Jatropha curcas and *Ricinus communis* display contrasting photosynthetic mechanisms in response to environmental conditions

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ABSTRACT: Higher plants display different adaptive strategies in photosynthesis to cope with abiotic stress. In this study, photosynthetic mechanisms and water relationships displayed by *Jatropha curcas* L. (physic nuts) and *Ricinus communis* L. (castor bean), in response to variations in environmental conditions, were assessed. *R. communis* showed higher CO_2 assimilation, stomatal and mesophyll conductance than *J. curcas* as light intensity and intercellular CO_2 pressure increased. On the other hand, *R. communis* was less effective in stomatal control in response to adverse environmental factors such as high temperature, water deficit and vapor pressure deficit, indicating lower water use efficiency. Conversely, *J. curcas* exhibited higher photosynthetic efficiency (gas exchange and photochemistry) and water use efficiency under these adverse environmental conditions. *R. communis* displayed higher potential photosynthesis, but exhibited a lower *in vivo* Rubisco carboxylation rate (*Vcmax*) and maximum electron transport rate (*Jmax*). During the course of a typical day, in a semiarid environment, with high irradiation, high temperature and high vapor pressure deficit, but exposed to well-watered conditions, the two studied species presented similar photosynthesis. Losing potential photosynthesis, but maintaining favorable water status and increasing non-photochemical quenching to avoid photoinhibition, are important acclimation mechanisms developed by *J. curcas* to cope with dry and hot conditions. We suggest that *J. curcas* is more tolerant to hot and dry environments than *R. communis* but the latter species displays higher photosynthetic efficiency under well-watered and non-stressful conditions.

Keywords: abiotic stress, castor bean, photosynthesis, physic nut, acclimation

Introduction

Photosynthetic performance in higher plants under adverse environmental conditions is largely dependent on plant species, which are able to trigger distinct adaptive mechanisms to deal with specific stressful conditions (Cousins et al., 2014). Plants display a set of acclimation strategies to maintain adequate photosynthesis rates in response to abiotic stress-inducers such as high temperature, drought and high light levels (Liu and Huang 2008; Chaves et al., 2009; Gonzalez-Cruz and Pastenes, 2012). To reach their potential or maximum photosynthesis, plants employ a fine metabolic coordination involving several inter-related processes, especially a close balance between photochemical activity and Calvin cycle reactions (Goh at al., 2012).

Abiotic stresses are able to disturb this balance, and affect especially CO_2 assimilation due to stomatal and biochemical limitations (Adams III et al., 2013). The degree of preservation of adequate synchrony between light harvest, energy conversion in photosystems and CO_2 assimilation, under stress conditions, is species-dependent and important to plant productivity (Athanasiou et al., 2010; Kramer and Evans, 2011; Murchie and Niyogi, 2011; Yamori et al., 2014).

In general, native species are able to survive under stressful environment conditions. These organisms are an important source of genes involved in stress tolerance and models for elucidating the steps that result in the limitation of photosynthesis efficiency. This feature is more relevant when these native plants have great agronomical potential like *Jatropha curcas* L. (physic nuts), a biofuel source of high quality (Achten et al., 2010).

Ricinus communis L. (castor beans) is widely cultivated worldwide as a source of special non-edible oil (Barbour and Buckley, 2007). These species are C3 plants and display contrasting tolerances in response to abiotic stress (Aragão et al., 2012; Babita et al., 2010; Dai et al., 1992; Silva et al., 2012). However, in these studies, the focus was on one of the species' response to isolated stresses. As an exception, Lima Neto et al. (2014) demonstrated that *J. curcas* and *R. communis* are contrasting in terms of salt tolerance and that the performance achieved by these species was related to distinct photosynthetic mechanisms. In this study, the photosynthetic mechanisms of the two species in response to different environmental conditions were compared.

Materials and Methods

Plant material

Jatropha curcas (L.) seeds, cultivar FT2, and *Ricinus communis* (L.) seeds, cultivar BRS 149 (nordestina), were utilized. The seeds were previously selected by size and weight and germinated in sand. Fifteen days after germination, the seedlings were transferred to

Lima Neto et al.

Jatropha curcas and *Ricinus communis* photosynthetic efficiency

plastic pots (4 L) containing vermiculite as substrate. Plants were grown for 45 days under natural conditions in a greenhouse situated in a semiarid region in Fortaleza, in the state of Ceará, Brazil (3°44' S; 38°34' W; 31 m altitude) between Jan and Mar 2012. The averages of the environmental parameters inside the greenhouse over the experimental period were as follows: 29 °C / 24 °C mean/minimum temperature, 62 % relative humidity, 1500 µmol m^{-2} s^{-1} maximum photosynthetic photon flux density (PPFD) and 12 h photoperiod. The plants were watered every two days with 300 mL of half-strength Hoagland and Arnon (1950) nutrient solution.

Dry matter, water status and cell integrity

Leaves were harvested at the end of experiment and weighed at freshly picked weight, then dried until constant weight in drying chambers. The relative water content (RWC) was calculated from the fresh, turgid and dry weight of leaf discs, as previously based on Lima Neto et al., 2014. The leaf pre-dawn water potential (Ψw) was evaluated immediately after sampling using the pressure chamber method (Scholander et al., 1965). Electrolyte leakage was assessed as described by Lima Neto et al. (2014) through the electrical conductivity of the leaf extract.

Gas exchange measurements

Gas exchange was monitored and photochemical measurements taken in plants grown under natural conditions of temperature, vapor-pressure deficit (VPD) and PPFD inside a greenhouse. The third fully expanded leaf from the bottom to the top was monitored throughout the experiment. The net CO_2 assimilation rate (P_N), transpiration (E), stomatal conductance (g_s) and intercellular CO_2 partial pressure (C_i) were regularly monitored with a portable gas exchange system.

