



# Sexual differences in gas exchange and chlorophyll fluorescence of *Torreya grandis* under drought stress

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## Abstract

**Key message** *Torreya grandis* seedlings showed significant gender difference under drought stress and females had a better performance in the process of photosynthesis.

**Abstract** Starting with saturated moisture content, the natural drought stress process was comprehensively investigated to clarify the possible sex differences of *Torreya grandis* and how the components of the entire photosynthetic electron chain respond to drought stress. We examined gas exchange, prompt chlorophyll *a* fluorescence (PF), delayed fluorescence (DF), and modulated 820 nm reflection (MR) in both male and female torreya seedlings that received a drought stress treatment for a total of 20 days. The net photosynthesis (P<sub>n</sub>) and stomatal conductance (G<sub>s</sub>) of these plants all decreased relative to the corresponding control groups (0 days), and the exchange capacity between primary quinone acceptor (Q<sub>A</sub>) to secondary quinone acceptor (Q<sub>B</sub>) became limited compared to the onset of drought. The oxygen-evolving complex (OEC) was also damaged, and the performance index on an absorption basis (PI<sub>ABS</sub>) was significantly reduced by drought. Drought stress affects either the oxidation of plastocyanin (Pc) and the PSI reaction center (P<sub>700</sub>) or the re-reduction of Pc<sup>+</sup> and P<sub>700</sub><sup>+</sup> over time. Our results showed that torreya seedlings were inhibited by prolonged drought stress, which significantly reduced their photochemical activities of photosystem II (PSII) and photosystem I (PSI), but PSII was more sensitive than PSI. When the gender differences in gas exchange were compared, females performed better than males under drought. In the aspect of fluorescence curves, female plants also showed a slower rate of damage in PSII and PSI under drought stress than males. Thus, we concluded that female individuals of torreya might possess better adaptability to drought stress than male individuals.

**Keywords** Delayed fluorescence · *Torreya* · Drought stress · Modulated 820 nm reflection · Prompt fluorescence · Gas exchange

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## Introduction

The case for the threat posed by global warming has been gaining strength in recent decades, as evidenced by worsening extreme weather conditions such as summer drought, which have resulted in a series of problems worldwide (Stocker 2014; Ummenhofer and Meehl 2017). As one of the major abiotic factors limiting plant growth, drought can reduce productivity and even lead to significant mortality under extreme conditions. Photosynthesis is a fundamental metabolic process in plants that is very sensitive to and thus significantly affected by drought (Kalaji et al. 2016). Under drought stress, plants will overheat because of the lack of transpiration cooling due to water shortage, which inhibits photosynthesis, and then lead to elevated levels of reactive oxygen (Fu and Huang 2001; Jedmowski et al. 2013). Therefore, studying how drought affects the process

of photosynthesis becomes necessary to the understanding of the mechanism of plants' drought response.

PSII and PSI capture photons and initiate photosynthesis, and then absorbed energy is transferred by photosynthetic electron transport chain (Li and Ma 2012). PSII is responsible for stripping electrons from water to reduce  $Q_A$ ,  $Q_B$ , plastoquinone (PQ) pool, cytochrome  $b_6/f$  complex (Cyt $b_6/f$ ), and Pc, while PSI oxidizes the reduced Pc to reduce the electron acceptors on the PSI receptor side in this transfer process (Strasser et al. 2010). Changes in any point in the electron transport chain affect photosynthetic efficiency. PSII electron donor side, PSI electron acceptor side and electron transfer between PSII and PSI, as the main part of photosynthetic electron transfer chain, can be studied by prompt *chlorophyll a* fluorescence (PF), delayed fluorescence (DF), and modulated 820 nm reflection (MR) measurements. (Duan et al. 2015; Yang et al. 2017).

To investigate the photochemical reactions of plants, a technique has been developed enabling the simultaneous measurement of PF, DF, and MR (Gao et al. 2014; Kar et al. 2021; Strasser et al. 2010; Wang et al. 2021). This technique is an in-situ, non-injurious method to measure functional aspects of the photosynthetic electron transport chain; hence, it is a thorough probe for monitoring the physiological state of a photosynthetic sample. The PF transient (OJIP) arises from the redox state of the PSII reaction centers (RC) and corresponds to the subsequent reduction of the acceptor side of PSII, the PQ pool, and the electron acceptors around PSI, which is conveyed in the recorded data (Huihui et al. 2020; Schansker et al. 2005). The DF can be detected by a flashing-light experiment, and this parameter represents the recombination between the reduced primary electron acceptor  $Q_A^-$  and the oxidized donor ( $P_{680}^+$ ) of PSII in the dark (Strasser et al. 2010; Zhou et al. 2019). Monitoring the modulated reflection mode at 820 nm (MR) is an effective way to investigate the redox state of PSI under conditions of continuous light (Oukarroum et al. 2013; Schansker et al. 2003). This technique has been applied to study the behavior of energy within the photosynthetic electron transport chain, based on simultaneous measurements of the kinetics of PF, DF, and MR (Gao et al. 2014). Accordingly, using simultaneous measurements can provide parallel and complementary information on the structure or function of the photosynthetic machinery (Dąbrowski et al. 2019; Strasser et al. 2010).

Sex differences in dioecious plants have been a topic of fascinating interest since Charles Darwin first recognized that the reproductive differentiation of dioecious plants creates specific resource requirements for each sex. A number of researchers have been working on morphological and ecological differences between male and female plants (Allen and Antos 1988; Dawson and Bliss 1989; Peng et al. 2012; Rana and Liu 2021; Salvatori et al. 2014; Stefanović et al.

2017). These studies have shown that females have higher reproductive costs than males. Thus, sex-linked specialization in certain traits can be interpreted as an evolutionary response allowing each sex to better meet their specific reproductive resource needs while maintaining its fitness (Dawson and Ehleringer, 1993; Espirito-Santo et al. 2003; Jones et al. 1999). In this context, most studies focused on aspects of plant growth, survival, spatial distribution, and resource allocation (Rana and Liu, 2021; Retuerto et al. 2000; Stefanović et al. 2017). On a smaller scale, some studies have found that male and female individuals have different presentation in physiological, ecological, and biochemical characters under different stresses (Chen et al. 2018; Xu et al. 2007). If drought can markedly affect leaf-level gas exchange, water use efficiency, and growth rate of male and female individuals, the sex ratio, reproductive capacity, and distribution of monoecious populations might well change so as to track changes of global warming-induced drought disturbances and perturbations to plant species. As a result, the structure and function of forest ecosystems in some drought prone areas are also likely to change due to the sex difference of dioecious plants in response to drought.

