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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 CO₂ 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 D₁ 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 photo-inhibition 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 photo-inhibition 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 *Pharmacosyrea* 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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in March and 1,750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$. 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

The following PSII parameters were calculated: $F_v/F_m = (F_m - F_0)/F_m$, $Y(\text{II}) = (F_m' - F_s)/F_m'$, $Y(\text{NO}) = F_s/F_m$, $Y(\text{NPQ}) = 1 - Y(\text{II}) - Y(\text{NO})$, $qP = (F_m' - F_s)/(F_m' - F_0')$ (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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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. $Y(\text{II})$ is the effective quantum yield of PSII; $Y(\text{NO})$ represents the inability of a plant to protect itself against damage from excess light energy. $Y(\text{NPQ})$ 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: $Y(\text{NA}) = (P_m - P_m')/P_m$, $Y(\text{I}) = P700_{\text{red}} - Y(\text{NA})$, $Y(\text{ND}) = 1 - P700_{\text{red}}$ (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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 300 ms after 10 s of far-red pre-

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