Net photosynthesis was measured in response to photosynthetic photon flux density (PPFD), leaf-to-air vapor-pressure deficit ($VPD_{leaf-to-air}$), leaf temperature and intercellular CO_2 partial pressure (C_i). Each of these conditions was separately isolated in the infrared gas analyzer (IRGA) leaf chamber. Changes in VPD were achieved by controlling the leaf and air temperature in the chamber, and the relative humidity through a drying column coupled to the IRGA. For the P_N-VPD response curve, gas exchange was measured after 20 min at each step (Young et al., 1997).

For instantaneous measurements, the PPFD was fixed at 1500 µmol m^{-2} s^{-1}, 29 °C, a leaf-to-air vapor-pressure difference ($VPD_{leaf-to-air}$) between 1.0 and 1.5 kPa, and external CO_2 at atmospheric partial pressure (38 Pa). The P_N-PPFD and P_N-Ci curves were determined according to Lieth and Reynolds (1987) and Sharkey et al. (2007), respectively. For the P_N-PPFD curve (0 – 1800 µmol m^{-2} s^{-1}), the $VPD_{leaf-to-air}$ was controlled between 1.0 and 1.5 kPa, and external CO_2 at atmospheric partial pressure (38 Pa). For the P_N-Ci curve (0 – 160 Pa) the PPFD was fixed at 1500 µmol m^{-2} s^{-1} and $VPD_{leaf-to-air}$

between 1.0 and 1.5 kPa. From these curves, several parameters were calculated including maximum photosynthetic rate (P_{Nmax}), maximum Rubisco carboxylation rate (V_{cmax}), maximum photosynthetic electron transport (J_{max}) and mesophyll conductance (g_m).

Chlorophyll *a* fluorescence measurements, P700 activity and estimation of photorespiratory rate

In vivo chlorophyll fluorescence was measured using a LI-6400-40 leaf Chamber Fluorometer coupled to the IRGA. The fluorescence measurements were taken by means of the saturation pulse method (Schreiber et al., 1994) in leaves exposed to light and 30 min-dark-adapted conditions. The intensity and duration of the saturation light pulse were 8,000 µmol m^{-2} s^{-1} and 0.7 seconds, respectively. The amount of blue light was set up to 10 % of the PPFD to maximize stomatal aperture (Flexas et al., 2007).

The following parameters were assessed: (i) the maximum quantum yield of photosystem II (PSII) [$F_v/F_M = (F_m-F_o)/F_m$], (ii) the effective quantum yield of PSII [$\Delta F/F_m' = (F_m'- F_s)/F_m'$], (iii) the non-photochemical quenching coefficient [$NPQ = (F_m-F_m')/F_m'$], and (iv) the actual flux of photons driving photosystem II [$ETR = (\Delta F/F_m'$ x PPFD x 0.5 x 0.84)]. To evaluate the apparent electron transport rate at PSII level (ETR), 0.5 was used as the fraction of excitation energy distributed to PSII, and 0.84 was used as the fraction of incoming light absorbed by the leaves.

The F_m and F_o are the maximum and minimum fluorescence of dark-adapted leaves, respectively; F_m' and F_s are the maximum and steady state fluorescence in the light-adapted state, respectively, and F_o' is the minimum fluorescence after the far-red illumination of the previously light-exposed leaves (Schreiber et al., 1994; Maxwell and Johnson, 2000). The estimation of the photorespiratory rate (P_R) was determined as described in Bagard et al. (2008) from the measurements of gas exchange (P_N and R_d) and chlorophyll *a* fluorescence-derived ETR parameter by the equation: $P_R = 1/12[ETR-4(A + R_d)]$.

Statistical analysis and experimental design

The experiments were arranged in a completely randomized design with five independent replicates for each species consisting of an individual pot containing a plant. Data were analyzed using one–way ANOVA and means were compared using the t-test ($p < 0.05$) with SigmaPlot (Systat Software, San Jose, CA).

Results

In order to compare the photosynthetic characteristics of *J. curcas* and *R. communis* plants in response to adequate and stressful environmental conditions, we performed a set of individual experiments. These assays involved changes in gas exchange parameters in response to varying light intensity, CO_2 partial pressure, temperature and a leaf-to-air vapor pressure deficit. Addition-

ally, we reproduced the conditions of seasonal variation in the major parameters of PSII and gas exchange and made evaluations over a typical day in a semiarid region.

Light and CO_2 response curves

The P_N-PPFD and P_N-Ci curves produced by *J. curcas* and *R. communis* leaves showed a pattern typical of C3 plants (Figure 1A-B) adequate for fitting in the models proposed by Lieth and Reynolds (1987) and Sharkey et al. (2007). All parameters calculated from these curves are presented in Table 1. The light compensation point of *R. communis* plants was higher than in *J. curcas*, indicating that the former species requires more light to produce a similar net CO_2 assimilation, compared with the latter (Figure 1 and Table 1). When exposed to increasing light intensity, *J. curcas* and *R. communis* plants presented light saturation points close to 1000 and 1500 µmol m^{-2} s^{-1}, respectively, with maximum CO_2 assimilation rates (P_{Nmax}) of 19 and 24 µmol m^{-2} s^{-1}, respectively (Figure 1A, Table 1). These responses indicated that *R. communis* is more able to use high light than *J. curcas* under well-watered conditions.

