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Original article

Differential responses of photosystems I and II to seasonal drought in two *Ficus* species

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ABSTRACT

Hemiepiphytic *Ficus* species exhibit more conservative water use strategy and are more drought-tolerant compared with their non-hemiepiphytic congeners, but a difference in the response of photosystem I (PSI) and photosystem II (PSII) to drought stress has not been documented to date. The enhancement of non-photochemical quenching (NPQ) and cyclic electron flow (CEF) have been identified as important mechanisms that protect the photosystems under drought conditions. Using the hemiepiphytic *Ficus tinctoria* and the non-hemiepiphytic *Ficus racemosa*, we studied the water status and the electron fluxes through PSI and PSII under seasonal water stress. Our results clearly indicated that the decline in the leaf predawn water potential (ψ_{pd}), the maximum photosynthetic rate (A_{max}) and the predawn maximum quantum yield of PSII (F_v/F_m) were more pronounced in *F. racemosa* than in *F. tinctoria* at peak drought. The F_v/F_m of *F. racemosa* was reduced to 0.69, indicating net photoinhibition of PSII. Concomitantly, the maximal photo-oxidizable P700 (P_m) decreased significantly in *F. racemosa* but remained stable in *F. tinctoria*. The fraction of non-photochemical quenching [Y(NPQ)] and the ratio of effective quantum yield of PSI to PSII [Y(I)/Y(II)] increased for both *Ficus* species at peak drought, with a stronger increase in *F. racemosa*. These results indicated that the enhancement of NPQ and the activation of CEF contributed to the photoprotection of PSI and PSII for both *Ficus* species under seasonal drought, particularly for *F. racemosa*.

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1. Introduction

When plants suffer from drought stress, they can minimize water loss through the reduction of stomatal conductance, and consequently through a decrease in photosynthesis (Brodribb and Holbrook, 2003). The decline in the activities of photosynthetic enzymes and the mesophyll conductance of CO_2 also leads to a reduction in photosynthesis (Cornic et al., 1992; Cornic, 1994; Flexas et al., 2002, 2004). A reduction in photosynthesis combined with the high levels of irradiation associated with drought conditions can produce excess excitation energy and an accumulation of NADPH, resulting in the production of reactive oxygen species (ROS) that suppress D_1 protein synthesis (Murata et al., 2007, 2012; Nishiyama et al., 2001, 2011) and cause photodamage to photosystem II (PSII) (Oguchi et al., 2009, 2011). Simultaneously, the acceptor side of photosystem I (PSI) may become over-reduced as a result of the over-accumulation of NADPH during drought stress, which results in the photoinhibition and degradation of the PSI complexes (Sonoike, 1999, 2006; Zhang and Scheller, 2004).

The enhancement of non-photochemical quenching (NPQ) and the activation of cyclic electron flow (CEF) can effectively protect the photosystems against drought stress (Gao et al., 2011; Huang et al., 2012; Wang et al., 2013). The activation of NPQ is based on the generation of a proton gradient across the thylakoid membrane (ΔpH) (Munekage et al., 2002, 2004). Linear electron flow (LEF) and CEF are the two major pathways for ΔpH formation. In drought-stressed plants, the electron yield through LEF may decrease, and thus, the LEF-dependent generation of a ΔpH is inhibited (Golding and Johnson, 2003). However, the activation of CEF simultaneously generates a ΔpH to promote NPQ, and consequently, the excess

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light energy can be harmlessly dissipated as heat (Munekage et al., 2002, 2004; Nandha et al., 2007; Huang et al., 2012). The CEF-dependent generation of a ΔpH promotes ATP synthesis to meet the demand for more ATP under drought stress. Moreover, the CEF-dependent generation of a ΔpH promotes the reverse transport of Ca^{2+} across the thylakoid membrane to increase the concentration of Ca^{2+} in thylakoid lumen, which is crucial for stabilizing the oxygen-evolving complex (OEC) (Takahashi et al., 2009). During short-term drought stress, plants can alleviate PSI and PSII photoinhibition through the activation of CEF (Golding and Johnson, 2003; Huang et al., 2012; Jia et al., 2008; Lehtimäki et al., 2010; Wang et al., 2013). However, during severe prolonged drought stress, severe PSI photoinhibition may lead to the inhibition of CEF (Huang et al., 2013).

Hemiepiphytic plants spend their early life in the canopies of trees with their roots suspended above the ground; in the adult phase, their roots are well established in the soil (Holbrook and Putz, 1996). The genus *Ficus* is a typical example of this shift in growth form from epiphytic to terrestrial phase. There were about 300 hemiepiphytic *Ficus* species, specifically, 280 belong to subgenus *Urostigma*, 1 belongs to subgenus *Pharmacosyea* and 20 belong to subgenus *Sycidium* (Berg and Corner, 2005). Previous studies have revealed that hemiepiphytic *Ficus* species exhibit conservative water use and are more drought resistant than non-hemiepiphytic *Ficus* species even during their adult phase when roots are established in the ground (Hao et al., 2010, 2011).

