. communis* showed that this species accumulates high contents of proline, total soluble sugars, amino acids and potassium after 33 days under water stress, and the sugars are the key players in osmotic adjustment in castor bean leaves [38].

Similarly, *Jatropha curcas* plants possess an efficient adaptive mechanism to prevent severe drought stress by maintaining good leaf water status and effective osmotic adjustment [39,40]. In soil matric potential of -3.0 kPa, both cultivars had significantly similar *Ψw* but with different *RWC* values (Fig.1 A, B).This indicates that although the status of the water within the cells was the same, the leaf hydration status and physiological water were different.

3.2 Leaf gas exchange

The cultivars showed different behaviors for *A/gs*, *A/E* and *Ci/Ca* when subjected to -183.0 kPa, with higher values for BRS Energia than for BRS 188 Paraguaçu (Fig.2 C, D and F). Both cultivars had *A*, *gs* and *E* constant at approximately 26 μmol m^{-2} s^{-1}, 0.45 mol H_2O m^{-2} s^{-1} and 3.8 mmol H_2O m^{-2} s^{-1}, respectively, after 18 days under matric potential in the substrate above -26.7 kPa (Fig.2 A, B, D), showing that gas exchange was not affected when the matric potential in the substrate exceeded -26.7 kPa, regardless of the cultivar. The reduction in the photosynthesis rate observed at -183.0kPa (Fig.2 A), in turn, was closely associated with the closure of stomata (Fig.2 B). The reduction in *gs* increases resistance to CO_2 diffusion into the leaves, affecting the accumulation of photoassimilates (Fig.4 A, B) [41]. If the plant loses water at a faster rate than its capacity to absorb and transport it, then the leaf water potential decreases, causing the closure of stomata and the reduction of photosynthesis (Fig. 1 B, Fig. 2 A, B) [42]. Similarly, in *J. curcas,* net photosynthesis was significantly reduced only when soil water availability dropped below 30% of field capacity. However, *gs* proved to be quite sensitive to soil water availability, and the strict stomatal regulation in this species was evident after 11 days of stress [39]. Compared to BRS 188 Paraguaçu, higher *A/gs* was observed in plants of BRS Energia subjected to increased water deficit (Fig. 2 C). This behavior is attributable to the rapid stomatic closure observed in BRS Energia to minimize water loss and thus maintain leaf *Ψw* (Fig. 2 B). The stomatal closure contributed to optimize the efficiency of water use in the plants under stress [43], allowing them to optimize CO_2 fixation *versus* water loss. Stomatal closure is considered a drought-avoidance mechanism [44].