*Torreya* is a genus of deciduous conifer trees and is valued for its production of nuts and timber in China, but its distribution is limited by its cultivated area and prevailing weather conditions. Many studies have investigated the effect of drought stress on the photosynthetic activity of *torreya* (Lin et al. 2019), however, comparatively little research has been done to elucidate the sex differences in *torreya* under drought stress. In this study, it is hypothesized that there are sexually different responses to drought, and we focus on the impact of drought stress on the electron transport chain to monitor plant responses to various drought stress conditions in a laboratory experiment. We used the simultaneous measurements of PF, DF, and MR to investigate and explore, in greater detail, sex-related changes occurring in photochemical activities during the drought stress process.

## Materials and methods

### Plant materials and drought treatment

Two-year-old *Torreya grandis* seedlings were obtained from the Zhuji Forestry Institute (29° 43' N, 120° 16' E). A total of 48 individuals, split between males ( $n=24$ ) and females ( $n=24$ ), were used in the drought stress experiment. The trees were grown individually in plastic pots (20-cm diameter  $\times$  18-cm deep) and arranged in a completely randomized design, with six replicates (one pot per replicate) for the drought treatment and six replicates for the counterpart control group per sex, in the greenhouse of Jiyang College of Zhejiang A&F University (Zhejiang Province, China;

29° 45' N, 120° 15' E). Each pot was filled with 6 kg loam soil (field water holding capacity of 33.2%), and the greenhouse environment was maintained under a 16-h/8-h (day/night) photoperiod at an average temperature of 32/26 °C (day/night), with a relative humidity of 70%. Continued watering was first applied for 15 days to acclimatize the plants to the greenhouse environment and restore the normal state before imposing the drought stress treatment. Seedlings were fully watered to saturation (about 0.5 L per pot, until the water ran out of the drain holes) and then allowed to naturally dry with no more water added to the pots. The entire experiment stopped at 20 days when most plants were severely stressed, as indicated by wilting, and obvious differences were observed among different treatments. During the drought period, we took measurements at 0, 6, 12, and 20 days after watering was stopped. Each measurement time represented a progressively more severe drought condition, from no drought at 0 days to the most severe drought at 20 days. In order to observe the changes of torreyia seedlings during drought stress, 0 days were used as control (He et al. 2016; Zhou et al. 2019).

### Soil moisture content and relative water content measurement

Soil moisture content (SMC) was measured with a soil temperature and moisture sensor (HSTL-TRSC02, Beijing, China) each day at 8 am and recorded. Each pot was measured three times and averaged.

Relative water content (RWC) was measured by the drying method. Every two days, the fresh leaves were collected and weighed to obtain their fresh weight (FW). Leaves were then soaked in purified water at room temperature for 4 h to obtain their saturated fresh weight (SW). Next, leaves were placed in a 70 °C oven for 6 h to determine the dry weight (DW). RWC was calculated as follows:  $RWC = (FW - DW) / (SW - DW) \times 100\%$ .

### Gas exchange measurement

Three leaves were selected from similar positions within the mid-portion of the main stem, and the Li-6400 portable photosynthetic measurement system (LI-COR, Lincoln, US) was used to measure leaf parameters. To ensure the the stabilization of gas concentrations, small steel cylinders filled with carbon dioxide were used in Li-6400. The process of light response under different soil moisture was measured during sunny days. From 9 to 11 am, each leaf was recorded three times, and the mean value was used for statistical analyses. The red and blue light sources were set as  $1200 \mu\text{mol s}^{-1} \text{m}^{-2}$ , with the light intensity in the same period kept the same. Automatic instrumentation recorded

stomatal conductance (Gs), net photosynthesis (Pn), and intercellular CO<sub>2</sub> concentration (Ci).

### PF, DF, and 820 nm reflection measurement

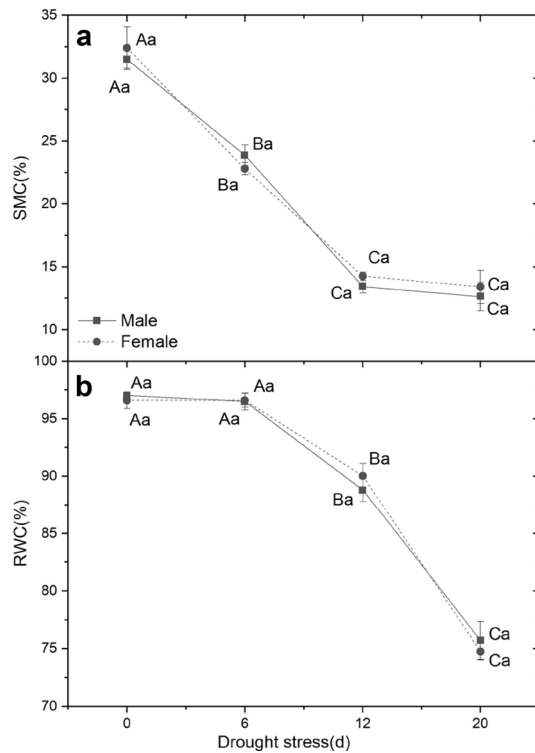
The leaf-level kinetics of PF, DF, and MR were measured by a Multifunctional Plant Efficiency Analyzer [M-PEA] (Hansatech Instruments, Pentney, UK). The light from actinic LEDs provided homogeneous illumination, with an intensity of  $5000 \mu\text{mol photons} / (\text{m}^{-2} \text{s}^{-1})$  for 60 s. The wavelengths were  $627 \pm 10 \text{ nm}$  for the red LED,  $820 \pm 25 \text{ nm}$  for the modulated moderate LED, and  $735 \pm 15 \text{ nm}$  for the far-red LED (Strasser et al. 2010). After 1 h of dark-adaptation, the M-PEA was used to measure the light absorption curve of rapid chlorophyll fluorescence induction kinetics (OJIP) every 2 days. Minimum reliable fluorescence intensity ( $F_0$ ) was at 20  $\mu\text{s}$ ; fluorescence at the J-step ( $F_J$ ) was at 2 ms; fluorescence at the I-step ( $F_I$ ) was at 30 ms. The ensuing curve was plotted on a logarithmic time scale to show the process unfolding in real-time. Red light induction for 1 s was implemented under saturated pulsed light, for which the measurement time was 2 s, with an initial rate of recording of 105 data points per second.

