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ORIGINAL ARTICLE

Regulation of the photosynthetic electron transport and specific photoprotective mechanisms in *Ricinus communis* under drought and recovery

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Abstract *Ricinus communis* is one of the major commercial non-edible oilseed crops grown in semiarid and arid environments worldwide and is reported as a drought tolerant species. Surprisingly, little is known about the mechanisms achieving this tolerance, especially in relation to photoprotection. The aim of this study was to analyze the association of the regulation of the photosynthetic electron transport and photoprotective mechanisms with drought tolerance in *R. communis*. Drought induced decreases in the relative water content, water potential and growth in *R. communis* exposed to 9 days of drought. After 6 days of rehydration, these parameters were completely recovered, demonstrating a potential of drought tolerance in this species. In addition, drought inhibited photosynthesis by stomatal and metabolic limitations (V_{cmax}, J_{max}, and Rubisco activity), with partial recovery after rehydration. Leaves displayed transient photoinhibition after 6 days of drought, which was completely recovered after 6 days of dehydration. The effective quantum yields and the electron transport rates of PSII and PSI were modulated to face drought avoiding the excess energy produced by decreases in CO_2 assimilation. NPQ was increased during drought, and it was maintained higher than control after the recovery treatment. In addition, the estimated cyclic electron flow was induced under drought and decreased after recovery. Photorespiration was also increased under drought and maintained at higher levels after the recovery treatment. Furthermore, antioxidative enzymes activities (SOD, APX, and CAT) were increased under drought to avoid ROS harmful effects. Altogether, we clearly showed that the modulation of photoprotective mechanisms and antioxidant enzymes are crucial to this species under drought. The implication of these strikingly strategies to drought tolerance is discussed in relation to agricultural and natural systems.

Keywords Antioxidative metabolism · Cyclic electron flow · Drought · Photochemical activity · Photorespiration · *Ricinus communis* · ROS

Abbreviations

Ψ_w	Water potential
APX	Ascorbate peroxidase
CAT	Catalase
CEF	Cyclic electron flow
DM	Dry matter
FM	Fresh matter
GO	Glycolate oxidase
LEF	Linear electron flow
PET	Photosynthetic electron transport
PPFD	Photosynthetic photon flux density
P_R	Photorespiration
ROS	Reactive oxygen species
RuBP	Ribulose 1,5 bisphosphate
RWC	Relative water content
PSI	Photosystem I
PSII	Photosystem II
SOD	Superoxide dismutase
TBARS	Thiobarbituric acid reactive substances
VPD	Vapor pressure deficit

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Introduction

Drought negatively impacts plant growth and development by disturbing several physiological process, such as photosynthesis and redox homeostasis (Flexas et al. 1999; Noctor et al. 2014). In fact, photosynthetic responses to drought are complex comprising a coordination of several morphological and physiological processes at different time scales and growth stage (Ogbaga et al. 2014). The ability to maximize water extraction from the soil, minimizing loss from leaves, is vital to plant tolerance to drought. Therefore, physiological adaptations to drought are related with changes in stomata density to maintain water status (Chaves et al. 2009), the accumulation of compatible solutes, as carbohydrates and amino acids, to lower the water potential and improve water uptake (Mcdowell et al. 2008) and the maintenance of photosynthetic efficiency by photoprotective mechanisms (Goh et al. 2011).

Photosynthetic responses to drought are influenced by the intensity, duration, and rate of progression of this stress (Zivcak et al. 2013). First, drought impairs photosynthesis through decreasing CO_2 availability to chloroplasts by stomatal and mesophyll restrictions. With the progression of the stress, the Calvin–Benson cycle reactions are affected leading to limitations on photosynthetic metabolism (Flexas et al. 2012). The CO_2 assimilation by the Calvin–Benson reactions is the main sink for the NADPH and ATP produced by the photosynthetic electron transport. Impairments on this important sink commonly induces an imbalance in the overall photosynthetic process, producing excessive energy in the thylakoids that could lead to an overproduction of reactive oxygen species (ROS) and eventually to photoinhibition (Takahashi and Murata 2008). Absorbed excessive energy is defined when it exceeds the capacity of photosynthesis to use it for assimilation (Murchie and Niyogi 2011). Although excess energy is potentially harmful, plants have several photoprotective mechanisms to manage the absorbed light and avoid ROS unbalance (Pérez-Torres et al. 2007).

The redox state in plant cells should be maintained in adequate levels by a delicate balance between ROS production and the scavenge system (Suzuki et al. 2012). Alterations in energy balance during drought in chloroplasts promote the generation of singlet oxygen ($^1O_2$) at PSII by excited triplet-state chlorophyll when the photosynthetic electron transport (PET) chain is overreduced (Nishiyama et al. 2006). In PSI, under excessive energy, electron transfer to oxygen might cause the production of H_2O_2 via radical superoxide ($O_2^{\cdot}$) (Asada 2006). To avoid oxidative stress, chloroplasts scavenge ROS effectively by multiple enzymatic and non-enzymatic mechanisms including superoxide dismutase (SOD), ascorbate peroxidase (APX), ascorbate, carotenoids, among others (Blokhina et al. 2003). However, these mechanisms are energetically demanding, requiring the synthesis of high amounts of antioxidants and enzymes (Stepien and Johnson 2009). An alternative strategy to avoid ROS burst is the regulation of the photosynthetic electron transport (Goh et al. 2011), avoiding photoinhibition and the excess energy in the thylakoids membranes (Lima Neto et al. 2014).