As a result of the rain-shadow effect, the valleys between the mountains of Yunnan province in southwest China have a hot and dry local climate, which is characterized by a pronounced dry season for over half of the year (Jin and Ou, 2000; Zhang et al., 2012). *F. tinctoria* and *F. racemosa* are distributed widely in the dry-hot valleys of this region. *F. tinctoria* belongs to subgenus *Sycidium*, a subgenus composed mainly of terrestrial species. However, *F. tinctoria* transits from epiphytic in the canopies of other trees to terrestrial in the adult phase, thus *F. tinctoria* shows the growth form of hemiepiphytism. In contrast, *F. racemosa* spends its whole life history with the roots well established in the soil. Based on a previous finding of a difference in photosynthesis and resistance to drought between the two growth forms, we chose hemiepiphytic *F. tinctoria* and non-hemiepiphytic *F. racemosa* for the present study. We hypothesized that PSI and PSII of the co-occurring hemiepiphytic and non-hemiepiphytic *Ficus* would differ in their responses to prolonged drought stress. To this end, we measured light energy partitioning of PSI and PSII for *F. tinctoria* and *F. racemosa* growing naturally in a dry-hot valley forest during the rainy season and the dry season. Previous studies have found that the PSII of savanna plants within this valley is quite resistant to drought (Zhang et al., 2007; Zhu et al., 2009). However, no direct study has been conducted to test whether PSI of the plants in a dry-hot valley is affected by drought stress. The following questions were addressed: (i) Are the activities of PSI and PSII less affected in the more drought-tolerant *Ficus* species than in the less drought-tolerant *Ficus* species? (ii) Does the activation of CEF play an important role in the photoprotection of the two *Ficus* species at peak seasonal drought?

2. Materials and methods

2.1. Study site and plant materials

This study was carried out at the Yuanjiang Research Station for Savanna Ecosystems (YRSSE, lat. 23°27′56″ N, long. 102°10′40″ E, elevation 481 m) at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yuanjiang county, Yunnan province, Southwest China. The climate is characterized by two distinct seasons: a rainy season (May to October) and a dry season (November to next April). Based on YRSSE meteorological records from 2011 to 2014, the mean annual temperature is 24.9 °C with a mean monthly temperature ranging from 16.5 °C (January) to 29.9 °C (May). The total mean annual precipitation was 666 mm, with 84% of the precipitation falling during the rainy season.

Dry-hot valley dwarf forests are distributed along both sides of the ravine streams, exhibiting a narrow-banded distribution. The dominant tree species in the dry-hot valley forests include *F. racemosa*, *Bischofia polycarpa* and *Garuga forrestii* (Du, 2005). From November 2012 to March 2013, the total precipitation at the study site was only 73.7 mm. The soil water potential was below −2 MPa during March 2013. The photosynthetic photon flux density (PPFD) was measured with a Li-1400 datalogger (Li-Cor, Lincoln, NE, USA) during March and July of 2013. The maximum PPFD was 1, 560 μmol photons m^{-2} s^{-1} in March and 1, 750 μmol m^{-2} s^{-1} in July.

Three mature trees each of *F. racemosa* and *F. tinctoria*, growing in a similar microenvironment, were chosen for this study. The diameter at breast height (DBH) of the sample trees was approximately 30 cm, with an approximate height of 8–10 m. During March and July 2013, at the end of the dry season and during the middle of rainy season, respectively, five terminal branches with fully sun-exposed leaves were harvested from the upper canopy of each species at predawn. The samples were sealed in black plastic bags and immediately transported in a sample box to the nearby YRSSE laboratory to measure the eco-physiological parameters. Three healthy, mature leaves were then selected from each branch to determine chlorophyll fluorescence and the P700 redox state, predawn leaf water potential (ψ_{pd}), and osmotic potential at the point of turgor loss (ψ_{tlp}).

2.2. Chlorophyll fluorescence and P700 redox state

The chlorophyll fluorescence and the P700 redox state of the detached leaves sampled at predawn were measured using a Dual-PAM-100 fluorometer (Heinz Walz, Effeltrich, Germany) connected to a computer with WinControl software. In this study, all measurements were conducted at room temperature (approximately 20–25 °C) in the laboratory at YRSSE. The relative air humidity was approximately 60%. The light response curves were measured after at least 20 min of light adaptation with a PPFD of 454 μmol m^{-2} s^{-1}. Light-adapted fluorescence parameters were recorded after 2 min of exposure to each PPFD level. Eight PPFD levels were used (94, 150, 297, 454, 684, 1,052; 1,311; 1,618 μmol m^{-2} s^{-1}).

