

Effects of drought stress on fluorescence characteristics of photosystem II in leaves of *Plectranthus scutellarioides*

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Abstract

Drought stress has multiple effects on the photosynthetic apparatus. Herein, we aimed to study the effect of drought stress on fluorescence characteristics of PSII in leaves of *Plectranthus scutellarioides* and explore potentially underlying mechanisms. Plants of *P. scutellarioides* were grown in a greenhouse and subjected to drought (DS, drought-stressed) or daily irrigation (control group). Leaf chlorophyll (Chl) index and induction kinetics curves of Chl *a* fluorescence and the JIP-test were used to evaluate effects of drought lasting for 20 d. Our results showed that both the leaf and soil relative water content decreased with increasing treatment duration. The leaf Chl index was reduced to half in the DS plants compared with the control group after 20 d. The minimal fluorescence in the DS plants was higher than that in the control plants after 10 d of the treatment. Maximum photochemical efficiency and lateral reactivity decreased with increasing treatment duration in the DS plants. With the continuing treatment, values of absorption flux per reaction center (RC), trapped energy flux per RC, dissipated energy flux per RC, and electron transport flux per RC increased in the earlier stage in the DS plants, while obviously decreased at the later stage of the treatment. In conclusion, drought stress inhibited the electron transport and reduced PSII photochemical activity in leaves of *P. scutellarioides*.

Additional key words: *Coleus*; electron transport; fluorescence transient; performance index; photoinhibition.

Introduction

Drought stress is one of important environmental stresses affecting plant photosynthesis and growth in arid and semi-arid regions (Ashraf and Foolad 2007). It has been widely known that the scarcity of water could damage metabolism and physiological processes of plant (Ranjbarfordoei *et al.* 2002, Shao *et al.* 2009). Cell dehydration, reduction in Chl content, decline of photosynthetic rate, and changes in Chl fluorescence parameters also occur under varying degrees

of drought stress (Ekmekci *et al.* 2005). PSII plays an important role in the response to environmental stresses, such as high salt (Centritto *et al.* 2003, Zushi *et al.* 2009), heat or chilling (Monneveux *et al.* 2003), and drought stress (Oukarroum *et al.* 2009). Besides, drought stress may influence the photochemical activity of PSII and electron requirement for photosynthesis, which results in an overexcitation and photoinhibition damage

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Abbreviations: ABS/RC – quantum yield of electron transport; DAT – day of treatment; DI₀/RC – trapped energy flux per reaction center; DM – dry mass; DS – drought-stressed; ET₀/RC – absorption flux per reaction center; F₀ – minimal recorded fluorescence intensity when all PSII reaction centers are open; FM – fresh mass; F_t – fluorescence intensity at t time; LRWC – leaf relative water content; M₀ – approximated initial slope of the fluorescence transient; OEC – oxygen evolving complex; PI_{abs} – dissipated energy flux per reaction center; PQ – plastoquinone; Q_A – primary quinone acceptor; Q_B – secondary quinone acceptor; RC/ABS – electron transport flux per reaction center; RCs – reaction centers; S_m – normalized total complementary area above the OJIP transient; SWC – soil water content; TM – turgid mass; TR₀/RC – quantum yield of dissipation; V_J – relative variable fluorescence intensity at the J-step; W_{OJ} – relative variable fluorescence for the normalization between F₀ and F_J; W_{OK} – relative variable fluorescence for the normalization between F₀ and F_{300μs}; Ψ₀ – lateral reactivity of PSII.

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to PSII reaction centers (RCs) (Souza *et al.* 2004, Akhka 2009). Under drought stress, Chl *a* fluorescence has been used as a rapid, accurate, and nondestructive probe to detect and analyze a function of PSII *in vivo* (Baker 2008, Sperdouli and Moustakas 2012). The analysis of changes in Chl *a* fluorescence induction kinetic curves (OJIP transient) has provided a wealth of detailed information, especially about PSII (Strasser and Srivastava 1995, Longenberger *et al.* 2009).

Plectranthus scutellarioides, a member of the Lamiales family, is native to Indonesia and commonly used as an ornamental plant with changeable leaf color and rich leaf shape (Zhou *et al.* 2011). Although many studies have

reported the effects of drought stress on PSII in different plants, such as barley (Oukarroum and Schansker 2009), *Phaseolus vulgaris* (Terzi *et al.* 2010), and lichen (Komura *et al.* 2010), specific effects of drought stress on fluorescence characteristics of PSII in leaves of *P. scutellarioides* still remains unclear. In the current study, we investigated the effects of drought stress on PSII in the *P. scutellarioides* leaves. Based on associated parameters, we attempted to investigate the changes in fluorescence characteristics of PSII under drought stress and explore the potentially underlying mechanisms for resistance to the drought stress.