The parameter ABS/RC (measure of the average total absorbance per active PSII RC),  $\Psi_0$  (the probability that an electron moves further than  $Q_A$ ),  $\phi P_0$  (maximum quantum yield of primary photochemistry),  $\phi E_0$  (quantum yield for electron transport),  $\Delta R_0$  (the efficiency of an electron beyond that reduced PSI acceptors), and  $PI_{\text{ABS}}$  (the performance index on an absorption basis) were collected from M-PEA.

Three healthy leaves were selected from similar positions within the mid-portion of the plant's main stem for measurement. Measurements were taken for 20 days until the leaves began to wilt. During this measurement cycle, the PF was measured at 7 am, and DF was recorded at 9 pm (after 3 h of dark adaptation). The first reliable MR time ( $MR_0$ ) point occurred at 0.7 ms at room temperature (25 °C). The  $MR/MR_0$  was calculated using the modulated reflection signal at 820 nm. The ratio of MR to  $MR_0$  reflects the change in REDOX status between  $P_{700}^+$  and  $P_c^+$  (Strasser et al. 2010).

### Statistical analyses

A two-way ANOVA, with sex and drought time as the main fixed factors plus a sex  $\times$  time interaction term, followed by Duncan's multiplerange test, was performed for each measured variable. When sex  $\times$  time interaction was significant, we conducted separate one-way ANOVAs for sex at each measurement time and for measurement time by each sex. All data were analyzed using SPSS 22.0 software (IBM, Armonk, USA), with the significant level set at the default  $\alpha = 0.05$ .



**Fig. 1** Changes in soil moisture content (SMC) and relative water content (RWC) during the imposed drought. The values are means  $\pm$  SE ( $n=6$ ). Different lowercase letters indicate a significant difference between different genders at  $P<0.05$ , and different uppercase letters indicate significant difference under drought stress at  $P<0.05$ , according to Duncan's test

## Results

### Soil moisture and relative leaf water content

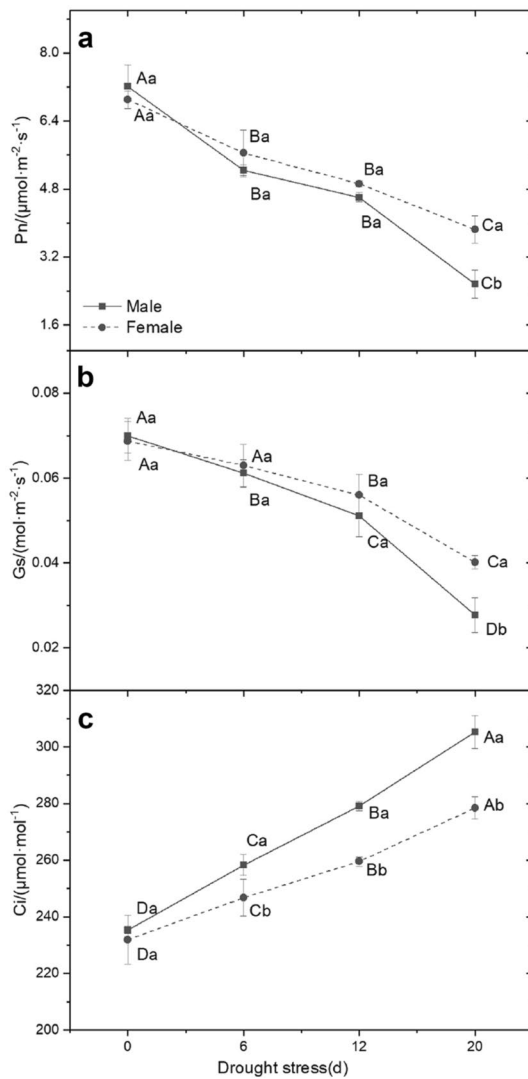
Changes in soil moisture content (SMC) and relative leaf water content (RWC) during the experiment are given in Fig. 1. Both SMC and RWC declined during the 20-day drying period. Compared with control, RWC decreased by 22.0% for males and 22.6% for females at 20 days, while SMC decreased by 59.8% for males and 58.6% for females at 20 days. In the same drought period, the SMC and RWC of male and female groups were basically synchronous, and the decreasing of SMC was fast firstly and then slowly, whereas RWC first decreased slowly and then quickly. Overall, the drought stress conditions experienced by the two sexes of the experimental torreyia plants were similar.

### Gas exchange

The gas exchange parameters were significantly influenced by both sex and the duration of drought, and a significant interaction of sex and drought was observed (Table 1). After 20 days of drought, males fell by 64.5% and females by 44.3% in terms of  $P_n$  (Fig. 2a), with corresponding declines of 60.4% and 41.5% for  $G_s$  (Fig. 2b), compared to control. By contrast, a 29.8% and 20.7% increase in  $C_i$  was observed for males and females, respectively (Fig. 2c).

**Table 1** Summary of significance levels (two-way ANOVA) for the effects of gender, drought, and their interaction on SMC, RWC, gas exchange parameters, fluorescence parameters, modulation parameters of 820 nm reflection, and parameters of delayed chlorophyll fluorescence

Source	SMC (%)	RWC (%)	$P_n$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$G_s$ ( $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$C_i$ ( $\mu\text{mol}\cdot\text{mol}^{-1}$ )	ABS/RC	$\Psi_0$	$\Phi_{P_0}$
<b>Gender (A)</b>								
MS (mean square)	0.9802	0.0058	1.4724	0.0002	1887.792	0.0201	0.0128	0.0005
<i>P</i> (probability)	0.3211	0.9349	0.001	0.0054	0.0001	0.0015	0.0001	0.0329
<b>Drought (B)</b>								
MS	638.4343	817.2148	20.4041	0.0019	4916.547	0.0384	0.015	0.0043
<i>P</i>	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
<b>Interaction (A×B)</b>								
MS	1.8124	1.7784	0.8529	0.0001	205.6879	0.0076	0.0012	0.0004
<i>P</i>	0.1569	0.1299	0.0007	0.0209	0.0004	0.0092	0.0035	0.0316
Source	$\Phi_{E0}$	$\Delta_{R0}$	$PI_{ABS}$	$V_{PSI}$	$V_{PSII-PSI}$	$I_1/I_2$	$(I_1 - D_2)/D_2$	
<b>Gender (A)</b>								
MS	0.0063	0.0015	115.8681	0.0244	0.0148	0.0013	0.5813	
<i>P</i>	0.0001	0.0033	0.0001	0.0005	0.0001	0.0612	0.0001	
<b>Drought (B)</b>								
MS	0.0159	0.0096	265.5478	0.0421	0.0225	0.0217	3.9864	
<i>P</i>	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	
<b>Interaction (A×B)</b>								
MS	0.0009	0.0015	13.9892	0.0102	0.0088	0.0013	0.4067	
<i>P</i>	0.032	0.0001	0.0003	0.0016	0.0001	0.0194	0.0001	