The dissipation of excess absorbed light into heat by the non-photochemical quenching (NPQ) represents a fast response of the photosynthetic membrane to excess light (Carvalho et al. 2015). A rapidly reversible component of NPQ (qE) dissipates the excess absorbed light energy in the light-harvesting antenna of PSII. qE is triggered by low thylakoid lumen pH and high ΔpH generated by the photosynthetic electron transport (Johnson et al. 2011). The low pH of the lumen activates qE by protonating the PsbS protein (Li et al. 2000) or indirectly by activating the xanthophyll cycle (Demmig-Adams and Adams 1993). In addition, under limitation of CO_2 assimilation, energy from the PET chain can be, in part, redirected to photorespiration (P_R) (Maurino and Peterhansel 2010). Photorespiration recovers the carbon diverted by the oxygenase activity of Rubisco, transporting and reducing equivalents from the chloroplast, mainly by the activity of malate shuttle. This mechanism would possibly prevent the overreduction of thylakoids and photoinhibition, as occurs in drought stress (Peterhänsel and Maurino 2010). This allocation of reducing equivalents by P_R is also important for nitrate assimilation in *R. communis* under salinity (Lima Neto et al. 2014). Nevertheless, photorespiration produces a great amount of H_2O_2 in the peroxisomes by the glycolate oxidase (GO) and in a minor extent $O_2^{\cdot}$ radical by peroxisomal superoxide dismutase (SOD) isoforms (Kangasjärvi et al. 2012). Catalase is an important enzyme scavenging the excess H_2O_2 in peroxisomes, mainly under high concentrations of H_2O_2 (Asada 2006).

The cyclic electron flow (CEF), activated in PSI, results in the generation of a pH gradient across the thylakoid membrane (ΔpH), driving ATP synthesis. Therefore, by inducing qE, light harvesting is regulated, without the accumulation of NADPH in chloroplasts (Joliot and Johnson 2011) and possibly dissipating absorbed energy by photosystem I (PSI) (Johnson 2011). CEF-PSI consists in two pathways, PGR5 and PGRL1 proteins dependent, whereas the minor pathway is mediated by NDH complex (Yamori et al. 2016). However, the complex regulation of the CEF in plants exposed to stress is not clearly yet. There is controversy over the contribution and regulation of this process as an effective photoprotective mechanism (Zivcak et al. 2013).

In view of this, it is pertinent to look critically at tolerance strategies of naturally drought tolerant plants to understand strategies to maintain crop productivity (Ogbaga et al. 2014). The aim of this study was to examine the physiological and biochemical responses of *R. communis* to drought and its capacity of recovery. In particular, we have focused identifying photoprotective mechanisms and antioxidative metabolism responses that could possible give rise to drought tolerance in this species. *R. communis* is a species well adapted to arid and semiarid environments as potential crop for biofuel production (Lima Neto et al. 2015).

Materials and methods

Plant material and growth conditions

Seeds of *R. communis* (L.), cultivar BRS 149, were provided by EMBRAPA, Brazil. Seeds were selected by size and weight and germinated in washed sand. Fifteen days after germination, the seedlings were transferred to plastic pots (8 L) with vermiculite and sand (1:1) as substrate. Plants were grown in a greenhouse located in a semiarid region (3°44′38″S and 38°34′11″W, 31 m altitude). The environmental conditions during the experimental period were: average air temperature of 29/24 °C (maximum/minimum); average air relative humidity of 62%, maximum photosynthetic photon flux density (PPFD) of 1800 µmol m^{-2} s^{-1}, and 12 h-photoperiod. Plants were watered every other day with distilled water, until drainage, and every 3 days with 400 mL of a half-strength nutrient solution at pH 6.0 (Hoagland and Arnon 1950). For the water deficit treatment, the irrigation of 45-day-old plants was withdrawn for 9 consecutive days. After these periods, a set of plants were harvested (drought) and another group was rewatered for 6 days (recovery). The well-watered plants (daily irrigated to near pot saturation) were used as control during all the experiment. Throughout the experimental period, the leaf gas exchange and chlorophyll *a* fluorescence were measured every 3 days between 9 and 10 h. On the ninth day of drought and after 7 days of recovery, full-expanded leaves were harvested, immersed in liquid N_2, and stored at −80 °C until biochemical determinations.

Leaf dry matter, relative water content, water potential, electrolyte leakage, and pigment content

The leaf fresh matter (FM) of each plant was measured just after harvesting. The leaf relative water content (RWC) was calculated from differences of fresh, turgid, and dry weight in leaf discs, as previously described (Lima Neto et al. 2015). Dry matter (DM) is the dry weight determined after 48 h in an oven at 75 °C and the turgid weight was measured after 6 h of saturation in deionized water at 4 °C in dark condition. The leaf predawn water potential (Ψ_w) was evaluated immediately after sampling using the pressure chamber (3000 Scholander PWSC, ICT international, Armidale, AUS) method (Scholander 1960). The electrolyte leakage was assessed as described previously (Lima Neto et al. 2015) and the photosynthetic pigments (chl *a*, *b*, total, and carotenoids) contents were assessed (Lichtenthaler and Wellburn 1983).

Leaf gas exchange, chlorophyll *a* fluorescence, and P700 redox state measurements

For the assessment of gas exchange and photochemical parameters, plants were transferred to a growth chamber, with controlled conditions of 29 °C, RH 70%, and PPFD of 700 µmol m^{-2} s^{-1}. After 1 h of plant acclimation to these conditions, the measurements were performed in the third full-expanded leaf. The net CO_2 assimilation rate (P_N), stomatal conductance (g_s), transpiration (E), and intercellular CO_2 partial pressure (C_i) were measured with a portable infrared gas analyzer system, equipped with a LED source (IRGA LI-6400XT, LI-COR, Lincoln, NE, USA). During the measurements, the conditions inside the IRGA chamber were set to PPFD of 1500 µmol m^{-2} s^{-1}, air CO_2 partial pressure of 38 Pa, air vapor pressure deficit of 1.2 ± 0.5 kPa, and air temperature of 28 °C. The amount of blue light was set to 10% of the PPFD to maximize stomatal aperture (Flexas et al. 2007). Measuring conditions were in accordance with the optimum one's for photosynthesis within the specie (Lima Neto et al. 2015). The P_N responses to changes in PPFD and CO_2 concentration were evaluated and fitted according to the models proposed by Lieth and Reynolds (1987) and Sharkey et al. (2007), respectively. From the photosynthetic response curves to PPFD and chloroplastidial CO_2 partial pressure (C_c), we were able to estimate the maximum Rubisco carboxylation rate (V_{cmax}), the maximum photosynthetic rate (P_{Nmax}), day respiration (R_d), mesophyll conductance (g_m), and the maximum rate of photosynthetic electron transport driving RuBP regeneration (J_{max}).