Increases in light intensity induced different responses in stomatal conductance (g_s) of the species studied. In *R. communis*, g_s rose steadily in response to the

increasing light, while in *J. curcas* the stomatal conductance was not dependent on light intensities above 150 µmol m^{-2} s^{-1}, indicating that this species required only a narrow range of intensity of low light to trigger stomatal

Table 1 – Parameters associated with photosynthetic efficiency calculated from the P_N/PPFD and P_N/Ci fitting curves in *J. curcas* and *R. communis* plants grown under optimal conditions. Light Γ* is the light compensation point, P_{Nmax} the maximum CO_2 assimilation rate, CO_2 Γ* the CO_2 compensation point, CO_2 P_{Nmax} the maximum CO_2 assimilation rate, V_{cmax} the maximum Rubisco carboxylation rate, J_{max} the maximum photosynthetic electron transport rate, g_m the mesophyll conductance, and P_R the photorespiration rate. Each point represents the mean of five replicates. Different letters represent differences between species (t test ($p < 0.05$).

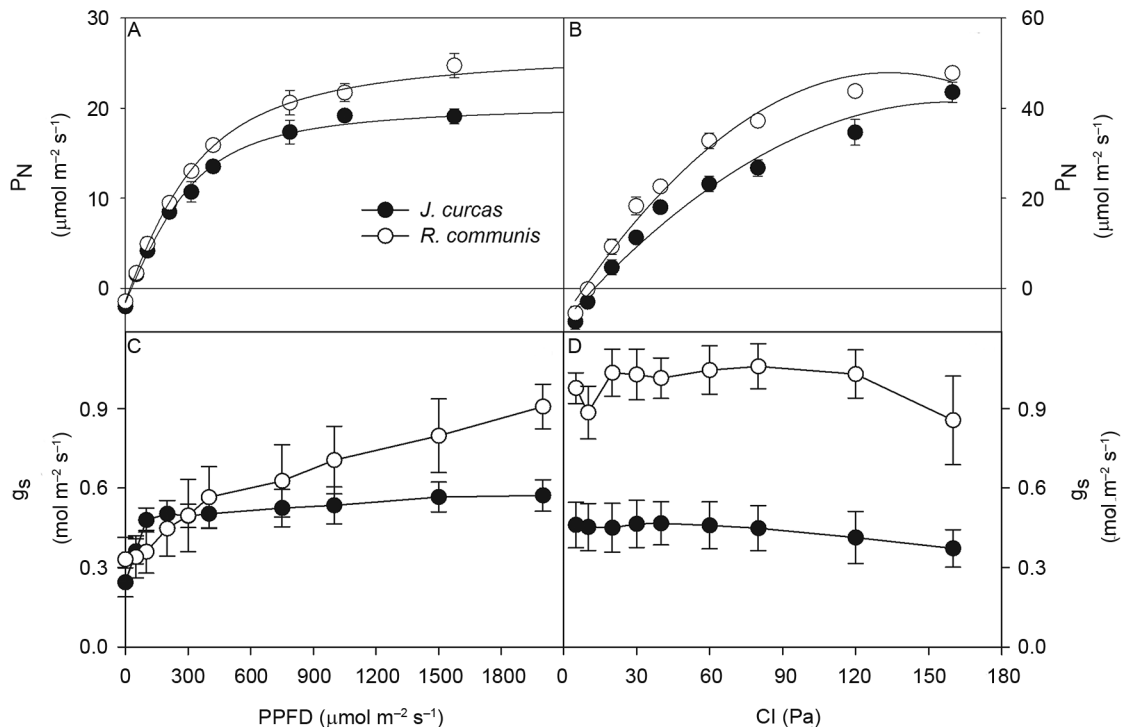|	*J. curcas*	*R. communis*
Light Γ* (µmol m^{-2} s^{-1})	20.71 b	26.82 a
Light P_{Nmax} (µmol m^{-2} s^{-1})	19.06 b	24.12
CO_2 Γ˙ (µmol m^{-2} s^{-1})	12.06 a	8.34 b
CO_2 P_{Nmax} (µmol m^{-2} s^{-1})	38.26 b	49.17 a
V_{cmax} (µmol m^{-2} s^{-1})	225.10 a	142.26 b
J_{max} (µmol m^{-2} s^{-1})	246.04 a	185.10 b
g_m (mol m^{-2} s^{-1})	0.23 b	0.59 a
P_R (µmol m^{-2} s^{-1})	7.52 a	3.46 b

Figure 1 – Curves of (A) CO_2 assimilation rates in response to increasing photosynthetic photon flux density, (B) to intercellular CO_2 partial pressure and (C) stomata conductance in response to increasing photosynthetic photon flux density and (D) to intercellular CO_2 partial pressure in young *J. curcas* and *R. communis* plants. For the PN/PPFD curve the CO_2 partial pressure was maintained at (38 Pa) and in the PN/Ci curve of the PPFD was fixed at 1,500 µmol m^{-2} s^{-1}. Each point represents the mean of five replicates (± SD). The standard deviation is shown when higher than the symbol.

opening, whereas *R. communis* maintained its stomata opening over a wide range of light intensity (Figure 1C). In response to increases in the intercellular CO_2 partial pressure, g_s did not change in either species, but *R. communis* showed much higher values (by 3-fold) compared with *J. curcas* (Figure 1D).