Materials and methods

Plant materials and growth conditions: The study was performed in the Jiangsu Academy of Agricultural Science, Nanjing City (31°40'N, 118°30'E), which was located on the plain of the Yangtze River Delta of eastern China. Seeds of *Plectranthus scutellarioides* were initially sowed with a seeding plug under greenhouse conditions (25–28/15–18°C of day/night temperature, natural sunlight, and 65–75% of relative humidity). The 30-d-old seedlings of approximately 10 cm height were transferred to plastic pots (8 L) containing a mixture of peat, garden soil, and perlite (volume ratio of 2:2:1) with one plant per pot. Each pot was weighed at 8:00 and 17:30 h every day and the mass difference was considered as the daily irrigation amount. A total of 100 plants with a similar stem height were selected and randomly divided into two groups (ten replicates of five pots): drought group (DS) and control group. After two weeks of growth, natural drought was simulated by cessation of watering in the DS group, and daily irrigation was performed as before to keep the soil moist in the control group. Plant water status, soil water content, Chl index, and OJIP transient were measured after 0, 5, 10, 15, and 20 d of the treatment (DAT).

Plant water status was estimated as a leaf relative water content (LRWC, [%]) and the soil water content (SWC, [%]). The fresh mass (FM) of the leaves was weighted rapidly after the sampling. The leaves were kept in distilled water for six hours in order to obtain the turgid mass (TM), and dried for 24 h at 80°C to obtain the dry mass (DM). FM, TM, and DM were all presented as average of ten plants. LRWC was calculated as $(FM - DM)/(TM - DM)$.

The SWC was measured using regular gravimetric techniques. Specifically, approximate 10 g of matrix about 5 cm depth in the plastic pots was taken out and weighed in a small aluminum box (M_1); the aluminum box was weighed previously as M_0 . After being dried for 12 h at 105°C, the matrix was weighed in the same aluminum box to obtain the dried mass (M_2). SWC was calculated as $(M_1 - M_2)/(M_1 - M_0) \times 100$.

Chl index and OJIP transient measurements: The Chl index of the third expanded leaf was measured using a non-destructive Chl meter *SPAD-502 Plus* (Konica Minolta Optics, Inc., Osaka, Japan).

A polyphasic OJIP transient was defined by O, J, I, and P steps, corresponding to the redox states of PSII and PSI, and to the efficiencies of electron transfer through the intersystem chain to the end electron acceptors at the PSI acceptor side. A polyphasic OJIP transient included the O to J phase (ending about 2 ms), the J to I phase (ending about 30 ms), and I to P phase (ending about at 600 ms). The photons captured by light-harvesting Chl of PSII were delivered to the RCs which were excited and transferred electron to PSII acceptor, including primary quinone acceptor (Q_A), secondary quinone acceptor (Q_B), and plastoquinone (PQ). The JIP test (Strasser and Strasser 1995), was used to explain the stepwise flow of energy through PSII at the RC level, as well as the level of the PSII cross-section. The fluorescence parameters with the calculation formula and illustrations derived from JIP-test of OJIP transient according to Lazár and Nauš (1998) were:

Fluorescence parameter	Biological significance
F_0	Minimal recorded fluorescence intensity when all PSII RCs are open
F_t	Fluorescence intensity at t time
F_m	Maximal recorded fluorescence intensity when all PSII RCs are closed
$W_{OJ} = (F_t - F_0)/(F_J - F_0)$	Relative variable fluorescence for the normalization between F_0 and F_J
$W_{OK} = (F_t - F_0)/(F_{300\mu s} - F_0)$	Relative variable fluorescence for the normalization between F_0 and $F_{300\mu s}$