The following PSII parameters were calculated: $F_v/F_m = (F_m - F_0)/F_m$, $Y(II) = (F_m' - Fs)/F_m'$, $Y(NO) = F_s/F_m$, $Y(NPQ) = 1 - Y(II) - Y(NO)$, $qP = (F_m' - F_s)/(F_m' - F_0')$ (Genty et al., 1989; Kramer et al., 2004). F_0 is the minimum chlorophyll fluorescence, and F_m is the maximum fluorescence of the predawn leaves following a saturation pulse of 10,000 μmol m^{-2} s^{-1} for 300 ms. F_0' and F_m' are the minimum and maximum chlorophyll fluorescence of light adapted leaves, respectively, and F_v is the variable chlorophyll fluorescence, which is equal to the difference between F_m and F_0. F_s' is the steady-state fluorescence under actinic light. Y(II) is the effective quantum yield of PSII; Y(NO) represents the inability of a plant to protect itself against damage from excess light energy. Y(NPQ) represents the efficiency of dissipation of excess light energy into harmless heat. qP is a measure of the proportion of open PSII centers.

The following parameters related to PSI were calculated: $Y(NA) = (P_m - P_m')/P_m$, $Y(I) = P700_{red} - Y(NA)$, $Y(ND) = 1 - P700_{red}$ (Pfündel et al., 2008; Klughammer and Schreiber, 2008). P_m is the maximal P700 change from the fully reduced to the fully oxidized state and is determined following a saturation pulse of 10,000 μmol m^{-2} s^{-1} for 300 ms after 10 s of far-red preillumination. $P700_{red}$ represents the fraction of overall P700 that is reduced in a given state. Y(I) is the effective quantum yield of PSI; Y(NA) is a measure of the acceptor-side limitation, which is enhanced by dark adaptation (i.e., deactivation of key enzymes of the Calvin–Benson cycle) and damage at the sites of CO_2 fixation. Y(ND) is a measure of the donor-side limitation, which is enhanced by a transthylakoid proton gradient (i.e., photosynthetic control at the cytb/f complex as well as the down-regulation of PSII). If CEF is activated, the ratio of Y(I)/Y(II) is greater than 1. Thus, this ratio has been used to indicate the activation of CEF (Harbinson and Foyer, 1991; Huang et al., 2012, 2013). The light response curves were fitted with the algorithm $Y = Y_{max} - a^{*}\exp(-b^{*}PPFD)$ (Iqbal et al., 1996); the maximum values of Y(I)/Y(II) and Y(NPQ) were calculated from the fitted equations.

2.3. Soil water potential and leaf predawn water potential

The soil water potentials (Ψ_{soil}) were measured at five different depths using a dewpoint potentiometer (WP4-T, Decagon, USA) during March and July of 2013. The soil was sampled along the soil profile at 20-cm intervals from the topsoil to a depth of 100 cm with three replicates from three sampling sites near the sample trees.

The predawn leaf water potential (Ψ_{pd}, MPa) was measured at predawn using a pressure chamber (PMS, Corvallis, OR, USA); five replicate measurements were taken from the sampled branches (described above) within 30 min after harvesting.

2.4. Measurement of pressure-volume curves

The pressure–volume (P–V) curves were generated using the bench-drying method (Schulte and Hinckley, 1985). The petioles of the terminal branches were held under water to rehydrate for several hours, and all leaves were then wrapped in black plastic bags. In the following morning, five mature and complete leaves were sampled for the determination of the P–V curves. The saturated weight of the leaf (SW) was determined with a balance, and the corresponding leaf water potential (Ψ_s) was immediately measured in a pressure chamber (PMS, Corvallis, OR, USA). The leaf fresh weight (FW) and the corresponding leaf water potential (Ψ_f) were measured as the leaves dried. When the water potential was no longer decreasing, the leaves were placed in an oven at 70 °C for 24 h, and the dry weight (DW) was recorded. The relative water content (%) was calculated as $RWC = [(FW - DW)/(SW - DW)] \times 100$. The P–V curves were fitted using a P–V curve analysis program (Sack and Pasquet-Kok, 2011). The osmotic potential at the turgor loss point (Ψ_{tlp}) was calculated from the fitted P–V curves.

2.5. Leaf gas exchange

Photosynthetic gas exchange measurements were made in the field on intact leaves of the same trees used for other physiological measurements from 9:00 to 11:00 h on sunny days using a portable gas analysis system (LI-6400, Li-Cor, Lincoln, NE, USA). The maximum photosynthetic rate based on leaf area (A_{max}) and the stomatal conductance (g_s) were determined under ambient CO_2 concentrations (~400 μmol m^{-2} s^{-1}) and saturated light conditions (1,000 μmol m^{-2} s^{-1}).