J. curcas presented a higher CO_2 compensation point (by 45 %) compared with *R. communis* (Table 1) but, in contrast, *R. communis* showed a higher maximum CO_2 assimilation rate than *J. curcas* under optimum external conditions. The maximum carboxylation rate of Rubisco (V_{cmax}), calculated from the P_N-Ci curves (Sharkey et al., 2007), was 58 % higher in *J. curcas* compared with *R. communis* and a similar trend was found for the maximum rate of photosynthetic electron transport (J_{max}), which was approximately 33 % higher in *J. curcas* plants (Table 1). Conversely, mesophyll conductance (g_m) was 157 % higher in *R. communis* compared with *J. curcas*, whereas the photorespiratory rate (P_R) was approximately twofold higher in *J. curcas* compared with *R. communis* (Table 1).

Taken together, these results indicate that photosynthesis in *R. communis* was more efficient in response to increases in both light intensity and CO_2 partial pressure compared with *J. curcas,* where the other environmental factors were non-limiting. This higher level of photosynthetic efficiency was closely associated with higher stomatal and mesophyll conductance. In contrast, *J. curcas* seedlings exhibited higher efficiency in transporting electrons from the photosystems to the Calvin cycle and a higher turnover rate of Rubisco.

Photosynthetic responses to increasing temperature and leaf-to-air vapor pressure deficit

Plants of both species exposed to increasing leaf temperatures had maximum photosynthesis at approximately 30 °C (Figure 2A). However, increasing the leaf temperature from 35 °C to 40 °C resulted in a decrease of 30 % in the P_N in *J. curcas* but the P_N remained unchanged in *R. communis* (Figure 2A). The intercellular CO_2 (C_i) partial pressure decreased in both species from 22 °C to 28 °C and did not change from 28 °C to 39 °C (Figure 2B). This early decrease in Ci in both species was correlated with the increase in P_N until it reached maximum CO_2 assimilation (Figure 2A-B).

The transpiration rate was positively correlated with increases in leaf temperature for both species, but *R. communis* showed higher transpiration rates at all temperatures (Figure 2C). The stomatal conductance (g_s) decreased steadily as the leaf temperature increased in both species. Overall, *J. curcas* showed a lower g_s compared with *R. communis*, indicating that the first one displays a more effective stomatal closing in response to increases in leaf temperature (Figure 2D).

Interestingly, when the leaf-to-air vapor-pressure deficit ($VPD_{leaf-to-air}$) increased from 1.0 to 5.5 kPa the P_N of both species did not change and both species had a similar increase in photosynthesis from 2.0 to 5.5 kPa (Figure 3A). In contrast to P_N, the C_i values were higher in *R. communis* compared to *J. curcas* over the VPD range studied (Figure 3B). Transpiration rates and g_s were also comparatively higher in *R. communis* than in *J. curcas*, increasing almost linearly from 0.5 to between 2.0 kPa in both species and remained practically constant from 2.0 to 4.0 kPa (Figure 3C). Overall, the g_s displayed a similar trend compared with E when the VPD changed from 0.5 to 2.5 kPa. Beyond this the g_s decreased in both species from 2.5 to 5.5 kPa. However, *R. communis* exhibited higher g_s values than *J. curcas* in response to the VPD range studied (Figure 3D).

The two species studied display contrasting responses to stomatal mechanisms regarding the changes in temperature and VPD (or heat and dry conditions). *R. communis* displayed a less effective mechanism to stomatal closure in response to heat and high VPD. However, the higher stomatal conductance shown by this species was not enough to allow CO_2 assimilation rates higher than those presented by *J. curcas* when both species were exposed to water restrictive conditions. Thus, the latter species presents higher water use efficiency under stomatal restriction conditions compared with *R. communis*.

Changes in gas exchange and photosystem II parameters over a typical day in a tropical semiarid region

The variations in a number of gas exchange and photosystem II parameters were evaluated over a day in plants cultivated under natural conditions where VPD and PPFD changed as on a typical day in a hot and dry tropical semiarid region. Under these conditions, the air temperature and VPD varied from a minimum of 27 °C and 0.9 kPa, respectively, at 9h00, to a maximum of 35 °C and 2.0 kPa, respectively at 13h00, while the PPFD reached maximum values (~ 1800 µmol m^{-2} s^{-1}) between 11h00 and 14h00 (Figure 4). Photosynthesis was similar for *J. curcas* and *R. communis*, increasing slightly from 7h00 to 13h00 and decreasing afterwards. The decrease in P_N rate was directly correlated with the decrease in PPFD (Figure 5A).