In vivo chlorophyll *a* fluorescence was measured using an LI-6400-40 Leaf Chamber Fluorometer (LI-COR, Lincoln, NE, USA) coupled to the IRGA. The fluorescence measurements were taken using the saturation pulse method (Klughammer and Schreiber 1994) in light and dark-adapted (30 min) leaves. The intensity and duration of the saturation light pulse were 8000 µmol m^{-2} s^{-1} and 0.7 s, respectively. The measurements of chlorophyll fluorescence in light-adapted samples were taken simultaneously to the measurements of leaf gas exchange,

under the same chamber conditions. The following parameters were assessed: the maximum quantum efficiency of PSII [$F_v/F_m = (F_m - F_o)/F_m$], the effective quantum efficiency of PSII [$\phi_{PSII} = (F'_m - F_s)/F'_m$], the non-photochemical quenching [$NPQ = (F_m - F'_m)/F'_m$], and the apparent electron transport rate through the photosystem II [$ETR_{II} = (\phi_{PSII} \times PPFD \times 0.5 \times 0.84)$]. To estimate ETR_{II}, 0.5 was used as the fraction of excitation energy distributed to PSII, and 0.84 was 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, F'_o, and F_s are the maximum, the minimum, and the steady-state fluorescence in the light-adapted samples (Maxwell and Johnson 2000). The estimation of the photorespiratory rate (P_R) was performed according to Bagard et al. (2008), as $P_R = 1/12[ETR_{II} - 4(P_N + R_d)]$.

The redox state of the PSI was measured using a DUAL-PAM 100 (Walz, Effeltrich, Germany). The photochemical quantum efficiency of PSI (ϕ_{PSI}) and the electron transport rate through PSI (ETR_I) were assessed. The estimation of the cyclic electron flow (CEF) was estimated by the ETR_I/ETR_{II} ratio (Yamori et al. 2011). Photochemical activity of PSI was measured under the same conditions described previously for measurements of PSII activity and leaf gas exchange.

Lipid peroxidation and hydrogen peroxide content

The lipid peroxidation was assessed evaluating the thiobarbituric acid reactive substances (TBARS) in accordance to Cakmak and Horst (1991), with modifications described by Bonifacio et al. (2011). Readings were taken by the difference in absorption of 660 and 532 nm. The concentration of TBARS was assessed by the absorption coefficient of 155 mM^{-1} cm^{-1} and the results expressed as nmol MDA-TBA g^{-1} FM. Hydrogen peroxide content was measured by the titanium tetrachloride ($TiCl_4$) method according to Brennan and Frenkel (1977). Fresh leaf discs were macerated with liquid N_2 containing 5% (w/v) TCA and centrifuged at 12,000*g* (4 °C), and the supernatant was used for the H_2O_2 determination. The measurement was performed after reaction of $TiCl_4$ with hydrogen peroxide and the H_2O_2 concentration was calculated from a H_2O_2 standard curve (Sigma). Readings were taken at 415 nm with a spectrophotometer and expressed as μmol H_2O_2 g^{-1} FM.

Preparation of leaf extract and enzyme activity assays

For preparation of leaf extracts, fresh leaf samples were grounded in liquid N_2 with a mortar and pestle and extracted with cold 100 mM Tris–HCl buffer, pH 8, 0.1 mM EDTA, 1 mM ascorbic acid, 20% glycerol, 3% PEG-6000 and 30 mM DTT. The enzymatic extract was stored at −20 °C until the determinations.

Total ascorbate peroxidase (APX) activity (EC 1.11.1.11) was measured by the ascorbate oxidation following the decreases in absorbance at 290 nm (Nakano and Asada 1981), with minor modifications described in Bonifacio et al. (2011). The activity was assayed with 0.5 mM ascorbate and 0.1 mM EDTA dissolved in 100 mM K-phosphate buffer pH 7.0 and leaf extract. The reaction started by adding 30 mM H_2O_2. The enzyme activity was measured by the decrease in absorbance at 290 nm and 25 °C over a 300 s period, being expressed as μmol ascorbate $(mg\ protein\ min)^{-1}$.

Total superoxide dismutase (SOD) activity (EC 1.15.1.1) was measured by the inhibition of the blue formazan by the nitroblue tretazolium chloride (NBT) photoreduction. The SOD activity was measured with the leaf extract in a mixture of 50 mM potassium phosphate buffer (pH 7.8), 0.1 mM EDTA, 13 mM L-methionine, 2 μM riboflavin, and 75 μm *p*-nitroblue tetrazolium chloride (NBT) in the dark. The reaction was exposed to illumination (30 W fluorescent lamp) at 25 °C for 6 min. The absorbance was measured at 540 nm (Giannopolotis and Ries 1977). A SOD activity unit (U) was defined as the amount of enzyme able to inhibit 50% of the NBT photoreduction. The activity was expressed as U $(mg\ protein\ min)^{-1}$.

Total catalase (CAT) activity (EC 1.11.1.6) was assessed by the oxidation of H_2O_2 at 240 nm. CAT activity was determined after the reaction of the enzymatic leaf extract in the presence of 50 mM potassium phosphate buffer (pH 7) with 20 mM H_2O_2. The absorbance at 240 nm was measured over 300 s (Havir and McHale 1987), and the catalase activity was calculated with the molar extinction coefficient of H_2O_2 (36 mM^{-1} cm^{-1}) and expressed as μmol H_2O_2 $(mg\ protein\ min)^{-1}$.

The glycolate oxidase (GO) activity (EC 1.1.3.15) was assayed by measuring the rate of glyoxylate-phenylhydrazone complex formation at 324 nm (Baker and Tolbert 1966). The GO activity was estimated from the molar extinction coefficient of the glyoxylate-phenylhydrazona complex (17 mM^{-1} cm^{-1}). The results were expressed as μmol glyoxylate $(mg\ protein\ min)^{-1}$.