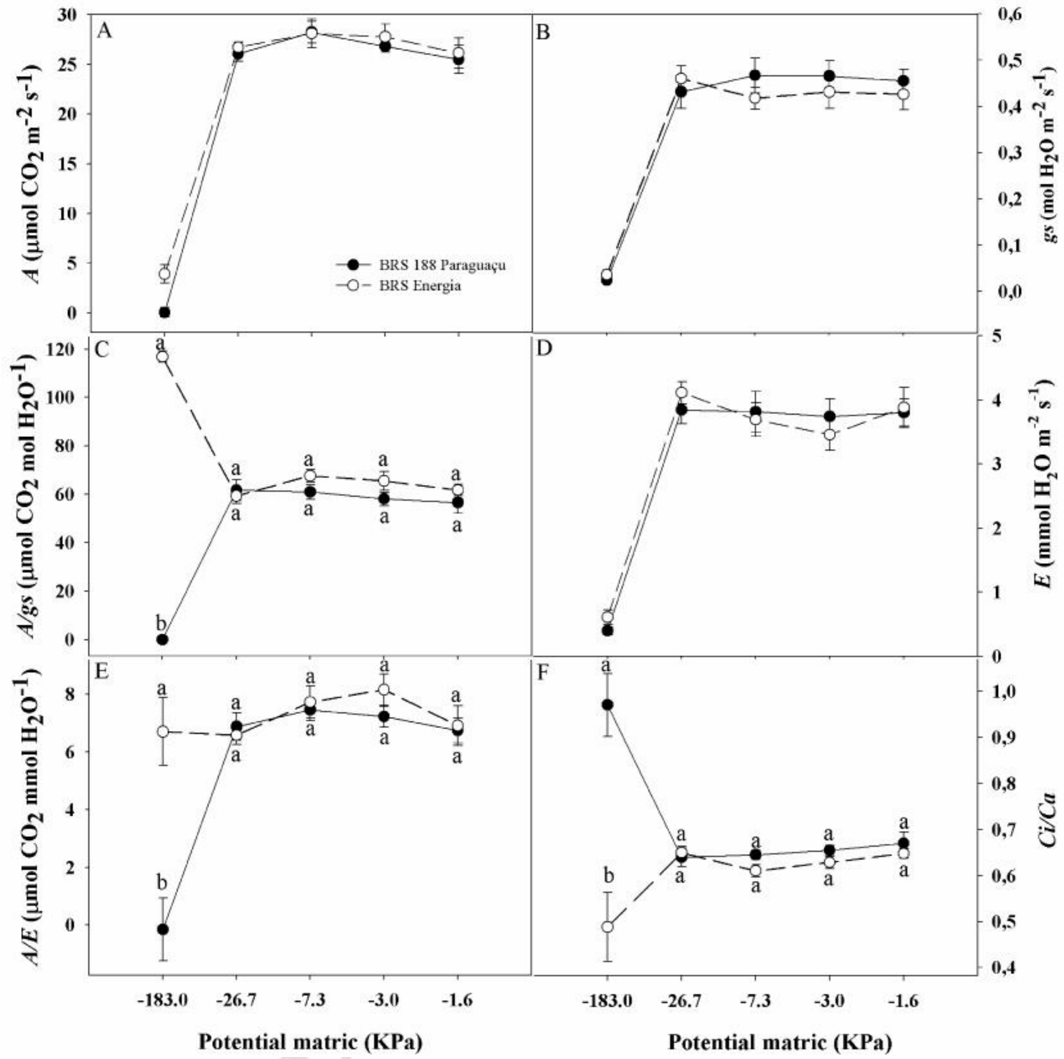

Fig. 2. (A) Net Photosynthesis rate (*A*); (B) stomatal conductance for water vapor (*gs*); (C) intrinsic water use efficiency (*A/gs*); (D) transpiration; (E) instantaneous water use efficiency (*A/E*) and (F) ratio (intercellular and atmospheric CO_2 concentrations) (*Ci/Ca*) of two castor bean cultivars cultivated in substrate with -1.6; -3.0; -7.3; -26.7 and -183.0 kPa of matric potential for 18 days after treatment application (DAAT). Points are mean (n=5), error bars are the standard error of the mean, and letters indicate significant differences (*P* = .05) by *t*-test between cultivars with the same water level.

This difference in behavior between the two cultivars was also observed in *Lotus corniculatus* where the transpiration rate, *RWC* and *gs* reflect specific physiological mechanisms in each cultivar, and allow for metabolic acclimatization to drought conditions [45]. [46] obtained similar results, and stated that the castor bean drought-resistance mechanism appears to be related to an initial response and increased growth, as well as efficient stomatal control, minimizing water loss from transpiration. Although the studies of *J. curcas* by [47] revealed that a reduction in water availability (100, 75, 50 and 25% field capacity) resulted in decreased *gs* and *E* in order to avoid loss of water, however, the *WUE* was reduced.

The rapid closing of stomata and the lower *E* observed in the lower matric potential of the substrate for BRS Energia in relation to BRS 188 Paraguaçu (Fig. 2 B, D) resulted in increased *A/gs* and *A/E* (Fig. 2 C, E). This improved the hydration of leaf tissue (Fig. 1 A), suggesting a conservative approach [48, 49, 50].