The C_i changed slightly throughout the day in both species but *R. communis* displayed higher C_i values compared with *J. curcas* (Figure 5B), corroborating the data previously observed (Figure 3B). The transpiration showed a variation pattern close to a parabolic function, similar to that observed for CO_2 assimilation, increasing from 7h00, reaching a maximum between 11h00 and 13h00 and decreasing afterwards (Figure 5C). The transpiration rates over the course of the day were slightly higher in *R. communis* compared with *J. curcas.* The former species presented higher g_s values from 7h00 until 13h00 than *J. curcas* but from 15h00 to 17h00 the two species studied showed similar stomatal conductance (Figure 5D). *J. curcas* exhibited higher water use efficiency (WUE), as expressed by µmol CO_2 fixed per mmol H_2O transpired, but mainly if the WUE is expressed on a stomatal conductance basis, thereby corroborating the previous data shown in Figure 3.
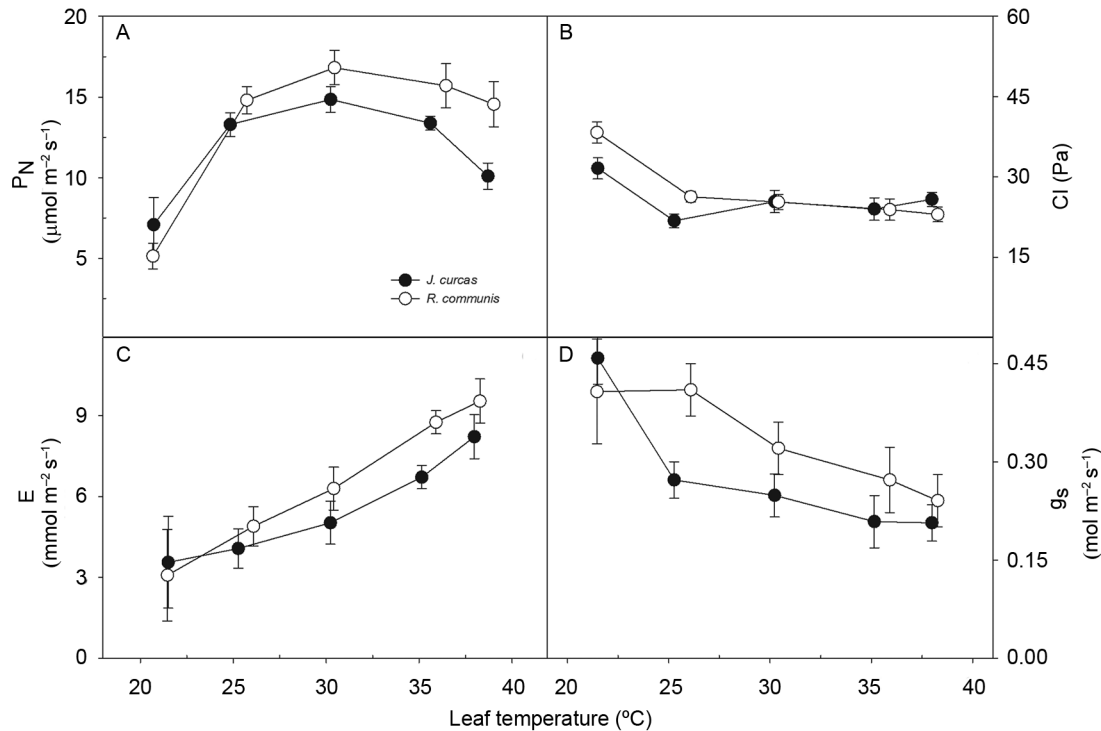
Figure 2 – (A) CO_2 assimilation rates, (B) intercellular CO_2 partial pressure, (C) transpiration rate and (D) stomatal conductance in response to increasing leaf temperature in young *J. curcas* and *R. communis* plants. The PPFD was fixed at 1,500 µmol m^{-2} s^{-1}, VDPleaf-to-air between 1.0 and 1.5 kPa, and external CO_2 at atmospheric partial pressure (38 Pa). Each point represents the mean of five replicates (± SD). The standard deviation is shown when higher than the symbol.

Both species displayed a similar trend in photochemical modulation during the course of the day (Figure 6 A-D). Fv/Fm, a ratio that expresses the potential yield of PSII, decreased during the driest and hottest hours of the day in both species, recovering late afternoon (Figure 6A). The effective quantum yield (ΔF/Fm') and the apparent electron transport of PSII (ETR) exhibited similar trends in both species, decreasing until 14h00 and recovering steadily afterwards (Figure 6 B-C). However, *R.communis* displayed higher photochemical efficiency and electron transport rate until 14h00 compared with *J. curcas*. The non-photochemical quenching (NPQ), an indicator of heat dissipation at PSII level, was triggered steadily in both species from 6h00 to 13h00, decreasing afterwards and reaching values near to those observed in the early morning.

Interestingly, *J. curcas* presented NPQ much higher than *R. communis* for most of the day (Figure 6D), indicating a great contrast between these species in terms of coping with excess energy. Altogether, the data obtained over a typical day in a semiarid region indicated that the two species had a significant contrast in photosynthesis under well-watered conditions and when exposed to varying conditions of PPFD and VPD (air temperature and humidity). The most contrasting mechanisms were stomatal control in which *R. communis* exhibited much

higher stomatal conductance associated with higher Ci compared with *J. curcas*. However, these two mechanisms were not closely correlated with CO_2 assimilation, indicating a certain biochemical limitation in *R. communis*. In contrast, *J. curcas* plants were more efficient in terms of photosynthesis per unit of water transpired, Ci and extent of stomatal opening. Both species exhibited good plasticity in PSII modulation but *J. curcas* was more efficient in terms of excess energy dissipation as heat by the NPQ mechanism.

R. communis displays under these environmental conditions higher leaf dry matter, relative water content and lower water potential compared with *J. curcas* plants exposed to the same condition. The electrolyte leakage, a common parameter for estimating membrane damage was practically the same in both species (Table 2).