Table continues on the next page

Fluorescence parameter	Biological significance
$V_J = (F_J - F_0)/(F_m - F_0)$	Relative variable fluorescence intensity at the J-step
$M_0 = 4(F_{300\mu s} - F_0)/(F_m - F_0)$	Approximated initial slope of the fluorescence transient
$S_m = (\text{Area})/(F_m - F_0)$	Normalized total complementary area above the OJIP transient (reflecting single-turnover Q_A reduction events)
$\phi_{P0} = \text{TR}_0/\text{ABS} = [1 - (F_0/F_m)] = F_v/F_m$	Maximum quantum yield of primary photochemistry (at $t = 0$)
F_v/F_0	Lateral reactivity of PSII
$\Psi_0 = \text{ET}_0/\text{TR}_0 = (1 - V_J)$	Probability that a trapped excitation transfers an electron into the electron transport chain beyond Q_A (at $t = 0$)
$\phi_{E0} = \text{ET}_0/\text{ABS} = [1 - (F_0/F_m)]\Psi_0$	Quantum yield of electron transport (at $t = 0$)
$\phi_{D0} = 1 - \phi_{P0} = F_0/F_m$	Quantum yield of dissipation (at $t = 0$)
$\text{ABS}/\text{RC} = M_0(1/V_J)(1/\phi_{P0})$	Absorption flux per RC
$\text{TR}_0/\text{RC} = M_0(1/V_J)$	Trapped energy flux per RC
$\text{ET}_0/\text{RC} = M_0(1/V_J)\Psi_0$	Electron transport flux per RC
$\text{DI}_0/\text{RC} = \text{ABS}/\text{RC} - \text{TR}_0/\text{RC}$	Dissipated energy flux per RC
$\text{RC}/\text{ABS} = (1/M_0)\phi_{P0}V_J$	Density of RCs based on absorbed energy
$\text{PI}_{\text{abs}} = (\text{RC}/\text{ABS})[\phi_{P0}/(1 - \phi_{P0})][\Psi_0/(1 - \Psi_0)]$	Performance index based on absorption of light energy
$W_k = (F_k - F_0)/(F_J - F_0)$	Ratio of variable fluorescence at K-step to the amplitude $F_J - F_0$
$\text{OEC} = [1 - (V_K - V_J)]_{\text{drought}}/[1 - (V_K - V_J)]_{\text{control}}$	The fraction of OEC in comparison with the control

The OJIP transients were measured at room temperature using a plant efficiency analyzer (*Handy-PEA*, *Hansatech Instruments Ltd.*, King's Lynn, Norfolk, UK) with high-time resolution (10 μs). Before the measurements, ten leaves per treatment were dark-adapted for 20 min using a leaf clip (*Hansatech Instruments Ltd.*, King's Lynn, Norfolk, UK). Light intensity reaching the leaf was 3,000 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$, which was enough to ensure closure of all PSII reaction centers and generate maximal fluorescence for all the treatments. The OJIP transient (F_0 to F_m) was recorded from 10 μs to 1s. The fluorescence intensity at 20 μs (considered as F_0), 100 μs , 300 μs (F_K), 2 ms (F_J), 30 ms (F_I), and maximal fluorescence (considered as F_m) were derived. The relative fluorescence between the step O and K: $W_{OK} = (F_t - F_0)/(F_K - F_0)$, and O and J: $W_{OJ} = (F_t - F_0)/(F_J - F_0)$ were normalized and displayed as $\Delta W_{OK} = W_{OK(\text{drought})} - W_{OK(\text{control})}$ and

$\Delta W_{OJ} = W_{OJ(\text{drought})} - W_{OJ(\text{control})}$ at different treatment time, which made the L-band (at about 120–150 μs) and K-band (at about 200–300 μs) visible, respectively.

Statistical analysis: All statistical tests were performed using a statistical software package *SPSS* for *Windows* (version 13). Normal distribution of data was determined by the *Shapiro-Wilk's W*-test. For data sets with parametric distribution, the *Student's t*-test was performed for determination of the significant differences between treatment means, while differences within group were analyzed with one-way analysis of variance (*ANOVA*). For data sets without parametric distribution, the *Mann-Whitney U*-test and *Kruskal-Wallis H*-test were performed in order to determine the significant differences between treatment means and within group, respectively. $P < 0.05$ was considered statistically significant.

Results

Changes of LRWC, SWC, and leaf Chl index: With increasing treatment duration, LRWC and SWC significantly decreased in the DS plants, while no significant difference was discovered in the control group (Fig. 1A,B). Specifically, there was considerably lower LRWC in the DS group (35%) than that in the control group (83%) after 15 DAT. Besides, SWC dropped to 9% in the DS group compared with 63% in the control group after 20 DAT. Furthermore, leaf Chl index showed a slight increase at 5 DAT and then significantly decreased in the DS group. Leaf Chl index was statistically lower in the DS group (16) than that in the control group (37.1) after 20 DAT (Fig. 1C).