The *Ci/Ca* ratio for both cultivars was maintained at 0.65 in substrates above -26.7 kPa. Water contents below -26.7 kPa led to a behavior contrary to that observed for *A/gs* (Fig.2 C, F); thus, the low value of *Ci/Ca* followed by an increase in the *A/gs* of BRS Energia plants are due to low *gs* [39]. On the other hand, the higher CO_2 concentration in intercellular spaces (*Ci*) subjected to low *gs* observed in BRS 188 Paraguaçu indicates that this cultivar was more sensitive to the *RDI* compared to BRS Energia (Fig.2 F). This behavior suggests the occurrence of non-stomatal limitations to photosynthesis, such as low mesophyll conductance, reduced activity and concentration of ribulose-1,5-bisphosphatecarboxylase-oxygenase (Rubisco), photoinhibition, and reduced photochemical efficiency of PSII [51,52,53].

3.3 Growth and biomass accumulation

Because the experiment consisted of two cultivars with different cycles,short-cycle BRS Energia (120-150 days) and long-cycle BRS 188 Paraguaçu (250 days), only the reproductive cycle of BRS Energia was evaluated. According to literature, the BRS 188 Paraguaçu cultivar begins the reproductive stage at 53 DAS [33]; however, in our study, no flowering was observed up to 66 DAS.

At 8 DAAT, due to the dry conditions, plant height was gradually reduced, especially in plants subjected to -183.0 kPa, with reductions of 38.81 and 33.28% compared to the controls in BRS Energia and BRS 188 Paraguaçu, respectively (Fig.3 A). At 34 DAAT, the reductions were even more significant, 51.48% and 40.17%, respectively (Fig.3 B).