Rubisco (EC: 4.1.1.39) activity was measured following the oxidation rate of NADH at 340 nm (Reid et al. 1997). The initial Rubisco activity was assessed from the extract added with 900 μL of the assay mixture, and the reaction was initiated with the addition of 0.5 mM RuBP. Total activity was measured when the reaction was started after 15 min of incubation of the mixture reaction in the absence of RuBP. Thereafter, 0.5 mM RuBP was added, and the total activity was measured following the oxidation NADH

at 340 nm. Both activities were expressed as μmol CO_2 m^{-2} s^{-1}. The Rubisco activation state was calculated by the initial activity/total activity ratio and expressed as percentage (%).

Statistical and experimental design

The experiments were arranged in a completely randomized design with five independent replicates, each one represented by an individual plant per pot. Data were analyzed using ANOVA and the means were compared using the Tukey's test ($P < 0.05$).

Results

Growth, water relations, and photosynthetic pigments content

Drought decreased the relative water content (RWC) and the water potential (Ψ_w) in *R. communis* leaves (Table 1). After 6 days of rehydration (recovery), the RWC reached the control level, whereas the Ψ_w was lower than control (Table 1). The electrolyte leakage, an indicator of the cell membrane integrity, was statically significant increased by two-fold in leaves exposed to drought. However, this parameter was completely recovered to control levels after 6 days of rehydration. The leaf dry matter was decreased by drought with a slightly increase after the recovery period (Table 1). The total chlorophyll content was decreased under drought and after the recovery was increased to higher levels compared with control. However, the chlorophyll *a*/*b* ratio was statically significant decreased by drought, with full recovery to control levels after the rehydration (Table 1). The total carotenoid content increased in leaves of *R. communis* under drought and this parameter was maintained after the recovery treatment (Table 1).

Table 1 Leaf relative water content (RWC), leaf water potential (Ψ_w), electrolyte leakage, leaf dry matter (DM), and photosynthetic pigments content in *Ricinus communis* plants under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery)

Traits	Control	Drought	Recovery
RWC (%)	82.2a	65.8b	79.2a
Ψ_w (MPa)	−0.71c	−2.34a	−1.12b
Electrolyte leakage (%)	20.3b	46.5a	21.15b
Leaf DM (g $plant^{-1}$)	8.34a	4.36b	5.26b
Total chlorophyll (mg g^{-1} DM)	6.02b	5.63c	6.78a
Chlorophyll *a*/*b*	2.1a	1.1b	1.89a
Carotenoids (mg g^{-1} DM)	0.36b	1.29a	1.23a

Different letters represent significant difference between treatments by Tukey's test ($P < 0.05$)

Gas exchange, fluorescence of chlorophyll, photorespiration, and $P700^+$ redox state

Net photosynthesis (P_N) was strongly decreased in *R. communis* plants exposed to drought, but after 6 days of rehydration, P_N was increased, but this increase was not able to reach control levels (Fig. 1a). Stomatal conductance (g_s) and transpiration (E) followed the same trend of P_N. However, these parameters were completely recovered after 6 days of rehydration (Fig. 1b, c). The internal partial pressure of CO_2 (C_i) was decreased during drought, and as g_s and E, it was completed recovered after rehydration (Fig. 1d). Regarding the $P_N - PPFD$ and $P_N - C_c$ response curve parameters, it was shown that *R. communis* presented metabolic limitation of photosynthesis after 9 days of continuous drought, as showed by the decreases in the maximum photosynthetic rate (P_{Nmax}), the maximum carboxylation rate of Rubisco (V_{cmax}), and the maximum photosynthetic electron transport rate driving RuBP regeneration (J_{max}). After the recovery treatment, these parameters were not completely recovered (Table 2). The mesophyll conductance (g_m), estimated from the $P_N - C_c$ modelling, was decreased after drought, and after the recovery treatment g_m was higher than control (Table 2).

It was possible that *R. communis* displayed both stomatal and metabolic limitation of photosynthesis during the drought treatment. In addition, the rehydration period could not be able to completely recover the metabolic limitation of P_N. To complement these results, we performed an in vitro activity of Rubisco (Fig. 2). The initial activity of Rubisco decreased by 62% in plants exposed to drought and it was not completely recovered, corroborating the previous data. In contrast, the activation state of Rubisco was maintained at control level for drought as well as for the recovery treatment (Fig. 2).

Ricinus communis plants displayed photoinhibition after 6 days of drought, as showed by decreases in F_v/F_m (Fig. 3a). In contrast, the effective yield of PSII (ϕ_{PSII}) and the electron transport rate at PSII (ETRII) were decreased from the third day of drought, and these parameters were completely recovered after the rehydration (Fig. 3b). It is plausible to note that this efficient modulation of the electron transport chain at PSII under drought could be modulated by the increase in the non-photochemical quenching, which, in some extent, was maintained after the recovery period (Fig. 3d). The effective quantum yield of PSI (ϕ_{PSI}) and the electron transport rate at PSI (ETRI) were decreased by drought, and these parameters presented complete recover after the rehydration period (Fig. 4a).