**Fig. 2** Variation in plant gas exchange parameters (Pn, net photosynthesis; Gs, stomatal conductance; and Ci, intercellular CO<sub>2</sub> concentration) of leaves between female and male *Torreyia grandis* under drought stress. The values are means  $\pm$  SE ( $n=6$ ). Different lowercase letters indicate a significant difference between different genders at  $P < 0.05$ , and different uppercase letters indicate significant difference under drought stress at  $P < 0.05$ , according to Duncan's test

Both male and female torreyia were significantly affected by the imposed drought stress (Fig. 2). Through the last day of drought, all parameters had changed significantly, but the effect size of each depended on plant sex.

### PF kinetics

With the extension of drought, the fluorescence kinetics of the counterpart control plant samples of the torreyia sex groups exhibited a polyphasic PF rise (Fig. 3). Their relative variable fluorescence of leaves was normalized to obtain the OJIP transients and the relative variable fluorescence at

steps J ( $V_J$ ) and I ( $V_I$ ). The L-band (Fig. 3g, h) and K-band (Fig. 3e, f) were significantly increased at 20 days compared to control, with the responses for males changing more than those of females under drought stress. Further, the PF transients under drought stress showed a J-step significantly higher than that recorded at control. After standardizing the transients between  $F_0$  and  $F_P$ , the correlation between the changed OJIP and the duration of the drought was apparent.

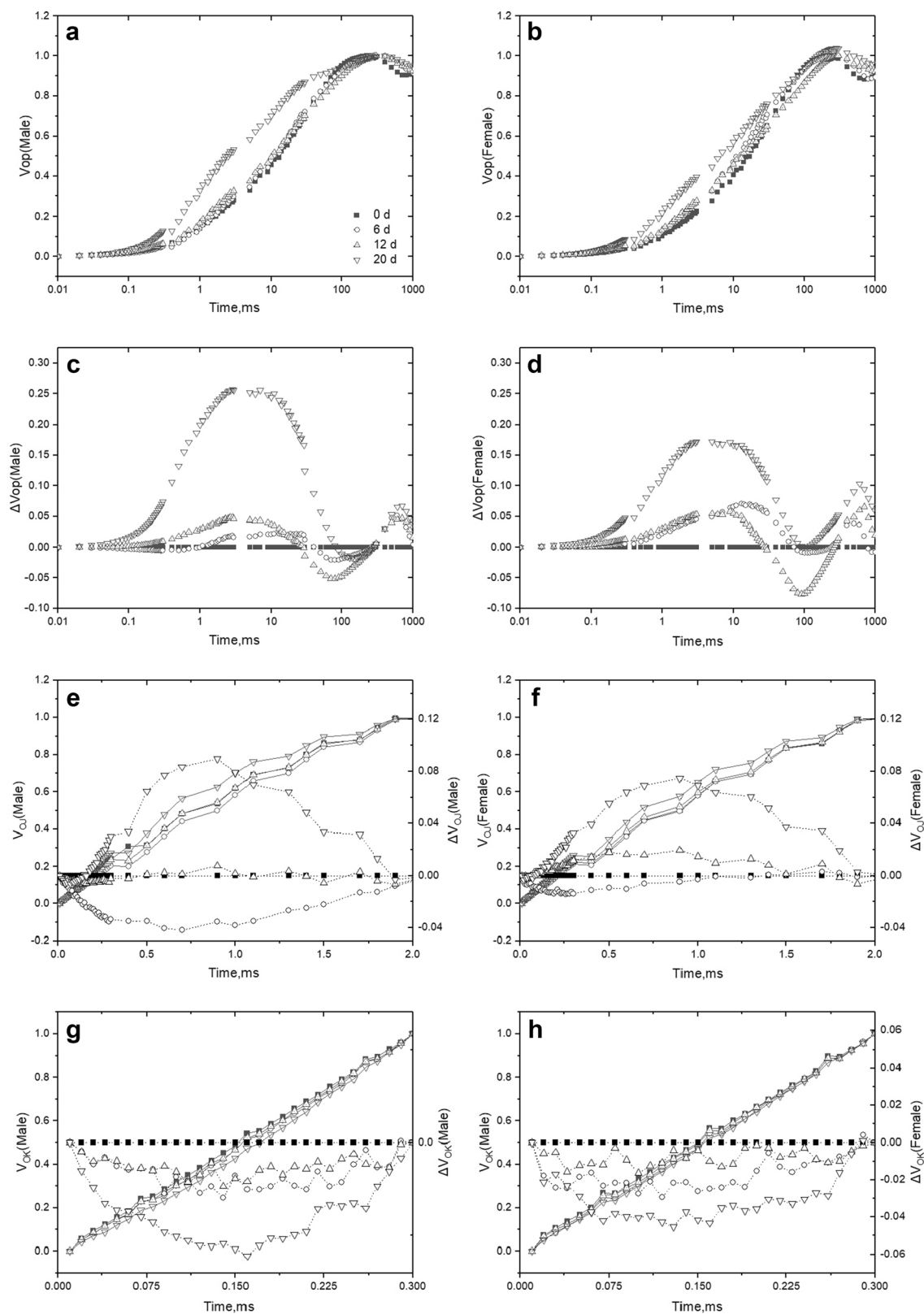
The parameters of PF in torreyia leaves were significantly influenced by both sex and the duration of drought, and a significant interaction of sex and drought was observed (Table 1). Under drought stress, the parameters  $\Psi_0$ ,  $\phi P_0$ ,  $\phi E_0$ ,  $\Delta R_0$ , and  $PI_{ABS}$  all decreased in both male and female individuals. When compared with control, the  $\Psi_0$  values for males decreased by 16.3%, and 9.0% in females at 20 days (Fig. 4b). There were corresponding declines of 7.4% and 4.0% detected for  $\phi P_0$  (Fig. 4c). The values of  $\phi E_0$ ,  $\Delta R_0$ , and  $PI_{ABS}$  declined by 18.9% and 11.7% (Fig. 4d), 27.1% and 12.7% (Fig. 4e), 63.0% and 39.0% (Fig. 4f) in male and female torreyia trees over the drought period, respectively. The drought-stressed males underwent a faster drop in their parameters than the females; however, the ABS/RC increased by 9.0% for males and 21.0% for females, compared with control (Fig. 4a). A two-way ANOVA showed that drought, sex and their interaction significantly affected PSI and PSII in torreyia leaves (Table 1). And, we observed that females showed higher ABS/RC,  $\phi P_0$ ,  $\phi E_0$ ,  $\Psi_0$ ,  $\Delta R_0$ , and  $PI_{ABS}$  than males under 20 days of drought stress, especially the  $\Delta R_0$  and  $PI_{ABS}$  (Fig. 4a–f).