2.6. Data analysis

Statistical analysis was performed using SPSS 16.0 software (SPSS Inc., Chicago, IL, USA). Prior to statistical analysis, all data were $\log_{10}$-transformed to improve normality and homoscedasticity. The values of Ψ_{pd} and Ψ_{tlp} were converted from negative to positive to facilitate the $\log_{10}$-transformation. However, Ψ_{pd} and Ψ_{tlp} were presented and interpreted as the usual negative values. Following transformation, two-way ANOVA was performed to assess the effects of season and species on the ecophysiological parameters. In addition, seasonal differences (between rainy season and dry season) in the ecophysiological parameters for each *Ficus* species were evaluated using a *T*-test for independent samples at a significance level of $P < 0.05$.

3. Results

3.1. Seasonal differences in soil and plant water status

During the rainy season, Ψ_{soil} remained at approximately −0.6 MPa throughout the soil profile (Fig. 1). Under peak seasonal drought, Ψ_{soil} decreased significantly and was −3.17 MPa in the topsoil (0–20 cm) and was lower, between −2.3 and −2.8 MPa, below the topsoil.

Compared with Ψ_{pd} during the rainy season, Ψ_{pd} during the dry season was significantly lower in both *Ficus* species. Ψ_{pd} during the dry season was −1.66 and −2.67 MPa for *F. tinctoria* and *F. racemosa*, respectively (Fig. 2a). The Ψ_{tlp} during the dry season was significantly lower than during the rainy season for *F. tinctoria*. For *F. racemosa*, the Ψ_{tlp} decreased slightly during the dry season, but the seasonal difference in Ψ_{tlp} was not significant (Fig. 2b). Two-way ANOVA showed that both season and species significantly affected Ψ_{pd} and Ψ_{tlp} (Table 1, $P < 0.05$).

3.2. Effects of drought on leaf gas exchange

The stomatal conductance (g_s) was strongly reduced in both *Ficus* species, but A_{max} was only significantly reduced in *F. racemosa* (Fig. 2c, d). Two-way ANOVA showed that A_{max} was significantly affected by season and species, whereas g_s was significantly affected by season but not by species (Table 1).

3.3. Effects of drought on chlorophyll fluorescence parameters

The ratio of F_v/F_m declined from 0.81 and 0.82 in the rainy season to 0.77 and 0.69 in the dry season for *F. tinctoria* and *F. racemosa*, respectively, and the seasonal differences in F_v/F_m were significant for both *Ficus* species (Fig. 2e, $P < 0.05$). The light response curves indicated that qP and Y(II) decreased significantly

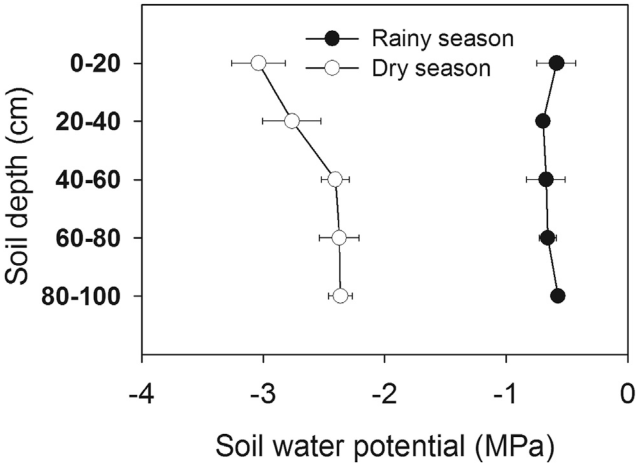

Fig. 1. Seasonal variation in the soil water potential at 20-cm intervals along the 100 cm soil profile. Values are means ± SE of three replicates at three sample sites near the sample trees.