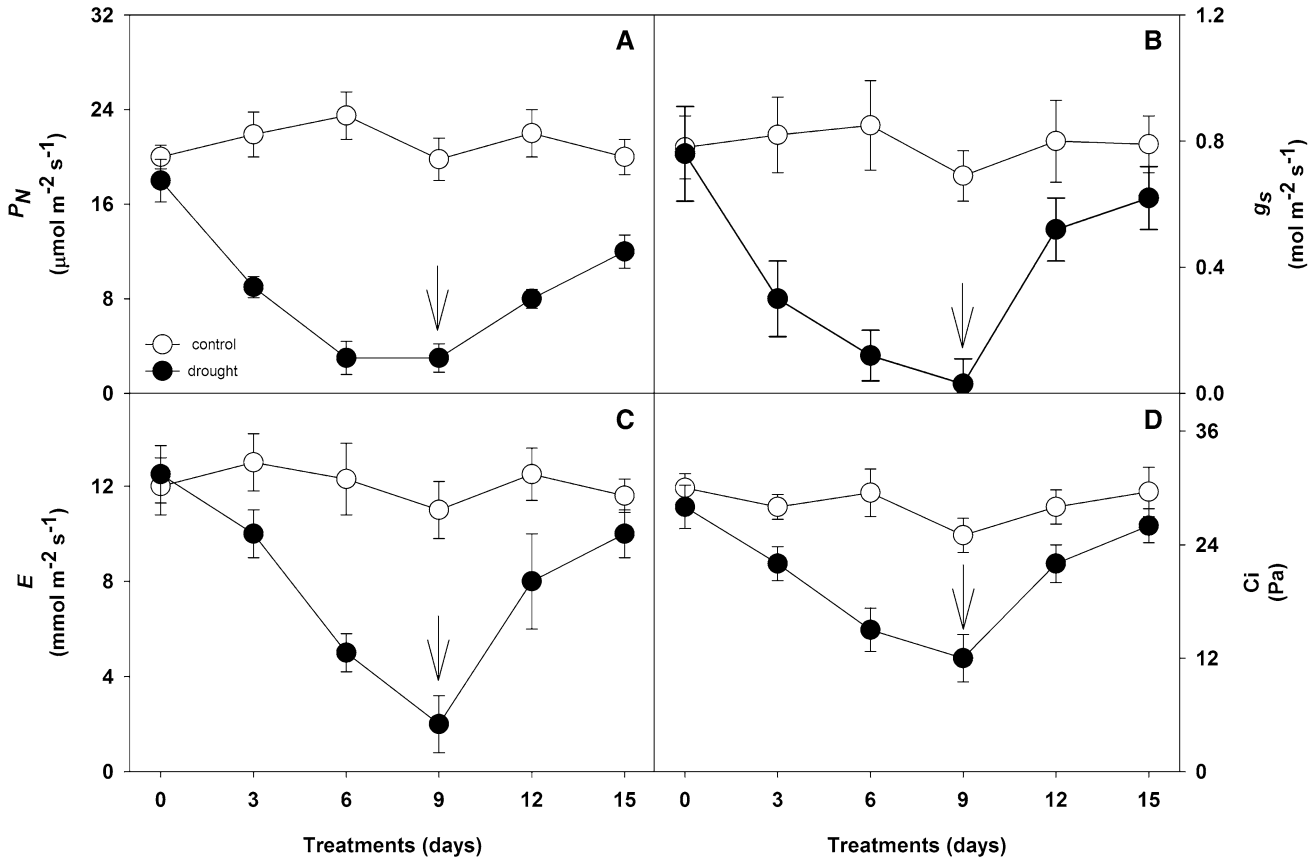

Fig. 1 Leaf gas exchange parameters in *R. communis* plants under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery). Photosynthesis (**a**), stomatal conductance (**b**), transpiration (**c**), and CO_2 internal partial pressure (**d**). *Down arrow* represents rehydration to near pot capacity. Data are the means of five replicates ± standard deviation (SD)

Table 2 Photosynthetic parameters derived from P_N − PPFD and P_N − C_c curves and Rubisco activity in *R. communis* under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery)

Traits	Control	Drought	Recovery
P_{Nmax} (µmol m^{-2} s^{-1})	34.2a	8.18c	22.5b
V_{cmax} (µmol m^{-2} s^{-1})	123a	21c	86b
J_{max} (µmol m^{-2} s^{-1})	131a	43c	112b
g_m (mol m^{-2} s^{-1})	0.075b	0.063c	0.082a

Different letters represent significant difference between treatments by Tukey's test ($P < 0.05$)

P_{Nmax} maximum photosynthetic rate, V_{cmax} maximum carboxylation rate of Rubisco, J_{max} maximum photosynthetic electron transport rate driving RuBP regeneration, g_m mesophyll conductance

Interesting to note that the relative decrease of ETRII was higher than the relative decrease of ETRI in plants exposed to drought, suggesting an increment of the cyclic electron flow (CEF) around PSI. To estimate the CEF, we calculate the ETRI/ETRII ratio (Yamori et al. 2011). This ratio clearly shows that the CEF was induced in plants exposed to drought and decreased during the recovery treatment (Fig. 4c).

Drought increased the estimated photorespiration (P_R) approximately by two-fold (Fig. 5a). Accordingly, there was a large increase in GO and CAT activities in *R. communis* under drought (Fig. 5b, c). These activities were maintained at higher levels after the recovery, compared with control. The glycolate oxidation to glyoxylate in higher plants is catalyzed by GO. The enzyme is present in the peroxisome and performs an essential step in P_R. Thus, GO activity is commonly used as a biomarker of P_R (Zelitch et al. 2009). CAT is located in the peroxisomes and virtually absent from chloroplasts, scavenging H_2O_2 by catalyzing its decomposition into O_2 and H_2O (Foyer et al. 2009). Therefore, CAT activity could be assessed as an indirect measure of P_R.

Lipid peroxidation, H_2O_2 content, and antioxidative enzymes

Drought increased the content of TBARS and H_2O_2 in *R. communis* leaves (Table 3). However, these parameters

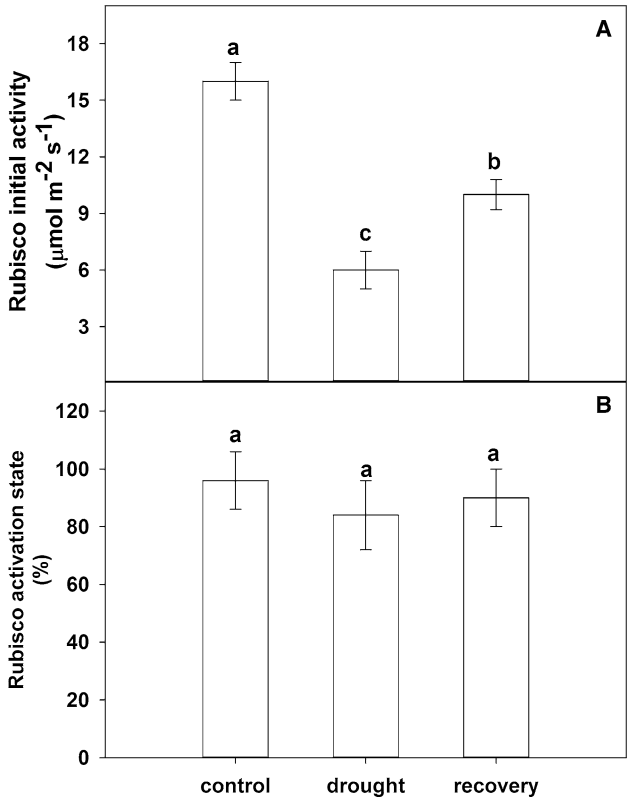

Fig. 2 Rubisco initial activity (**a**) and Rubisco activation state (**b**) in *R. communis* plants under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery). Data are the means of five replicates ± standard deviation (SD) and *different letters* represent a significant difference between treatments by Tukey's test ($P < 0.05$)

were maintained at higher levels, compared with control, after the recovery period. Probably, the regulation of the photosynthetic electron transport chain and the photoprotective mechanisms were not able to maintain the H_2O_2 at control level, leading to lipid peroxidation and membrane damage. Nevertheless, the activities of APX and SOD, important antioxidative enzymes, were increased under drought, and these enzymes activities were maintained at higher levels after the recovery treatment (Table 3).