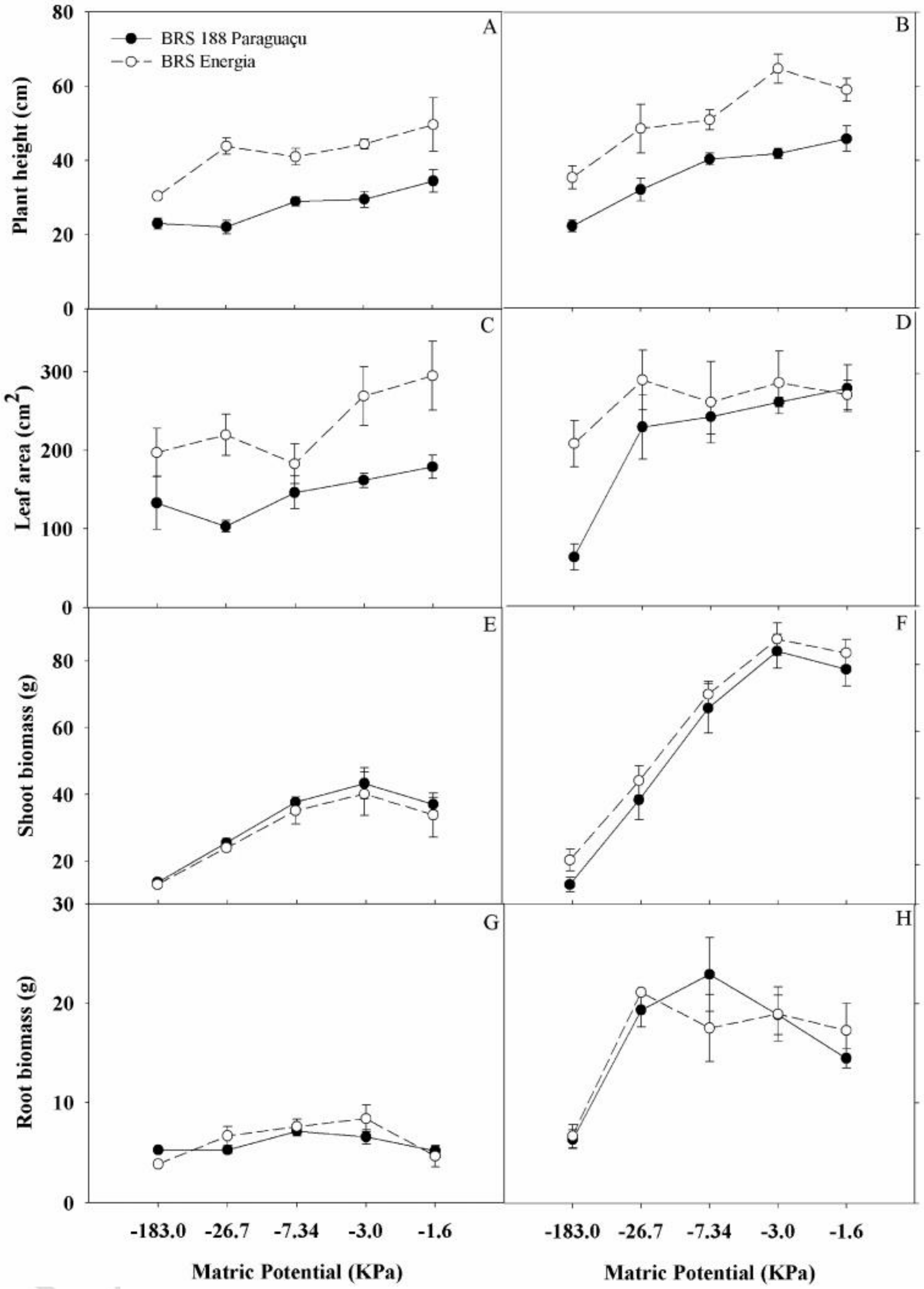

Fig. 3. Plant height (cm), leaf area (cm^2), shoot biomass (g) and root biomass (g) of two castor bean cultivars grown in substrate with -1.6; -3.0; -7.3; -26.7 and -183.0 kPa at 8 DAAT (A, C, E and G) and 34 DAAT (B, D, F and H).Points are mean (n=5), error bars are the standard error of the mean.

This indicates that the plant height of cultivars is determined, among other factors, by the water supply [54], which inhibits cell elongation more than division, affecting various physiological and biochemical processes such as photosynthesis, respiration, translocation, absorption of ions, carbohydrates, nutrient metabolism, and growth factors [55].

Reductions in height were also observed by [56] in cultivars BRS 149 Nordestina and BRS 188 Paraguaçu, with reductions of 40.24, 24.89 and 13.83% in treatments with 40, 60 and 80% available water compared to plants in soil maintained at field capacity.

After 8 DAAT there was a reduction in leaf area with increasing water stress, soon after the plants were subjected to the treatments (Fig. 3 C).

Similarly, [57] reported a leaf-area reduction of more than 60% in BRS 188 Paraguaçu under excess water stress and deficiency in only six days, and stated that in the juvenile stage until the first 52 days after seedling emergence, this cultivar is very sensitive to water stress.

At 34 DAAT, under greater water stress, the plants showed a quite compromised leaf area, with reductions of 75.58% and 23.13% compared with the control, for BRS 188 Paraguaçu and BRS Energia, respectively (Fig. 3 D). According to [58], the reduction in leaf area, due to selective leaf senescence combined with decreases in *A* and *A/gs* (Fig. 2 A, C), allows plants to maintain an "above-lethal" water potential. The same authors observed a similar behavior in *J. curcas* after 18 days of water stress. The reduction in leaf area and gas exchange during dry conditions reduces not only water loss but also carbon assimilation, with consequent slower growth [59]. The smaller reduction in leaf area observed in BRS Energia compared to BRS 188 Paraguaçu, especially at -183.0 kPa, resulted from the ability of the former to produce leaves, although small, whereas BRS 188 Paraguaçu lost leaves. According to [45], the regrowth process generates small turgid leaves that are physiologically acclimated to drought, showing obvious morphological changes resulting from changes in growth and leaf development. At 34 DAAT, the longer period of drought had significantly affected the shoot biomass of plants of both cultivars. At -183.0 kPa, cultivars BRS Paraguaçu and BRS Energia showed reductions of 79.02 and 85.44% respectively, compared to control plants (Fig. 3 F).