Discussion

Our data strongly suggest that *J. curcas* and *R. communis* plants display contrasting photosynthetic mechanisms in response to different environmental conditions. Apparently, *J. curcas* is better adapted to dry and hot conditions like those that prevail in semi-arid regions. Indeed, this species displays efficient stomatal control to avoid water loss and high excess
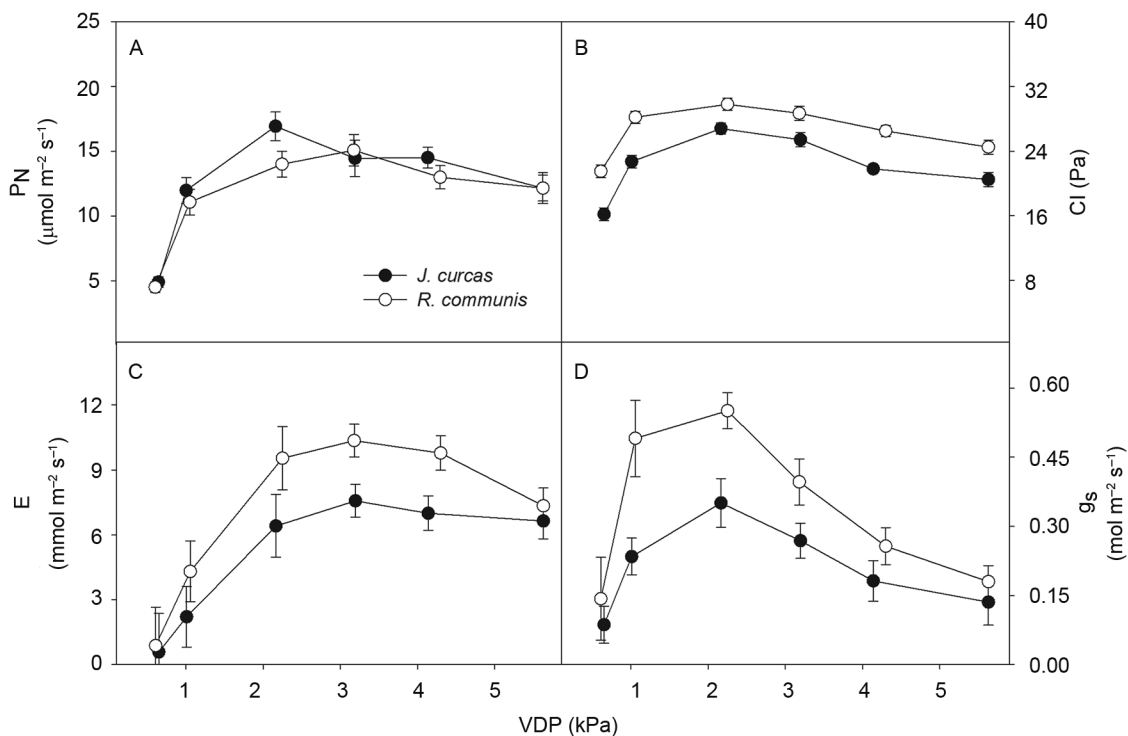
Figure 3 – (A) CO_2 assimilation rates, (B) intercellular CO_2 partial pressure, (C) transpiration rate and (D) stomatal conductance in response to increasing air VPD (kPa) in young *J. curcas* and *R. communis* plants. The PPFD was fixed at 1,500 µmol m^{-2} s^{-1} and external CO_2 at atmospheric partial pressure (38 Pa). Each point represents the mean of five replicates (± SD). The standard deviation is shown when higher than the symbol.
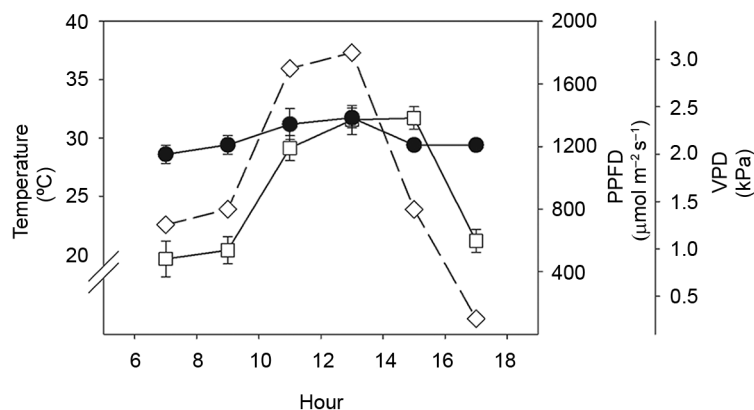

Figure 4 – Changes in environmental parameters over a typical day in the greenhouse. (-•-) Air temperature, (-◇-) photosynthetic photon flux density (PPFD) and (-□-) vapor pressure deficit (VPD). Each point represents the mean of three independent measurements taken on different days. The standard deviation is shown when higher than the symbol.

energy dissipation by NPQ, corroborating previous results in response to water deficit alone (Maes et al., 2009a; Maes et al., 2009b; Silva et al., 2010a), drought combined with high temperature (Silva et al., 2012), drought with high CO_2 (Meng et al., 2013) and salinity alone or in combination with high temperature (Silva et al., 2010a; Silva et al., 2010b).