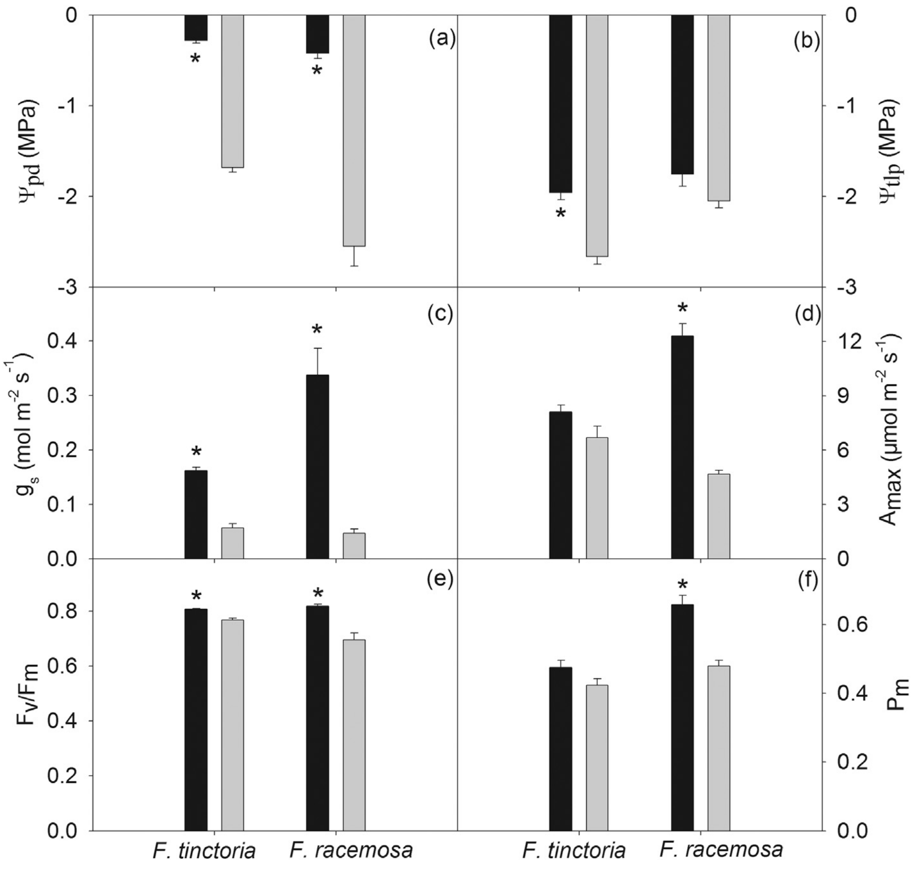

Fig. 2. Seasonal variation (means ± SE) in (**a**) predawn leaf water potential (Ψ_{pd}), (**b**) osmotic potential at the turgor loss point (Ψ_{tlp}), (**c**) stomatal conductance (g_s), (**d**) maximum photosynthetic rate based on leaf area (A_{max}), (**e**) maximum quantum yield of photosystem II (F_v/F_m) and (**f**) maximum photo-oxidizable P700 (P_m) between *F. tinctoria* and *F. racemosa*. The black and gray bars represent the rainy season and the dry season, respectively. The asterisks (*) above the black bars indicate significant differences between the rainy and dry season at the significance level of $P < 0.05$.

Table 1
Two-way ANOVA results of the effects of season and species on predawn leaf water potential (Ψ_{pd}, MPa), osmotic potential at the turgor loss point (Ψ_{tlp}, MPa), stomatal conductance (g_s, mol m^{-2} s^{-1}), maximum photosynthetic rate based on leaf area (A_{max}, μmol m^{-2} s^{-1}), maximum quantum yield of photosystem II, maximum photo-oxidizable P700 (P_m), maximum rate of the quantum yield of non-photochemical quenching $[Y(NPQ)]_{max}$ and maximum ratio of effective quantum yield of PSI to that of PSII $[Y(I)/Y(II)]_{max}$ in the two *Ficus* species.

Parameters	Season		Species		Season × Species	
	F	Sig.	*F*	Sig.	*F*	Sig.
Ψ_{pd}	274.1	0.000	21.8	0.000	11.8	0.003
Ψ_{TLP}	33.4	0.000	22.1	0.000	5.6	0.032
g_s	58.7	0.000	2.3	0.150	32.2	0.000
A_{max}	49.8	0.000	7.8	0.013	9.9	0.006
F_v/F_m	37.5	0.000	5.3	0.035	9.5	0.007
P_m	29.4	0.000	32.1	0.000	8.9	0.009
$[Y(NPQ)]_{max}$	40.6	0.000	11.2	0.004	0.4	0.553
$[Y(I)/Y(II)]_{max}$	24.6	0.000	4.0	0.062	6.9	0.019

during peak drought at all levels of PPFD for both *Ficus* species, but the reductions in qP and Y(II) for *F. racemosa* were more pronounced than for *F. tinctoria* (Fig. 3a–d). Y(NPQ) showed an opposite trend, such that Y(NPQ) increased during the dry season at all PPFD levels for both *Ficus* species, and the increase in Y(NPQ) with increasing PPFD levels was greater for *F. racemosa* than for *F. tinctoria* (Fig. 3e, f). Y(NO) remained steady at ~0.2 for both *Ficus* species during both seasons (Fig. 3g, h). Two-way ANOVA showed that F_v/F_m and $Y(NPQ)_{max}$ were significantly affected by season and species (Table 1, $P < 0.05$).

By the end of the dry season, P_m in *F. racemosa* had declined significantly compared with value of the rainy season, but P_m in *F. tinctoria* decreased only slightly without a statistically significant seasonal difference (Fig. 2f). Two-way ANOVA showed that P_m was significantly affected by season and species (Table 1, $P < 0.05$). The light response curves showed that during the peak drought period, Y(I) declined at all PPFD levels compared with the rainy season for both *Ficus* species (Fig. 4a, b), although a stronger reduction was observed in *F. racemosa*. In contrast, the increase in the magnitude of Y(ND) during the dry season was more pronounced for *F. racemosa* than for *F. tinctoria* (Fig. 4c, d). At peak drought, Y(NA) decreased slightly and remained at a low value at high PPFD levels for both *Ficus* species (Fig. 4e, f).