### Modulated reflection at 820 nm

The normalized MR/MR<sub>0</sub> signals differed between males and females on MR<sub>820</sub> kinetics (Fig. 5). It was observed that the first red light induced an initial oxidation of Pc and P<sub>700</sub> followed by a full reduction for control. With the increase of drought stress, the maximum decreasing slope of the MR/MR<sub>0</sub> transient ( $V_{PSI}$ ) increased, yet the maximum increasing slope of the MR/MR<sub>0</sub> transient ( $V_{PSII-PSI}$ ) decreased. Compared with control, there was a 23.3% and 8.2% increase in  $V_{PSI}$  and a 22.9% and 5.8% decline in  $V_{PSII-PSI}$  in males and females at 20 days, respectively (Fig. 6). The parameters of MR at 820 nm in torreyia leaves were significantly influenced by both sex and the duration of drought, and a significant interaction of sex and drought was observed (Table 1).

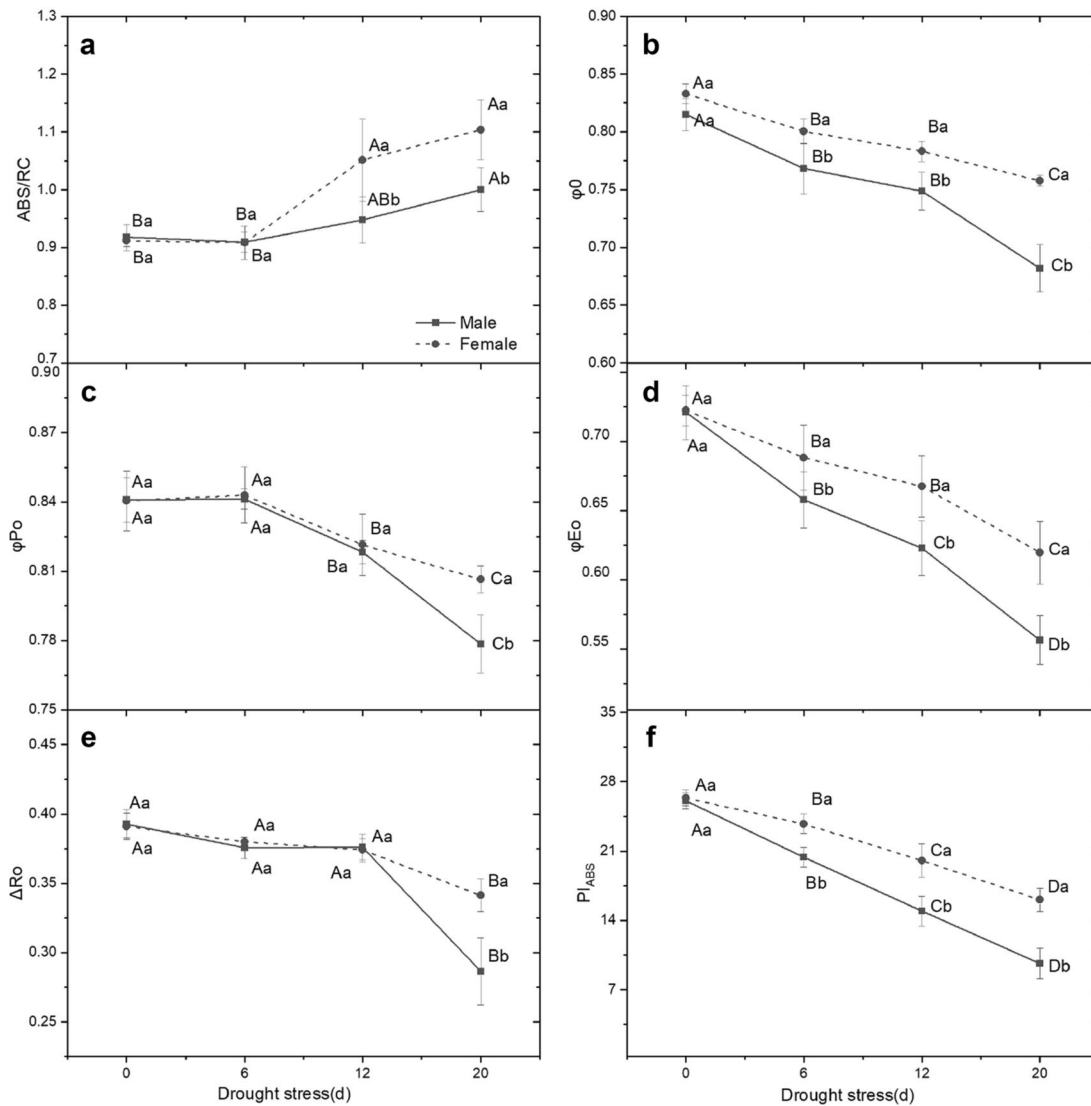
### DF induction and decay kinetics

As depicted in Fig. 7, all the treatments showed the typical DF induction curves, with obvious changes. To illustrate the shapes of DF on a time scale directly, these induced curves were calculated and averaged (Fig. 7b, d). After 20 days of drought, the values of  $I_1$  and  $I_2$  had decreased.