In contrast to *J. curcas*, *R. communis* display less effective stomatal control and NPQ triggering under dry and hot conditions. This species has more efficient photosynthesis under non-limiting conditions of soil water availability, light and temperature. Dai et al. (1992) reported that *R. communis* presents high photosynthetic capacity under low VPD conditions which was compa-
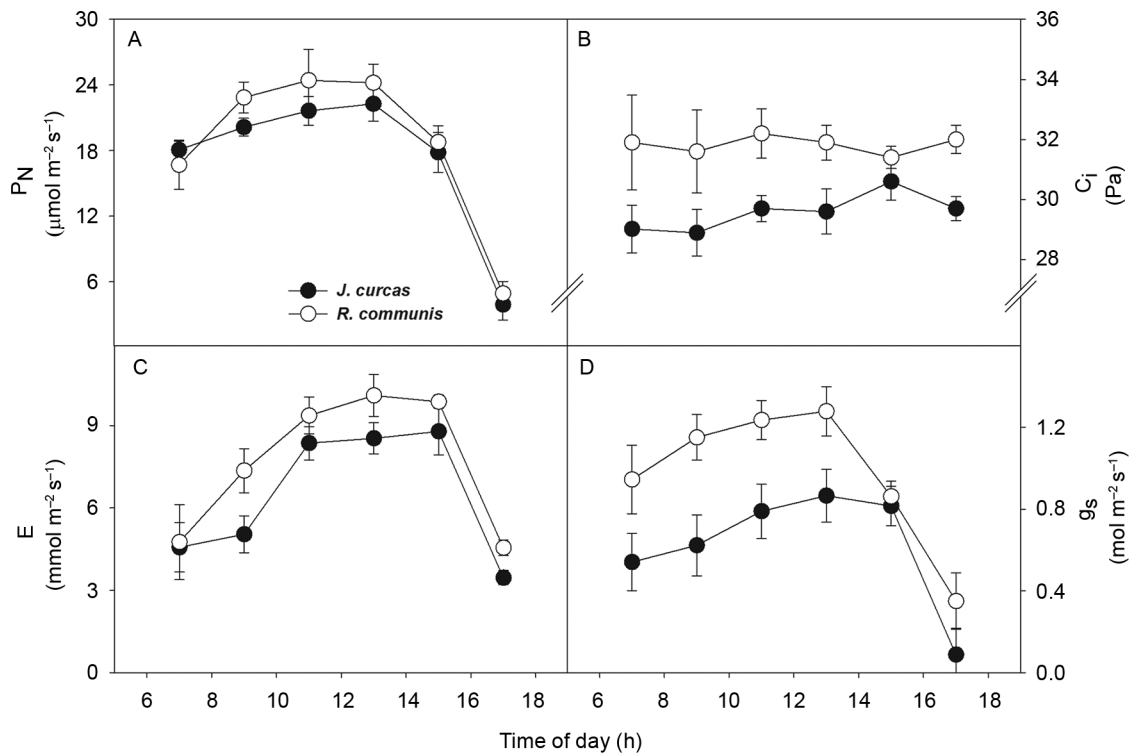
Figure 5 – Daily courses of (A) CO_2 assimilation rates, (B) intercellular CO_2 concentrations, (C) transpiration rates and (D) stomatal conductance, in young *J. curcas* and *R. communis* plants. The average environmental parameters over the experimental period were as follows: 29 °C / 24 °C mean/minimum temperature, 62 % relative humidity, 1,500 µmol m^{-2} s^{-1} maximum photosynthetic photon flux density (PPFD). Each point represents the mean value of five replicates (± SD). The standard deviation is shown when higher than the symbol.

Table 2 – Leaf dry matter, relative water content, water potential and electrolyte leakage in *J. curcas* and *R. communis* plants grown under greenhouse conditions in a semiarid region. Each point represents the mean of five replicates. *represents a difference between species (t test, $p < 0.05$).

	R. communis	J. curcas
Leaf DM (g per plant)	5.41*	4.91
RWC (%)	81.43*	63.24
Water potential (MPa)	-0.31*	-0.19
Electrolyte leakage (%)	21.18	21.69

rable to a C4 plant (maize). However, similar to the data we obtained, photosynthesis was remarkably reduced as VPD increased in parallel to an excessive loss of water by transpiration. Our data are also corroborated by Barbour and Buckley (2007), who have suggested that *R. communis* is a "mal-adaptive" species when faced with dry conditions since it maintains high stomatal conductance even under high VPD. *R. communis* plants presented stomatal limitation to photosynthesis under drought and maintained high g$_s$, resulting in low water use efficiency (Babita et al., 2010).

Under field conditions *R. communis* and *J. curcas* require different crop management and climate conditions to reach optimum productivity. The former species require good soil water supply and low VPD to express their genetic potential for high photosynthesis. In contrast, *J. curcas* is less able to exhibit similar photosynthetic efficiency under the conditions required by *R. communis* but, in contrast, it adapts better to hot and dry conditions. Thus, the photosynthetic characteristics presented by these two species are typical for both the more tolerant (*J. curcas*) as well as the less tolerant (*R. communis*) to drought condition (Flexas and Medrano, 2002; Chaves et al., 2003).