The light response curves showed that the ratio of Y(I)/Y(II) during the dry season increased at all PPFD levels for both *Ficus* species, with a much greater increase in *F. racemosa* (Fig. 5). The maximum ratio of Y(I)/Y(II) for *F. tinctoria* was only 1.40 in the dry season (Fig. 5a). The maximum ratio of Y(I)/Y(II) was low in the rainy season for *F. racemosa*, even in high light; however, Y(I)/Y(II) almost reached a maximum value (1.73) from medium PPFD (454 μmol m^{-2} s^{-1}) to high PPFD at peak drought (Fig. 5b). Two-way ANOVA showed that $[Y(I)/Y(II)]_{max}$ was significantly affected by season but was not significantly affected by species (Table 1).

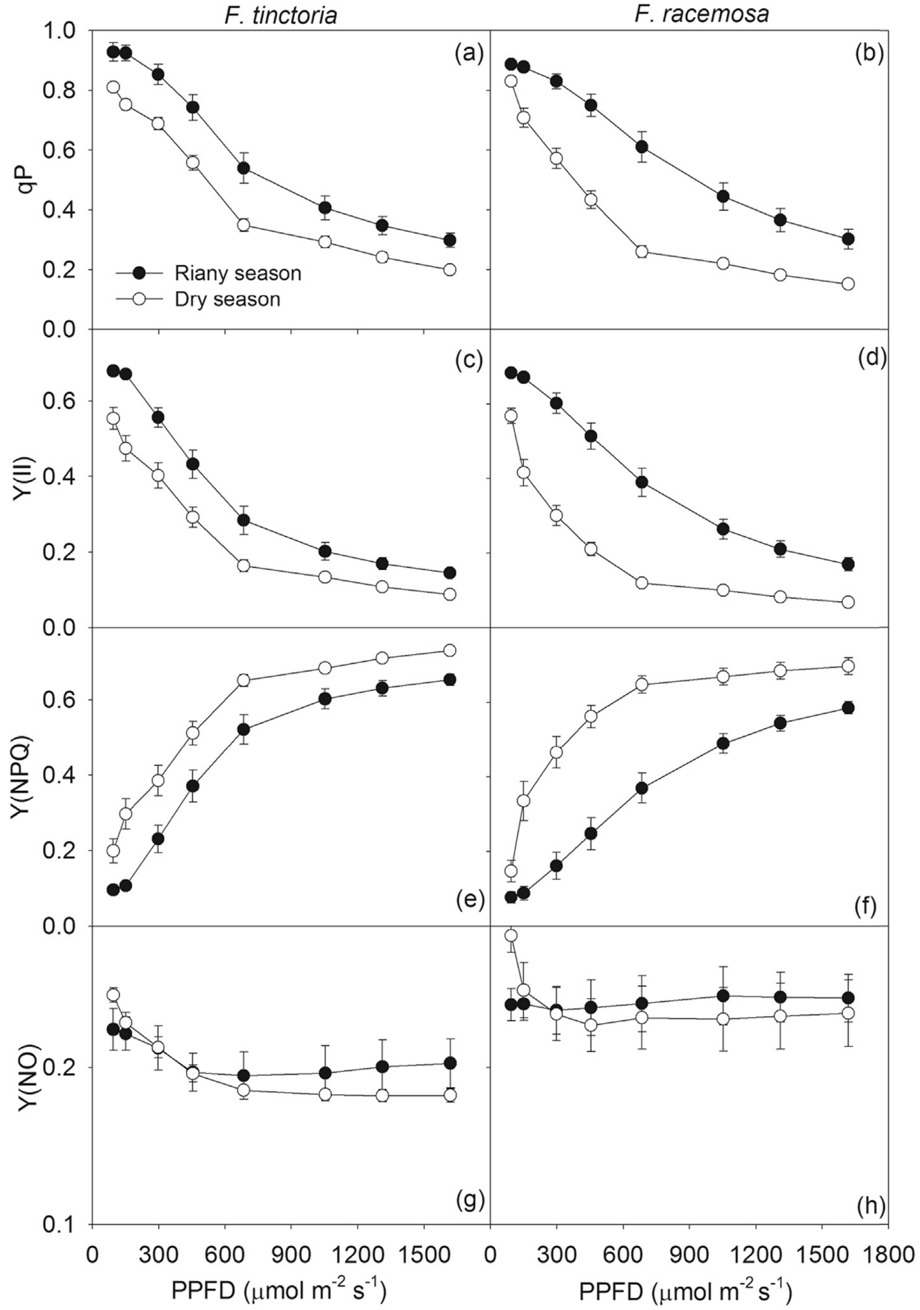

Fig. 3. . Seasonal variation (means ± SE) in the light response curves of photosystem II for *F. tinctoria* and *F. racemosa*. (**a**–**b**) Coefficient of photochemical quenching (qP); (**c**–**d**) the effective quantum of PSII [Y(II)]; (**e**–**f**) the quantum yield of regulated energy dissipation [Y (NPQ)]; (**g**–**h**) the quantum yield of non-regulated energy dissipation [Y(NO)].