Discussion

The better understanding of physiological traits triggered by drought tolerant plants is crucial to crop yield, so that these can be transferred into new varieties. In this study, *R. communis* plants, an oilseed species, commonly used to biofuel production in arid and semiarid were studied. *R. communis* is a Euphorbiaceae described as drought tolerant triggering osmotic adjustment to avoid the harmful effects of drought (Babita et al. 2010). In addition, it was shown that *R. communis* has a high photosynthetic capacity under high humidity and a pronounced sensitivity to high water vapor pressure deficit (VPD) (Dai et al. 1992), displaying high transpiration rate and stomatal conductance (Barbour and Buckley 2007).

In the current study, we show that drought impacts some important physiological traits in *R. communis*, but after rewatering, this species could continue growth and development. Drought induced decreases in leaf dry matter, relative water content (RWC), water potential, and membrane damage in *R. communis* leaves, with decreases in chlorophyll content and increases in carotenoids concentration. However, 6 days of rehydration could recover the water status and membrane integrity in this species (Table 1). These data clearly show that *R. communis* has a potential to recover growth after short drought period. Interesting to note that after the recovery treatment, *R. communis* leaves presented higher content of total chlorophyll and carotenoids compared with control. Possibly, these increases in photosynthetic pigments were important to avoid the excess energy (Ogbaga et al. 2014) produced by the stomatal closure during drought leading to lower CO_2 assimilation rate (Fig. 1). Commonly, changes in chlorophyll concentration and composition are related with a reorganization of the photosynthetic apparatus in response to drought (Ogbaga et al. 2014). In addition, increases in carotenoid content are commonly reported as a photoprotector mechanism acting on singlet oxygen quenching within the reaction center complex (Ballottari et al. 2014; Finazzi et al. 2004).

R. communis plants displayed stomatal limitation of photosynthesis during drought as shown by decreases in g_s, E, and C_i (Fig. 1). However, the stomatal control was efficient in *R. communis* recovery after rehydration (Fig. 1), showing increases in g_s, E, and accumulation in C_i. It was previously shown that *R. communis* has high photosynthetic capacity under low vapor pressure deficit (VPD) conditions which was comparable to maize (Dai et al. 1992). In contrast, under drought, this species maintains a significant level of transpiration (Fig. 1c), resulting in a low water use efficiency which is in accordance with Barbour and Buckley (2007) and Babita et al. (2010). Nevertheless, after rehydration, the CO_2 assimilation rate was not completely recovered (Fig. 1a), possibly due to metabolic limitation of photosynthesis, as showed by decreases in V_{cmax}, J_{max} (Table 2), in vitro Rubisco activity and increases in C_i (Fig. 2). It was previously demonstrated that increases in C_i at moderate-to-severe drought are closely related to metabolic impairment in photosynthesis, reflecting the impairment on Rubisco activity and regeneration of RuBP content (Flexas 2002). As stomata close, C_i primarily declines with the stress and then increases as drought becomes more severe (Chaves et al. 2009).