To display favorable stomatal mechanisms to cope with drought, *J. curcas* exhibits another important adaptive characteristic, that is, a rapid and efficient triggering of excess energy dissipation by NPQ at PSII level. Indeed, this response is very important for adaptation to a wide range of stressful conditions (Niyogi 1999; Chaves et al., 2009; Driever and Baker, 2011; Takahashi and Badger, 2011). Under drought conditions, the impairment of CO_2 assimilation causes an imbalance between the electron transport rate in the photosynthetic electron transport (PET) chain and the plant's capacity to utilize NADPH (reduced nicotinamide adenine dinucleotide phosphate) and ATP (adenosine tri-phosphate) in the Calvin cycle (Chaves et al., 2009). Under this CO_2-limiting condition, photorespiration is proposed as an important alternative pathway for consuming the excess reducing equivalents from the photochemical reactions, avoiding photoinhibition (Bagard et al., 2008; Takahashi and Badger, 2011).
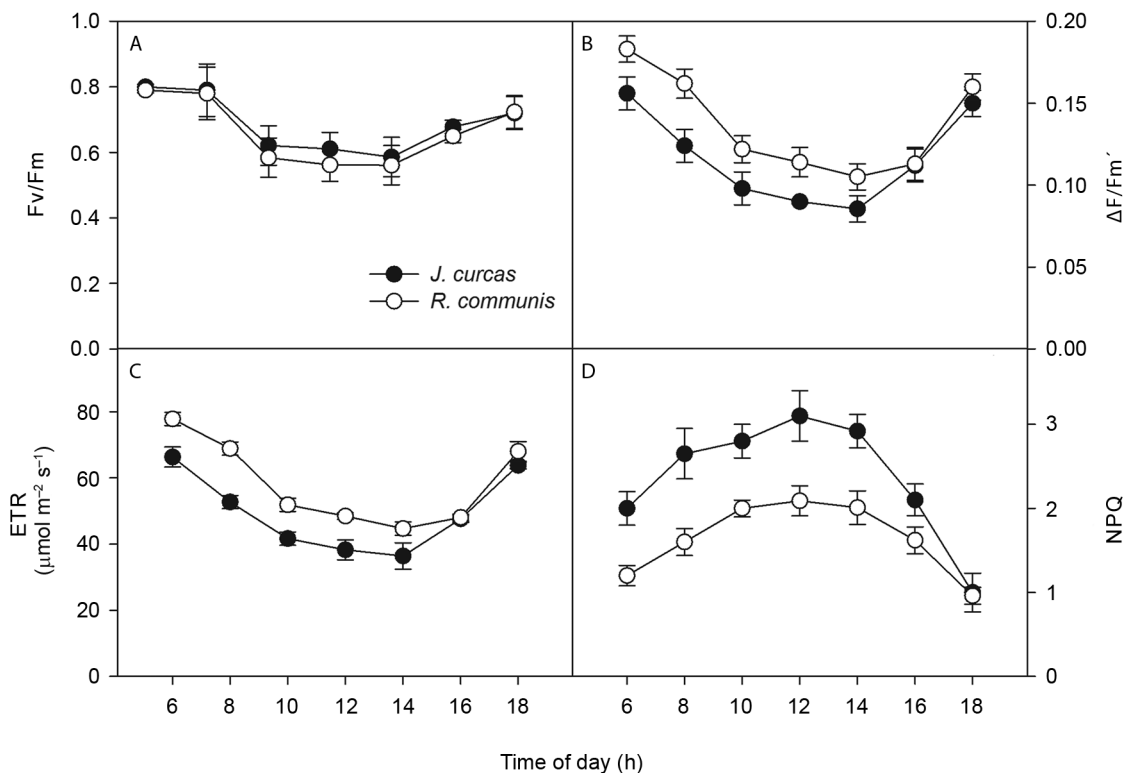
Figure 6 – Daily courses of (A) potential yield of PSII, (B) effective yield of PSII, (C) electron transport rate of PSII and (D) non-photochemical quenching, in young *J. curcas* and *R. communis* plants. The average environmental parameters over the experimental period were as follows: 29 °C / 24 °C mean/minimum temperature, 62 % relative humidity, 1,500 µmol m^{-2} s^{-1} maximum photosynthetic photon flux density (PPFD). Each point represents the mean value of five replicates (± SD). The standard deviation is shown when higher than the symbol.

Plants must achieve a fine balance between photochemistry, CO_2 assimilation, and alternative electron sinks in order to cope with different environment conditions and avoid photoinhibition (Murchie and Niyogi, 2011). Any disturbance of this equilibrium will disrupt the photosynthetic efficiency and result in excess energy on the thylakoid membranes (Niyogi 1999). This excess energy might produce reactive oxygen species that in high concentrations can be harmful to lipids, and protein structure in chloroplasts and the whole cell (Osmond and Förster, 2006). However, plants have developed distinct photo-protective mechanisms that control the excess energy to preserve the structures of chloroplasts and metabolism. Aragão et al. (2012) have previously reported that *J. curcas* plants exposed to salinity use nitrate assimilation as an alternative excess energy dissipation mechanism. In addition, Lima Neto et al. (2014) demonstrated that *R. communis* displayed higher increases in photorespiration compared with *J. curcas* after exposure to high salinity.

J. curcas has lower potential photosynthesis but higher *in vivo* Rubisco activity (*Vcmax*) and maximum electron transport rate (*Jmax*) compared with *R. communis* under optimum growth conditions. Moreover, over a typical day in a semiarid environment, with high irradiance, VPD and temperature, but exposed to well-watered conditions, *J. curcas* had similar photosynthesis and higher water use efficiency, compared with *R. communis*. These responses were related to efficient stomata control and the increase in NPQ to prevent photoinhibition in *J. curcas*. The maintaining of high P_N during the driest hours of the day (high VPD levels) is related to low stomata control in *R. communis* in response to VPD as described previously by Barbour and Buckley (2007). A high transpiration rate linked with low photosynthesis is not an advantageous physiological characteristic for plants that face abiotic stress factors like those predominating in semiarid environments.

Does *R. communis* have stomatal characteristics suitable for coping with dry and hot environments such as those found in semiarid regions? In fact, the stomatal conductance and water use efficiency presented by *R. communis* are less effective in dealing with drought compared with *J. curcas*. Thus, apparently, the initial growth phase is critical to *R. communis* for survival and it will grow under dry conditions. In contrast, this species requires good water supply and mild vapor pressure deficit to achieve maximum photosynthetic efficiency. However, as both *R. communis* and *J. curcas* are deciduous species, they could display low photosynthetic efficiency under the very dry conditions prevailing in semiarid re-

gions. In practical terms, *J. curcas* are more adapted to survivjng under extreme conditions of heat and dryness in comparison with *R. communis*. In contrast, under irrigated conditions, the latter species might exhibit higher photosynthesis rates.

In conclusion, under non-limiting water supply *R. communis* plants have high photosynthetic efficiency associated with an efficient use of light and CO_2 and high stomatal and mesophyll conductance. In contrast, *J. curcas* is resistant to hot and dry conditions due to an efficient excess energy dissipation mechanism at PSII level by NPQ. This photochemical response in *J. curcas* is associated with an effective stomatal mechanism that might restrict water loss, which allows it to maintain high water use efficiency under abiotic stress conditions.

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