The root development was also strongly influenced by growing conditions. At 34 DAAT, the root biomass at -183.0 kPa was lower than in the control, with reductions of 61.25 and 56.04% in BRS Energia and BRS 188 Paraguaçu, respectively (Fig. 3 H). This indicates that both cultivars showed no root growth in the most intense drought conditions, reducing the shoot:root ratio. [60] noted that root growth is usually less affected by drought stress than shoot growth. A decrease in the shoot:root ratio is a common observation under drought stress, which results either from an increase in root growth or from a relatively larger decrease in shoot growth than in root growth, as a result of pre-conditioning deficit-irrigation processes. Furthermore, as the matric potential of the substrate decreased, the percentage of shaded roots in the BRS 188 Paraguaçu plants increased possibly the result of suberization of the exodermis to protect the roots from adverse conditions [60].

Within a short period of time (8 DAAT), the plants subjected to water-deficit treatments showed a significant decrease in total biomass (*TB*) due to the reduction of the matric potential in the substrate (Fig.4 A), indicating high sensitivity of growth to reduced water availability. When subjected to severe water deficit (-183.0 kPa),total biomass decreased by 56% in both cultivars compared to the control (Fig. 4 B). Leaves comprised most of the *TB* (Fig.3 D). This reduction in growth of biomass observed in both species is attributable to a survival strategy.

The reductions in growth and biomass accumulation observed in the plants subjected to water deficit, especially in BRS 188 Paraguaçu, are due to decreases in *Ψw*, which has been associated with a reduction in the coefficient of cell division and in cell expansion [61], mainly driven by leaf turgor pressure (*Ψp*). Similar behavior was observed in *J. curcas* after 18 days of stress [58].

After 34 DAAT (Fig. 4 B), water deficits below -3.0 kPa reduced (*TB*) production, by 18.21, 25.47 and 75.97% in BRS Energia and 3.57, 35.10 and 80.95% in BRS 188 Paraguaçu at-7.3; -26.7 and -183.0 kPa in comparison with the control, respectively. With the reduction in water availability, the water consumption (evapotranspiration) decreased linearly to values of 11.71, 7.41, 6.43, 4.14 and 0.53 L (BRS 188 Paraguaçu) and 11.35, 7.60, 5.69, 3.98 and 0.71 L (BRS Energia), with mean daily consumption of 1.46, 0.93, 0.80, 0.52 and 0.07 L (BRS 188 Paraguaçu) and 1.41, 0.95, 0.71, 0.50 and 0.09 L (BRS Energia) at -1.6, - 3.0, - 7.3, - 27.7 and -183.0 MPa, respectively, over 8 DAAT (Fig. 4 C). Even so, there were no significant differences between the cultivars. Similar results were observed for the same castor bean cultivars where the highest water consumption (2534 mm) occurred with 100% available water over the 180 days of the crop cycle [62].