**Fig. 3** Changes in the shape of the Chl *a* fluorescence transient curves in leaves of *Torreya grandis* under drought stress (left: male, right: female). **a** and **b**  $V_{OP} = (F_t - F_0)/(F_M - F_0)$ ; **c** and **d**  $\Delta V_{OP} = V_{OP}(\text{treatment}) - V_{OP}(\text{control})$ ; **e–h**  $V_{OI} = (F_t - F_0)/(F_J - F_0)$ , and between  $F_0$  and  $F_K$ :  $V_{OK} = (F_t - F_0)/(F_K - F_0)$  were normal-

ized and displayed as  $\Delta V_{OI} = V_{OI}(\text{treatment}) - V_{OI}(\text{control})$  and  $\Delta V_{OK} = V_{OK}(\text{treatment}) - V_{OK}(\text{control})$ . The left side is a solid line, and the right side is a dashed line. Each point is the mean of six replicates



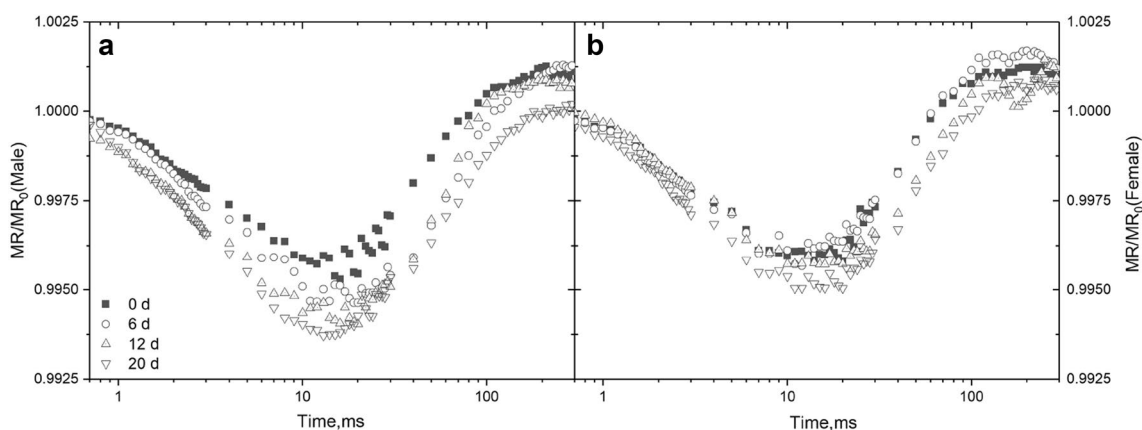
**Fig. 4** Sexual differences for six fluorescence parameters under drought stress (ABS/RC, measure of the average total absorbance per active PSII RC;  $\Psi_0$ , the probability that an electron moves further than  $Q_A$ ;  $\phi_{P_0}$ , maximum quantum yield of primary photochemistry;  $\phi_{E_0}$ , quantum yield for electron transport;  $\Delta R_0$ , the efficiency of an electron beyond that reduced PSI acceptors; and  $PI_{ABS}$ , the perfor-

mance index on an absorption basis) in *Torreyia grandis* leaves. The values are means  $\pm$  SE ( $n=6$ ). Different lowercase letters indicate a significant difference between different genders at  $P < 0.05$ , and different uppercase letters indicate a significant difference under drought stress at  $P < 0.05$ , according to Duncan's test

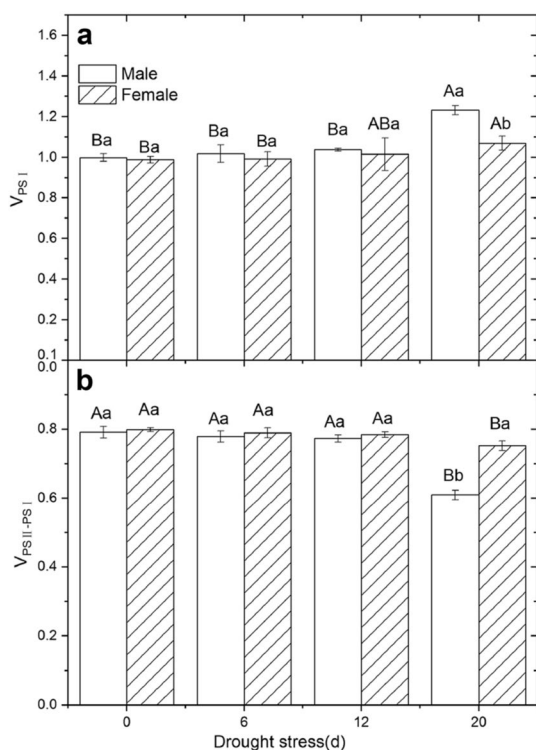
The change in the ratio of  $I_1/I_2$  was similar to the changed ratio of  $(I_1 - D_2)/D_2$ , in that they were all significantly lowered compared to control. Two-way ANOVA indicated that drought, sex, and their interaction significantly influenced the parameters of DF in torreyia leaves (Table 1). Yet, under drought pressure, the males experienced more pronounced numerical fluctuations than the females.

### Discussion

RWC commonly exhibits a descending trend under drought treatment (Cocozza et al. 2010). It has been found that the RWC of trees with weak drought resistance is lower than that of trees with strong drought resistance, as higher RWC of plants could be used to ensure more favorable internal water relationship (Berova and Zlatev 2003; Sivakumar et al. 2014). In our study, there was little gender difference in RWC (Fig. 1b), and no significant interaction of sex and drought was observed in SMC and RWC of torreyia



**Fig. 5** Sexual differences in the curves of modulated reflection at 820 nm under drought stress (left: male, right: female *Torreya grandis*). The values are means  $\pm$  SE ( $n=6$ )



**Fig. 6** Study on modulation parameters of 820 nm reflection ( $MR/MR_0$ ) in torreyia leaves of different sex under the different duration of drought stress.  $V_{PSI}$ , maximum slope decreases of  $MR/MR_0$ ;  $V_{PSII-PSI}$ , maximum slope increases of  $MR/MR_0$ . Different lowercase letters indicate a significant difference between different genders at  $P < 0.05$ , and different uppercase letters indicate a significant difference under drought stress at  $P < 0.05$ , according to Duncan's test

(Table 1), suggesting that both males and females of torreyia seedlings were similarly affected by drought.