4. Discussion

Our results revealed that *F. racemosa* was more significantly affected by severe seasonal drought than *F. tinctoria*, as indicated by a stronger reduction in Ψ_{pd}, A_{max} and PSI and PSII activities (Fig. 2 a, d, e, f). By the end of the dry season, the predawn F_v/F_m remained close to 0.8 in *F. tinctoria*, but it decreased to 0.69 in *F. racemosa*. This indicates some photoinhibition of PSII induced by drought and thus inhibition of LEF in *F. racemosa*.

By the end of dry season, consistent with the lower Ψ_{pd} and the stronger inhibition of PSII in *F. racemosa*, P_m had declined to a significantly greater extent in contrast with the relatively stable P_m of *F. tinctoria* (Fig. 2f). It has been reported that the photoinhibition of PSI is primarily induced by the over-reduction of the acceptor side of PSI (Sonoike, 1999, 2006). The greater decline in Y(II) could result in more excessive light energy in *F. racemosa* during seasonal drought. Excess light energy may result in the generation of hydroxyl radicals and the over-reduction of the acceptor side of PSI (Smirnoff, 1998; Takahashi et al., 2009). Because the repair of the photo-damaged PSI reaction centers is a slow process that requires several days (Huang et al., 2013), the drought-induced decline in PSI activity in *F. racemosa* can be regarded as an accumulation of photodamage to PSI during seasonal drought stress.

The enhancement of NPQ and the activation of CEF are considered important mechanisms that protect PSII and PSI against drought stress (Huang et al., 2012; Jia et al., 2008; Lehtimäki et al.,

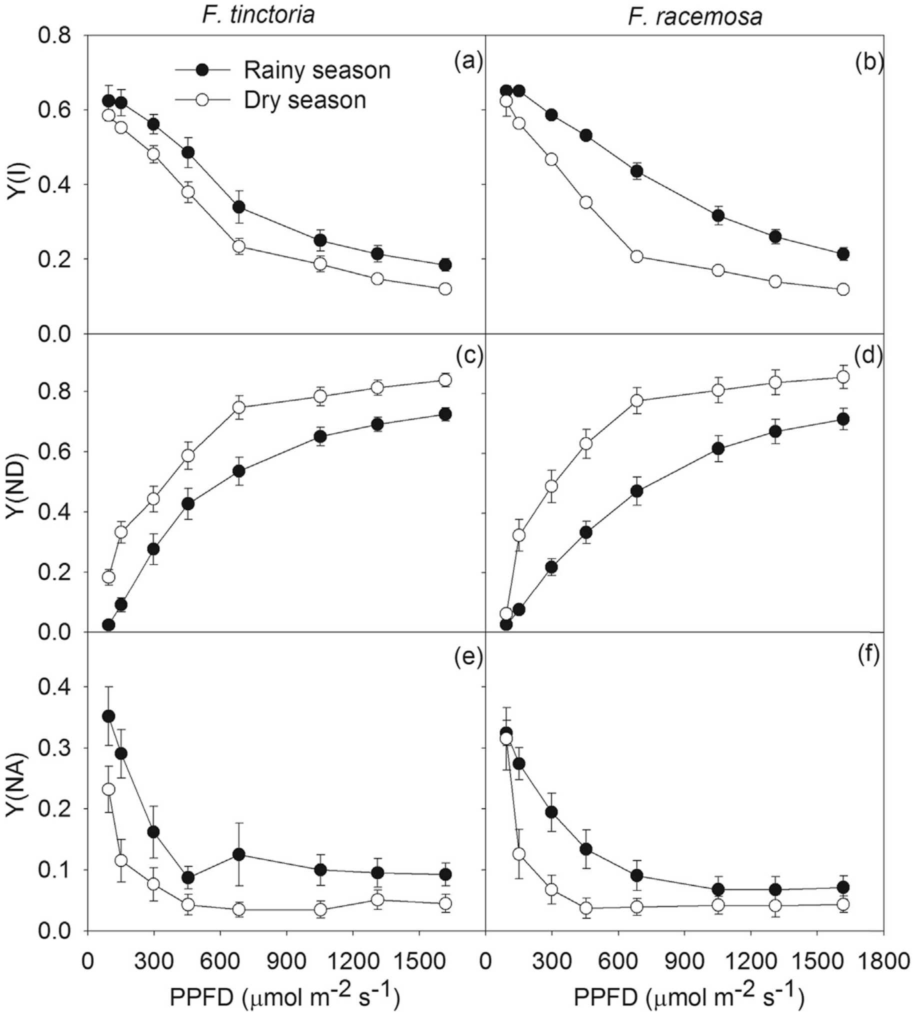

Fig. 4. . Seasonal variation (means ± SE) in the light response curves of photosystem I for *F. tinctoria* and *F. racemosa*. (**a**–**b**) The photochemical quantum yield of PSI [Y(I)]; (**c**–**d**) the fraction of overall P700 oxidized in a given state [Y(ND)]; (**e**–**f**) the fraction of overall P700 that cannot be oxidized in a given state [Y(NA)].