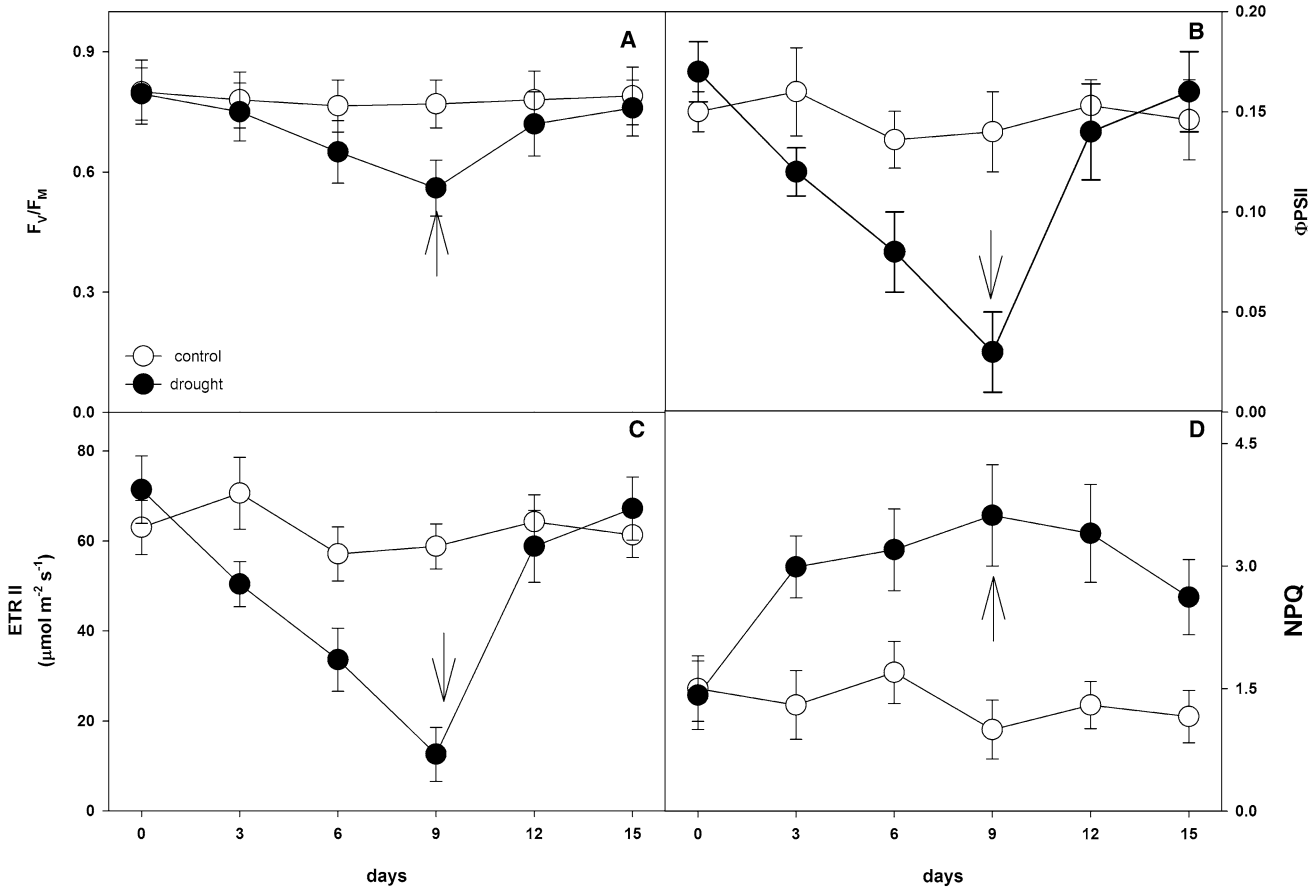

Fig. 3 Potential quantum yield of PSII (**a**), effective quantum yield of PSII (**b**), electron transport rate at PSII (**c**), and non-photochemical quenching in *R. communis* plants under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery). *Arrows* represent rehydration to near pot capacity. Data are the means of five replicates ± standard deviation (SD)

However, the effects of drought on the mechanisms that control Rubisco activity are unclear (Galmés et al. 2011).

Interesting to note that the activation state of Rubisco was not affected by drought under the experimental conditions applied (Fig. 2b). Rubisco activation by reaction with CO_2 resulting in the carbamylation of a lysyl residue in its active site is crucial to the activity of this enzyme (Sage et al. 2009). Drought through changes in stomatal and mesophyll conductance induces a decrease in CO_2 concentration in leaves and in the amount of activator CO_2 bound by carbamylation to Rubisco (Ristic et al. 2009). Galmés et al. (2011) show that the activation state of Rubisco is maintained under mild-to-moderate water stress, depending on the species and declining under severe water stress, which is in accordance with our data.

Inhibition of CO_2 assimilation by drought resulted in down-regulation of PSII yield and ETRII, with increases in NPQ (Fig. 3b–d). NPQ is an important photoprotective mechanism related with the dissipation of excess energy as heat (qE) produced by the decreases in CO_2 assimilation (Ruban 2016). In addition, decreases in ϕ_{PSI} and ETRI (Fig. 4) were lower compared with PSII (Fig. 3), probably by increases in the CEF (Fig. 4). The cyclic electron flow is important to sustain a ΔpH across the thylakoids membranes maintaining NPQ (Zivcak et al. 2014) and possibly preventing photoinhibition of PSII (Goh et al. 2011) and PSI. Overreduction of both photosystems can lead to ROS production (Joliot and Johnson 2011; Sejima et al. 2016; Takagi et al. 2016). It is interesting to note that after the recovery period, the NPQ was maintained at higher levels compared with control (Fig. 3d) with a concomitant decrease in CEF (Fig. 4c). This could be plausible due to increases in the linear electron flow (LEF) and increases in CO_2 assimilation after recovery, sustaining the ΔpH necessary for the NPQ development (Johnson 2011). In addition to the CEF, an NAD(P)H dehydrogenase (NDH) and plastid terminal oxidase (PTOX) could be involved in the chlororespiratory pathway, alleviating the electron pressure on PSI acceptors by recycling electrons to the PQ and ultimately to PTOX (Rumeau et al. 2007). Chlororespiration helps avoiding the overreduction of the electron acceptors of PSI removing ROS and protecting PSI

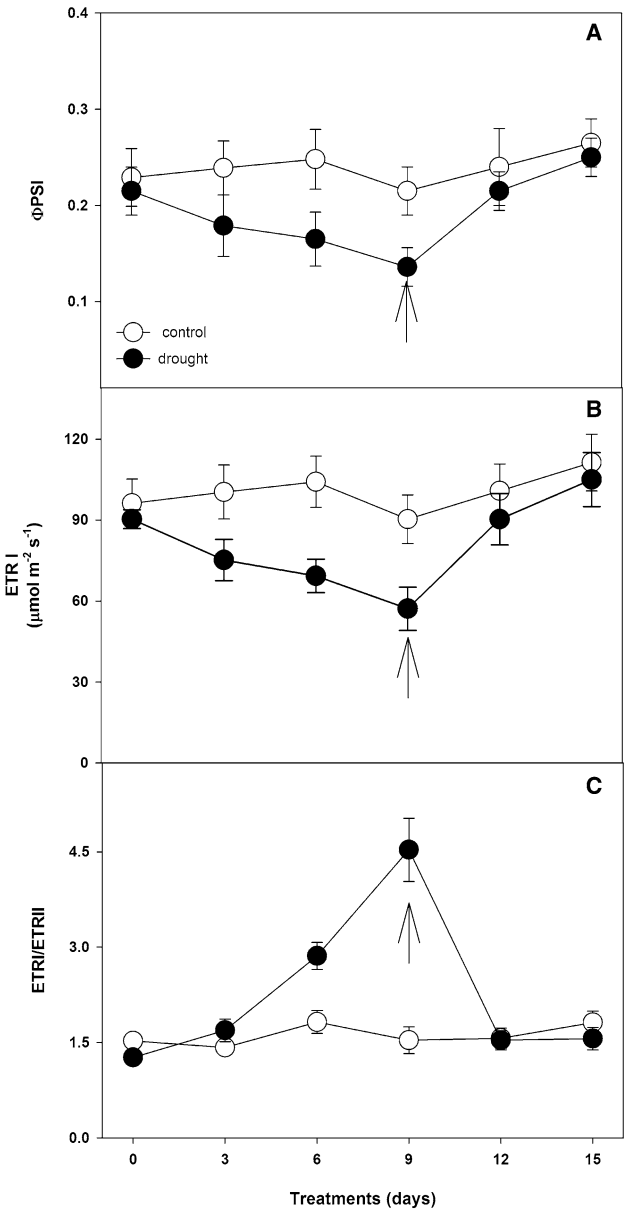

Fig. 4 Effective quantum yield of PSI (**a**), electron transport rate at PSI (**b**), and ETRI/ETRII ratio (**c**) in *R. communis* plants under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery). *Arrows* represent rehydration to near pot capacity. Data are the means of five replicates ± standard deviation (SD)