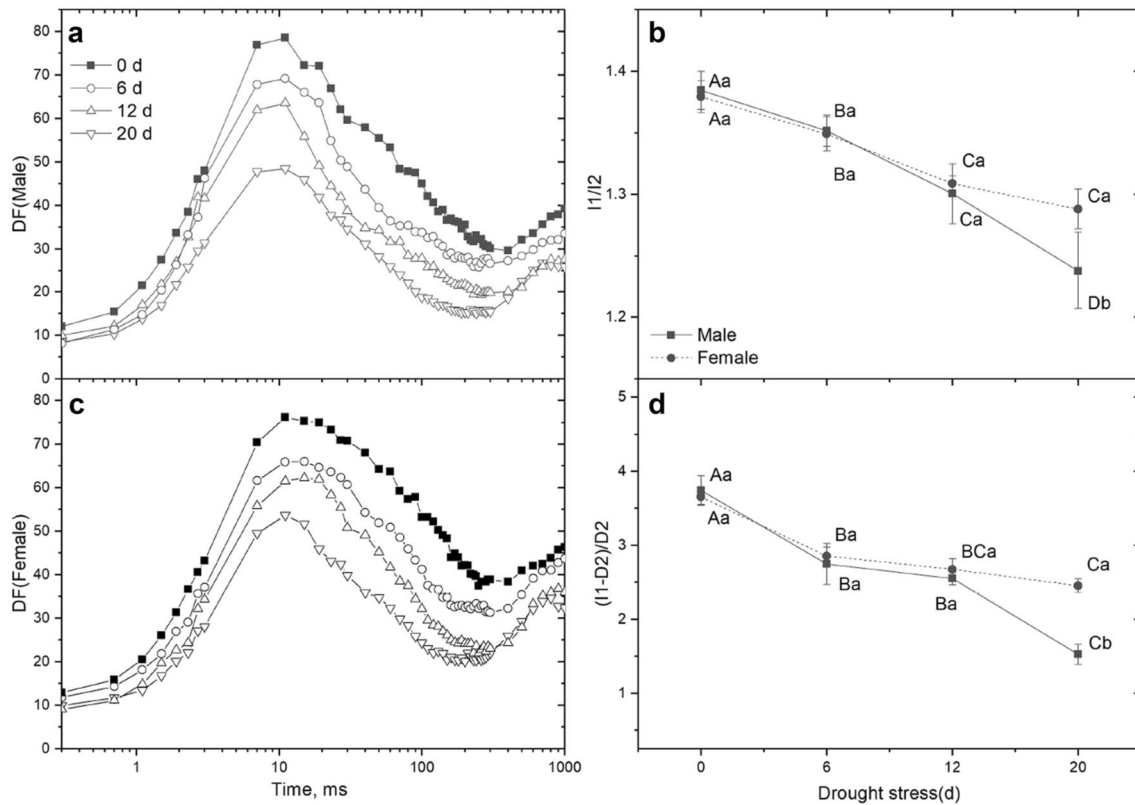
We found differences in gas exchange parameters between males and females, most of which became significant after 6 days of drought stress (Fig. 2). Compared with males,

females had higher values of Pn and Gs, and lower values of Ci. This result suggested that the female was more tolerant of severe drought, which is consistent with the study of *ginkgo biloba* (He et al. 2016). Stomatal factors and non-stomatal factors are the main reasons for the changes of plant photosynthesis under drought stress (Farquhar and Sharkey, 1982). The results of this experiment showed that Pn and Gs decreased but Ci increased in both males and females of torreyia trees under drought stress (Fig. 2), indicating that the decrease of Pn was caused by non-stomatal limitation (Wang et al. 2003). Meanwhile, the gas exchange parameters of torreyia were significantly affected by drought, gender and their interaction effects (Table 1), suggesting that the gas exchange activities with different genders were significantly different.

We used simultaneous measurements of PF, DF, and MR to investigate changes in the photosynthetic transport chain of torreyia seedlings under drought stress conditions, as well as the variation characterizing each parameter. The results confirmed that drought stress had a significant impact on the photosynthetic electron transport process of torreyia, and there were significant differences between males and females under drought stress (Table 1). Under the same degree of drought (i.e., duration in days), males are more vulnerable to photosynthetic apparatus and ability than females.

The rapid rise of PF is usually accompanied by the accumulation of  $Q_A^-$  and inhibition beyond the redox couple  $Q_A/Q_A^-$ . We found that torreyia seedlings showed a higher fraction of inactive RCs with the aggravating of drought stress (Fig. 3a–d). A reduction in the active RCs was also reported in *sorghum landrace* under drought (Jedrowski et al. 2013). At early drought stages, the proportionally lower fraction of inactivated RCs indicates that torreyia seedlings likely had a higher ability to downregulate their photochemistry against drought. At the later drought stage, it is probable that photo-oxidative destruction of a large proportion





**Fig. 7** Study on modulation parameters of delayed chlorophyll fluorescence (DF) induction and decay kinetics in leaves of *Torreya grandis* under drought stress. Each curve is the average of six replicates

of RCs might have occurred as indicated by the stepper fluorescence rise and increased peaks at the J-step (Fig. 3e, f). Photo-oxidative appeared to suffer less serious destruction during drought treatment in females than in males, which may be another causation why females showed higher Pn than males under drought.

An increased K-band often relates to a limitation on the donor side of PSII (Guisse et al. 1995; Srivastava et al. 1997), and  $W_K$  (normalized relative variable fluorescence in K-step) has been widely used as a specific indicator of injury to the OEC (Zhang et al. 2012). Raised fluorescence in K-bands can be observed in plant species stressed by high temperature (Konôpková et al. 2018; Li et al. 2009; Toth et al. 2005) or drought stress (De Ronde et al. 2004; Oukarroum et al. 2007, 2009). In this study, the emulated natural drought process induced a clear K-band in torreyia seedlings (Fig. 3e, f). Similarly, a salt-induced K-band was also observed in perennial ryegrass (Dąbrowski et al. 2016). These observations suggest that drought stress can destroy the OEC and weaken the electron transfer capacity of the donor side of the PSII. Since OEC is involved in the photo-oxidation of water during photosynthesis, our results suggested that the oxidation of water under drought stress was altered. Less impact of OEC was detected in females than in

males during drought treatment, suggest that females own better drought resistance than do males.

A negative L-band is influenced by the excitation energy transfer between PSII units, commonly denoted as connectivity or grouping (Strasser and Stirbet 1998). Changes in respectively the L and K-bands of the fluorescence transients OJIP were shown to have predictive value with respect to the vitality of leaves and the tolerance of the varieties to drought stress (Oukarroum et al. 2007). During the course of drought, the negative L-band deviation of torreyia leaves increased (Fig. 3g, h); hence, the PSII connection (or grouping) per unit of energy increased. In other words, torreyia is a plant species with drought tolerance, and that makes no difference between male and female torreyia trees in connectivity. After 12 days of drought stress, males significantly fell by 11.3% and females by 6.3% in terms of  $\phi E_0$  (Fig. 4d), with corresponding declines of 8.1% and 6.0% for  $\Psi_0$  (Fig. 4b), compared to control, which indicated the inhibition of photosynthetic electron transfer beyond  $Q_A$  (Sheng et al. 2016). The parameter  $\Delta R_0$ , often used as a semi-quantitative indicator of the relative change of PSI, also underwent no significant decrease during 12 days of imposed drought. This result indicates that the photochemical activity of PSII is more sensitive than PSI to moderate drought.