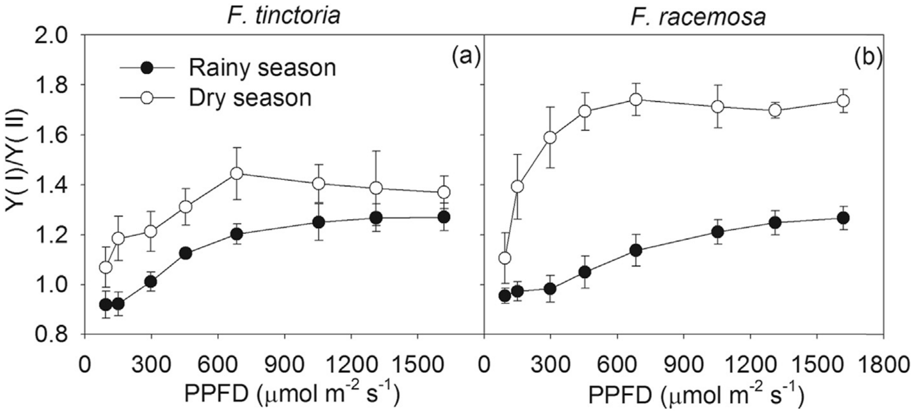

Fig. 5. Seasonal variation (means ± SE) in the light response curves for the ratio of Y(I)/ Y(II) in *F. tinctoria* and *F. racemosa*.

2010; Wang et al., 2013). For both *Ficus* species, Y(NPQ) and Y(I)/Y(II) increased during peak drought (Fig. 3e, f; Fig. 5a, b), suggesting stronger activation of CEF that could generate a ΔpH, and promote the harmless dissipation of excess light energy (Huang et al., 2012; Nandha et al., 2007). The stronger activation of CEF could also compensate for ATP synthesis, which is used for the repair of photosynthetic reaction centers during drought stress (Gao et al., 2011; Huang et al., 2012, 2013; Miyake et al., 2005). The stronger activation of CEF-dependent generation of a ΔpH in *F. racemosa* could alleviate photodamage to the OEC, and decrease the rate of photodamage to PSII (Takahashi et al., 2009). Increasing NPQ reduced the production of ROS and therefore prevented inhibition of the repair to photo-damaged PSII by allowing D1 protein synthesis. Moreover, the activation of CEF might alleviate the over-reduction of the acceptor side of PSI, thus protecting PSI against photodamage (Huang et al., 2012; Munekage et al., 2002, 2004). Our results showed that during the dry season, Y(ND) increased and remained above 0.8 even in high light for both *Ficus* species (Fig. 4c, d), indicating that the excess light energy could be dissipated harmlessly and that the PSI complexes were well protected by the activation of CEF. In addition, a low value of Y(NA) suggested prevention of over-reduction of the PSI acceptor side in both *Ficus* species. Recently, it was reported that the decrease in electron flow from PSII to PSI can increase the value of Y(ND) (Tikkanen et al., 2014). Thus, the lower value of Y(NA) during the dry season was partially due to the depression of LEF.

Our results suggested that PSI and PSII activities were more severely inhibited in *F. racemosa* than in *F. tinctoria* during peak drought. In this study, by peak seasonal drought, the Ψ_{pd} had decreased more greatly in *F. racemosa* than in *F. tinctoria*, and the Ψ_{pd} was lower than the Ψ_{tlp} in *F. racemosa* but was still higher than the Ψ_{tlp} in *F. tinctoria* (Fig. 2a, b). Concomitantly, *F. racemosa* showed greater decreases in Y(II) and Y(I) than *F. tinctoria* by the end of the dry season (Fig. 3a, b; Fig. 4a, b). In addition, *F. racemosa* displayed larger decreases in g_s and A_{max} (Fig. 2c, d). The restriction of the Calvin cycle aggravates the production of ROS at the acceptor side of PSI (Murata et al., 2007), which not only inhibits the repair of photo-damaged PSII (Takahashi et al., 2009) but also causes photodamage to PSI.

5. Conclusions

In conclusion, PSI activity was more sensitive to seasonal drought in *F. racemosa* than in *F. tinctoria*. At peak seasonal drought, the enhancement of NPQ and CEF contributed to the photoprotection of PSI and PSII activities for both *Ficus* species, but it contributed more significantly to *F. racemosa*. Our results provide new information that contributes to an understanding of the photoprotection of *Ficus* species with contrasting growth forms.

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