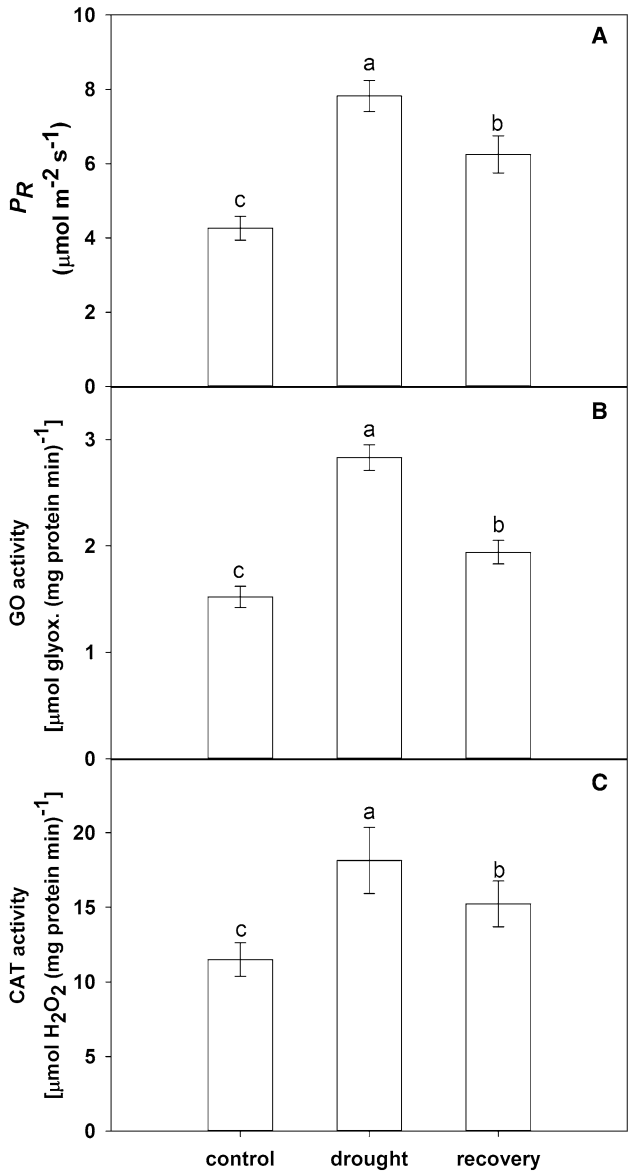

Fig. 5 Estimated photorespiration (**a**), glycolate oxidase activity (**b**), and catalase activity (**c**) in *R. communis* plants under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery). Data are the means of five replicates ± standard deviation (SD) and *different letters* represent significant difference between treatments by Tukey's test ($P < 0.05$)

(Saroussi et al. 2016). However, due to the low abundance of the complex, NDH-mediated electron flows bioenergetically insignificant to ATP production (Joliot and Joliot 2005).

In addition, we show that photorespiration (P_R) could be an important photoprotective mechanism in *R. communis* under drought (Fig. 5). Drought induced increases in P_R, and even after the recovery treatment, P_R were at higher level compared with control. Photorespiration is difficult to be measured (Busch 2013). Nevertheless, we performed GO and CAT activities to corroborate the estimated P_R from fluorescence and gas exchange measurements (Fig. 5b, c). P_R has the potential to sustain photons in a non-assimilatory pathway, protecting the photosynthetic apparatus against photoinhibition (Peterhänsel and Maurino 2010). In addition, P_R is very important in biochemical recycling, particularly to N-compounds under restrictive metabolic conditions such as drought consuming NADH and reduced ferredoxin (Kangasjärvi et al. 2012). Recently,

Table 3 Lipid peroxidation (TBARS), H_2O_2 concentration, APX, and SOD activities in *R. communis* under well-watered conditions for 15 days (control), exposed to 9 days of water withholding (drought) and exposed to 9 days of drought plus 6 days of rehydration (recovery)

Traits	Control	Drought	Recovery
TBARS (ηmol g^{-1} FM)	38.3c	95.26a	56.2b
H_2O_2 (μmol g^{-1} FM)	10.25c	21.36a	15.22b
APX [μmol AsA (mg protein min)$^{-1}$]	0.61c	1.14a	0.82b
SOD [U (mg protein min)$^{-1}$]	1.56c	3.25a	2.52b

Different letters represent significant difference between treatments by Tukey's test ($P < 0.05$)

photorespiration was described as an important mechanism providing the CEF to operate for the redox-regulation of P700 in sunflowers leaves (Takagi et al. 2016), preventing PSI photoinhibition and reducing ROS burst at PSI level.

The enzymatic ROS scavenging system was induced in *R. communis* plants under drought (Table 3; Fig. 5). The activities of APX, SOD, and CAT, important antioxidative enzymes, were increased by drought, and were maintained in higher levels compared to control after the rehydration treatment. Altogether, the data presented show that *R. communis* trigger diverse photoprotective mechanisms to maintain the integrity of the photochemical apparatus, preventing the harmful damages of the excess energy in the thylakoids produced by drought. An efficient stomatal control in accordance with increases in NPQ, CEF, and P_R is important to drought acclimation in this species. In addition, antioxidative enzymes are responsive to drought, scavenging the excess of ROS produced by the overreduced PET chain (Foyer et al. 2012).

Author contribution statement MCLN and JAGS designed the experiments. MCLN, JVAC, and JRC performed the experiments. MCLN, JAGS, and JRC wrote the manuscript. All authors contributed have seen and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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