OJIP transient and standardized analysis at different treatment times: The fluorescence intensity in the OJIP transient significantly decreased with increasing treatment

duration in the DS group, while the fluorescence intensity showed no obvious change in the control group (Fig. 2). The relative fluorescence of the L- and K-bands as well as the value of ΔW_{OK} and ΔW_{OJ} , however, obviously increased with the increasing treatment time (Fig. 3).

Changes in fluorescence parameters at different treatment times: The fluorescence intensity in F_0 in the DS group was higher than that in the control group from 10 DAT, and it was 1.45 times higher than that in the control group at 20 DAT (Fig. 4A). F_v/F_m decreased with increasing treatment duration in the DS group and was significantly lower compared with that of control on 15 and 20 DAT (Fig. 4B), and the same as F_v/F_0 (Fig. 4C). Along with the increase of treatment duration, ABS/RC and TR_0/RC increased in the DS group at the earlier stage of the treat-

ment, reaching the peak at 10 DAT, and then decreased, but were still higher compared with that in the control group (Fig. 4D,E). ET_0/RC exhibited a slight elevation after 5 DAT, and then declined continuously in the DS group (Fig. 4F). The change of DI_0/RC was similar with that of ABS/RC and TR_0/RC (Fig. 4G). RC/ABS showed a trend of a gradual decline and reached an obviously different level compared with that of control at 10 DAT (Fig. 4H). The performance index based on absorption of light energy, PI_{abs} , was found to be reduced with the increasing treatment duration (Fig. 4I).

Parameters including S_m , M_0 , Ψ_0 , and Φ_{E0} mainly

Discussion

Many studies have shown that PSII was injured under environmental stresses (Logan 2005). In this study, we explored the drought stress effect on PSII in leaves of *P. scutellarioides* and the potentially underlying mechanism. Results showed that SWC and LRWC significantly decreased in the DS group with increasing treatment duration, as well as the OEC content, while in the early stage of drought, there was no significant decrease of the leaf Chl index in the DS group. Besides, inhibition of electron transport and decrease of PSII photochemical activity were identified as a response to drought stress. Furthermore, PI_{abs} was found to be significantly decreased in the DS group, which might be used as an indicator to determine the extent of drought stress in the leaves.

Water deficit in soil could cause a decrease of LRWC which is related to drought resistance of a plant (Flower and Ludlow 1986). Lawlor and Cornic (2002) have pointed that photosynthesis became irreversibly depressed when LRWC fell to around 60–70%. Consistent with previous study (Flower and Ludlow 1986), the present study showed that LRWC of *P. scutellarioides* significantly decreased to 24% after 15 d under drought stress when PI_{abs} was only 35.3% of that in control, indicating that the activity of PSII RCs was irreversibly damaged. Furthermore, the OEC content was found to be reduced with increasing treatment duration, which also indicated the serious injuries of PSII in *P. scutellarioides* under drought stress. On the other hand, the Chl index was an essential parameter for photosynthesis and was considered as a key factor reflecting a growth state of a plant. A previous study (Akhkha *et al.* 2011) reported a pot experiment in order to evaluate effects of water stress in wheat; the Chl content was found to ascend in the first stage while descend at the last stage under drought. Our result showed that the Chl index ascended in the earlier stage and descended in the later stage under drought stress, which was in accord with the findings and conclusions from previous investigations (Daie 1986).

The OJIP transient and JIP-test are key indicators for studying the response of plants to environmental stress (Baker 2008). It has been reported that drought stress

reflected the change of the PSII acceptor side, and OEC and W_k mainly reflected the change of the PSII donor side. With the treatment duration prolonging, the biggest change among these parameters was in M_0 . M_0 increased and peaked after 15 DAT in the DS group, which was 2.2 times higher in the DS group than that of the control group. S_m , Ψ_0 , and Φ_{E0} were found to be decreasing, while W_k increased, with the treatment duration in the DS group. Besides, the OEC content declined from 5 DAT and reached the minimum at 20 DAT. It was shown that these parameters did not change significantly at different treatment times in the control group (Fig. 5).