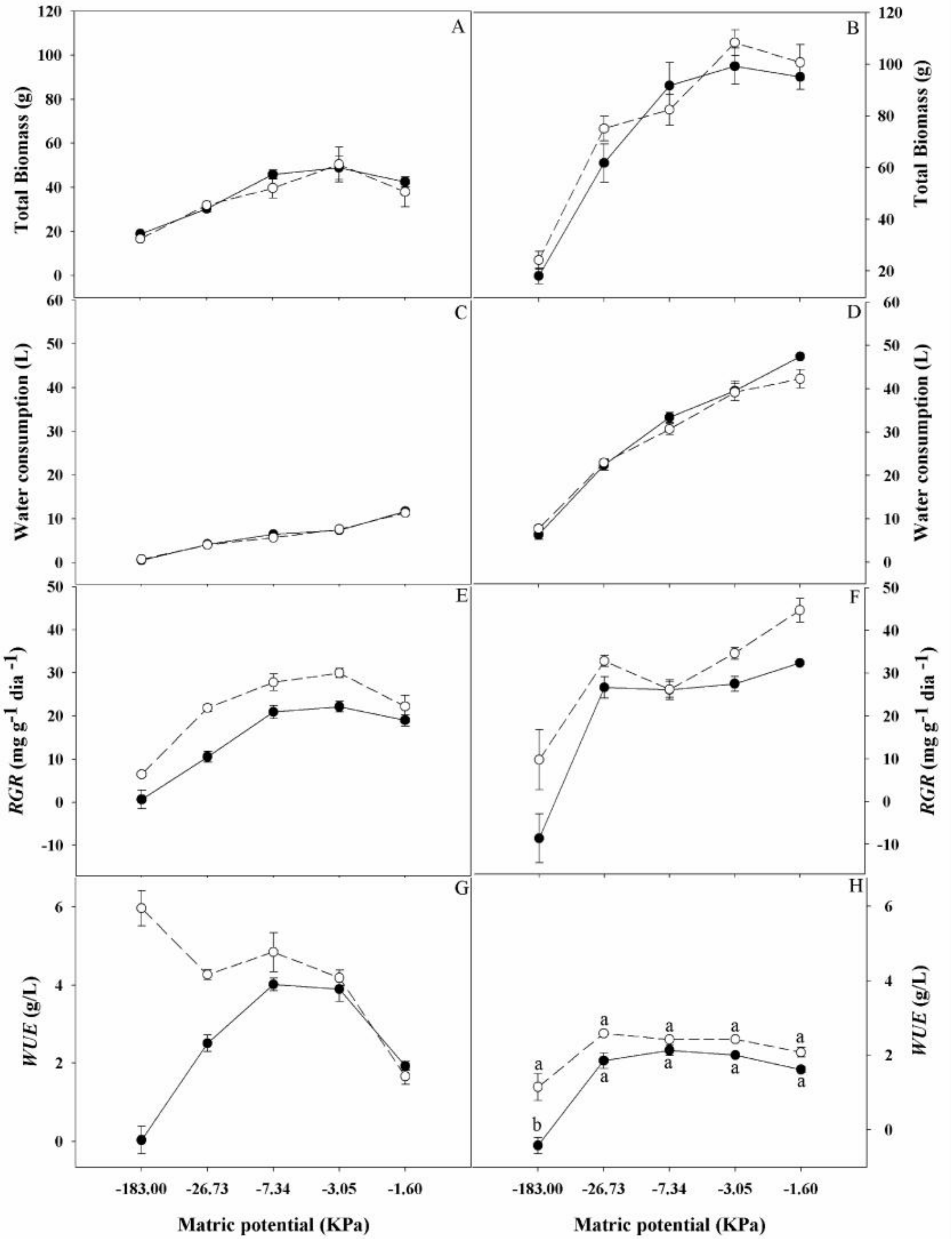

Fig. 4. Total biomass (*TB*), cumulative water consumption (WC), relative growth rate in biomass (*RGR*) and water use efficiency (*WUE*) of two castor bean cultivars cultivated in substrate with -1.6; -3.0; -7.3; -26.7 and -183.0 kPa for 8 DAAT (A, C, E and G) and 34 DAAT (B, D, F and H). Points are mean (n=5), error bars are the standard error of the mean, and

letters indicate significant differences (*P* = .05) by *t*-test between cultivars with the same water level.

During the entire experiment (34 DAAT), the final water consumption was 47.47, 39.53, 33.40, 22.41 and 6.33 L in BRS 188 Paraguaçu and 42.31, 39.22, 30.69, 22.94 and 7.72 L in BRS Energia at -1.6, - 3.0, -7.3, -26.7 and -183.0 MPa of soil water, respectively, with a mean daily consumption of 1.40, 1.16, 0.98, 0.66 and 0.19 L (BRS 188 Paraguaçu) and 1.24, 1.15, 0.90, 0.67 and 0.23 L (BRS Energia) (Fig. 4 D). Despite the different plant architectures of the two cultivars, there were no differences in evapotranspiration.

BRS 188 Paraguaçu had a reduced *RGR* when subjected to -1.60 kPa water in the substrate at 8 DAAT (Fig. 4 E). Similar results were found by [63], who attributed the delay in development and consequent limitation of the respiratory process of BRS 188 Paraguaçu to the 4.80% reduction in growth of the root system at the highest soil water content, which was 100% field capacity.