After 20 days of drought stress, the  $\phi P_0$ ,  $\phi E_0$ , and  $\Psi_0$  values decreased significantly while that of ABS/RC increased significantly. These coordinated changes drove a decrease in  $PI_{ABS}$  under drought stress, which indicated that torreyia leaves reduced PSII activity (Tsimilli-Michael and Strasser, 2008). The significant increases in both  $V_J$  and  $V_I$ , as well as the sustained decrease in  $\Delta R_0$ , suggest that the 20-day drought treatment applied inhibited the entire electron transport chain from the donor side of the PSII to the PSI-end electron acceptors. Moreover, females showed less susceptibility to drought treatment and  $PI_{ABS}$  was 66% higher than males after 20 days of drought, which suggested that females suffer less disruption in the PSII electron transport process. Thus, we infer that there are significant differences between male and female trees, and the male tree is more vulnerable to drought stress.

MR changes reflect altered redox states of Pc and  $P_{700}$  (Guo et al. 2020; Strehler and Arnold, 1951); thus measuring the MR signal can supplement the partial ‘blind area’ of PF measurements (Chow et al. 2012; Gao et al. 2014). The result showed the minimum value of MR signal in both sexes under drought stress conditions (Fig. 5), which might due to the limited blocking of PSII electron transport to  $cytb_6f$  and PSI and the acceptor side of PSI (Lazar, 2009).  $V_{PSI}$  and  $V_{PSII-PSI}$  reflect the oxidation reduction rate of Pc and  $P_{700}$ , and are obtained by the absolute values of minimum and maximum slopes of  $MR_{820}$  signal linear regression (Guo et al. 2020).  $V_{PSI}$  and  $V_{PSII-PSI}$  for each parameter’s range in males exceeded that in females, and there were significant differences between different sex in  $V_{PSI}$  and  $V_{PSII-PSI}$ , indicating a greater impact of drought on male than female trees (Table 1). After 12 days of drought, the values of  $V_{PSI}$  and  $V_{PSII-PSI}$  did not change significantly when compared with control. This indicates that PSI is more resistant to drought than PSII. The decrease of  $V_{PSII-PSI}$  means that  $P_{700}$  and Pc are both affected by drought stress, and the re-reduction rate of  $P_{700}^+$  and  $Pc^+$  is decreased, corresponding to inhibition of PSI (Fig. 6). It can be interpreted as there were too few electrons going pass to PSI to reduce  $P_{700}^+$  and  $Pc^+$  under drought stress. This indicates that drought stress affects either the oxidation of Pc and  $P_{700}$  or the re-reduction of  $Pc^+$  and  $P_{700}^+$ . A wider fluctuation of  $V_{PSI}$  and  $V_{PSII-PSI}$  suggested that there was faster oxidation of Pc and  $P_{700}$  and a slower re-reduction of  $Pc^+$  and  $P_{700}^+$  in males than females, which might be the reason why females perform better to drought.

DF has become a useful tool for testing plant response under stress conditions due to its sensitive response to photosynthetic process (Guo et al. 2020; Guo and Tan, 2009; Lambrev and Goltsev, 2001). As drought duration increased, DF induction kinetics significantly changed in torreyia leaves. The decrease in  $I_1$  and  $I_2$  suggests that severe drought stress (i.e., 20 days without water) was destroying the photosynthetic electron transport chain

and reducing the net photosynthetic rate and the ability to adapt to circumstances. At the same time, this damage happened at a faster rate in males than females, suggesting that males were more adversely affected by drought. Our results demonstrated that drought, sex, and their interaction were capable of exerting a significant differential effect on the  $(I_1 - D_2)/D_2$  of both sexes of torreyia seedlings (Fig. 7). The change process of ratio  $I_1/I_2$  was similar to that of ratio  $(I_1 - D_2)/D_2$ , which reflects the electron transfer rate of PSII acceptor side (Lazár, 1999; Mehta et al. 2011). The significant change of the  $(I_1 - D_2)/D_2$  ratio under drought can be explained by the loss of PSII activity and the functional damage to the PSI. These results showed that both males and females were damaged under drought stress, though, in males, the changes were more pronounced. This indicated that females torreyia seedlings suffered less damage in electron transport from drought than males.

There have been many reports on the sex differences in the photosynthetic index of dioecious plants (Gehring and Monson 1994; Wang and Griffin 2003; Zhao et al. 2018). For example, female plants of *Ginkgo biloba* show better adaptability than males under drought stress (He et al. 2016). *Populus cathayana* males have a stronger ability to balance growth and carbohydrate accumulation when compared to females (Yang et al. 2015). In *Populus tremuloides*, Wang and Curtis (2001) found that males were characterized by a higher photosynthetic efficiency than females. In other work, the net photosynthetic rate of *Ilex aquifolium* females exceeded that of males under low light conditions, but this was reversed under saturated light (Strasser and Srivastava, 1995). A study on *Populus yunnanensis* provided evidence for different adaptive responses between plants of different sexes exposed to elevated  $CO_2$  and salinity (Li et al. 2013), which reported that females were more sensitive and suffered from greater negative effects than males under salt stress. Therefore, our study and previous studies together suggest that sex-linked differences in photosynthesis of dioecious plants are not consistent among species, which can be interpreted as species-specific adaptation.

To conclude, significant differences in gas exchange, PF, DF, and MR curves between the males and females of torreyia seedlings under drought stress were demonstrated in this experimental study. This different yet seemingly coordinated sex-based response may be caused by the inhibition of PSII and PSI under drought stress, thus affecting the electron transport chain, which changes faster and more substantially in the male than female seedlings. Therefore, we suggest that males of this species are more sensitive than females to negative influences from abiotic stress factors.

**Author contribution statement** SJ conceived and designed the experiment. JW, YX, WC and YH performed experiments. JW and YL analyzed the data. JW, YL and GW wrote the manuscript. JW and YL contributed equally.

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## Declarations

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

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