Reductions in *RGR* were evident after 34 DAAT, in particular in BRS 188 Paraguaçu, where the *RGR* was negative (-8.58 mg g^{-1} day^{-1}) (Fig. 4 F). Considering that the *RGR* corresponds to the amount of new material produced in relation to the pre-existing material over time [64], the cultivar BRS 188 Paraguaçu had stopped growth, which explains why the *RGR* was negative. BRS Energia, in contrast, still showed positive values of *RGR* (9.8 mg g^{-1} day^{-1}) even under a severe soil water deficit (Fig. 4 F). Those results suggest that the cultivar BRS 188 Paraguaçu is less tolerant to water deficit compared to BRS Energia.

The lower water availability resulted in a decrease in *A* (Fig. 2 A) and consequently in the production of carbohydrates, contributing to a reduction in biomass accumulation (Fig. 4 E, F) of the plants. Similar results were found in *J. curcas*, in terms of CO_2 assimilation, stomatal conductance, transpiration, growth, biomass and water use efficiency which progressively reduced in response to decreasing soil moisture content [47].

3.4 Water use efficiency (WUE)

The *WUE* was evaluated taking into account the evapotranspiration of water (soil evaporation + leaf transpiration) and dry biomass production. For both, pots containing only substrate were covered with plastic to estimate evaporation, but the estimate was very low and was therefore disregarded. Shading of the pot’s surface by leaves further reduced evaporation, so that the evaporation was higher than the transpiration. The *WUE* of BRS Energia increased linearly with decreased matric potential in the substrate at 8 DAAT, reaching a *WUE* of up to 6 kg m^{-3}(Fig.4 G). This behavior can be attributed to increased branching and length of the roots. This can minimize the depletion of water around the roots, thereby minimizing resistance to transport of water to the root system [65].

The substrate with a matric potential of -1.6 kPa reduced the *WUE* of BRS 188 Paraguaçu at 8 DAAT (Fig.4G). Our results are not consonant with those obtained by [62], who in studies involving BRS 188 Paraguaçu found increased *WUE* in the treatment with 100% available water in relation to the lowest level (40%), with values of 2.78 and 0.28 kg m^{-3}, respectively. This discrepancy can be attributed to the time when the analyses were performed: in the studies conducted by [62] the cultivation time was 180 days, and the present study lasted 66 days.

At 34 DAAT, only for *WUE*, indicating that the cultivars have different behaviors as a function of watering regimes (Fig.4 H). In contrast, the *WUE* of the BRS Energia plants was significantly higher (2.1, 2.4, 2.6 and 1.1 kg m^{-3}) than that of the BRS 188 Paraguaçu plants (1.6, 2.0, 1.9 and -0.4 kg m^{-3})at-1.6, -3.0,-26.7 and -183 kPa, respectively (Fig.4H). In the same period, the *WUE* of the plants was reduced in soil with the highest water deficit, regardless of the cultivar. The lower efficiency recorded for BRS 188 Paraguaçu in relation to BRS Energia may possibly be attributed to the decrease in *gs* during water deficiency, which reduces the assimilation efficiency (0.05 μmol m^{-2} s $^{-1}$) through photosynthesis, since BRS Energia showed higher values than BRS 188Paraguaçu at -26.7 and -183.0 kPa. Similarly, is was found in *J. curcas* a reduction in *WUE* under dry conditions most likely due to the negative effect of the higher potentials on the production of plant biomass [66]. However, in this study, soil with matric potential greater than -183.0kPa allowed the plants to maintain *WUE*.

4. CONCLUSION

Among the variables studied here, the relative water content, predawn leaf water potential, biomass, and relative growth rate were more sensitive to regulated water deficits. The cultivar BRS Energia was more promising in relatively drier conditions compared to BRS 188 Paraguaçu, since it was able to maintain a larger leaf area and more-hydrated tissues, maximizing the efficiency of water use. The carbon assimilation decreased in both castor bean cultivars only under severe water stress (-183.0 kPa), suggesting that the use of the deficit irrigation technique may be viable leading to lower water consumption and higher photosynthesis efficiency.

COMPETING INTERESTS

The authors declare that there is no conflict of interests.

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