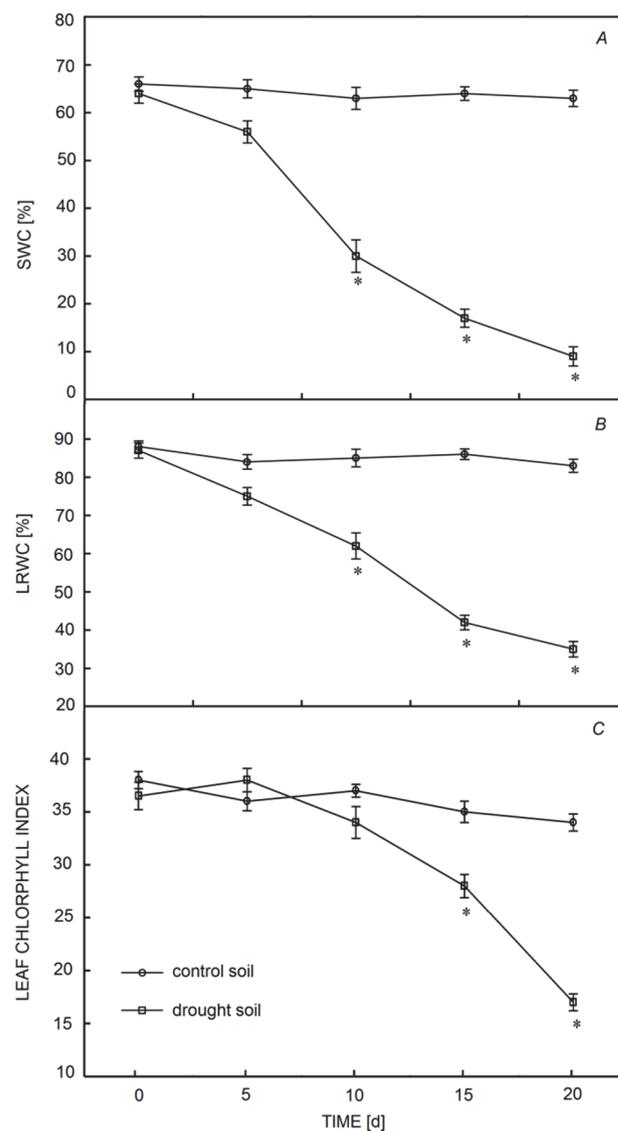


Fig. 1. Changes of soil water content (SWC) (A), leaf relative water content (LRWC) (B), and leaf chlorophyll index (C) in control and drought group at different treatment times. * $P < 0.05$ compared with the control group.

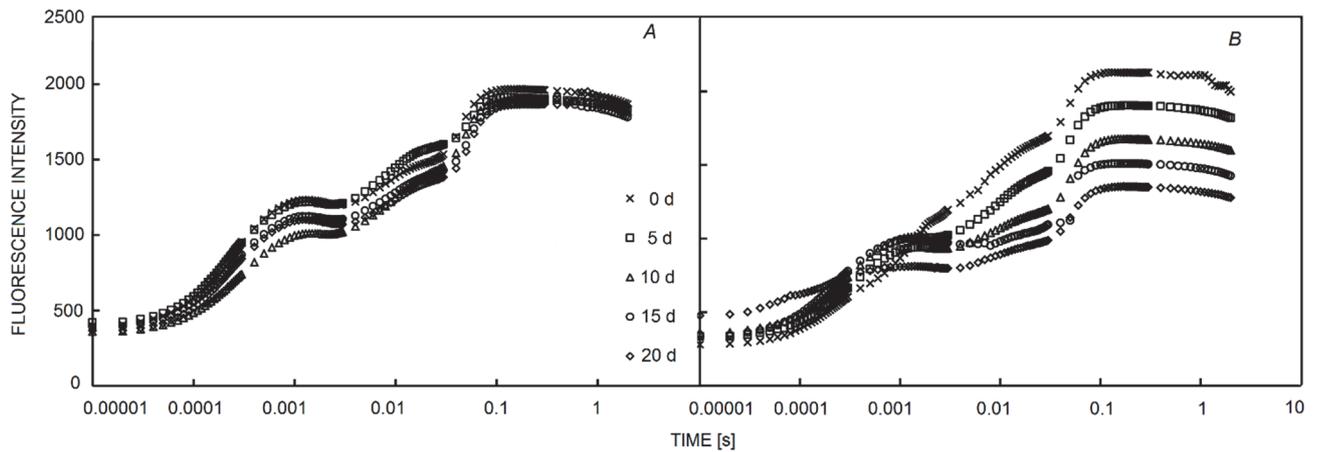


Fig. 2. Chlorophyll *a* fluorescence induction kinetics curves (OJIP transient) in the control group (A) and drought-treated group at different treatment times (B). Each OJIP transient was plotted on a logarithmic time scale from 10 μ s to 2 s.

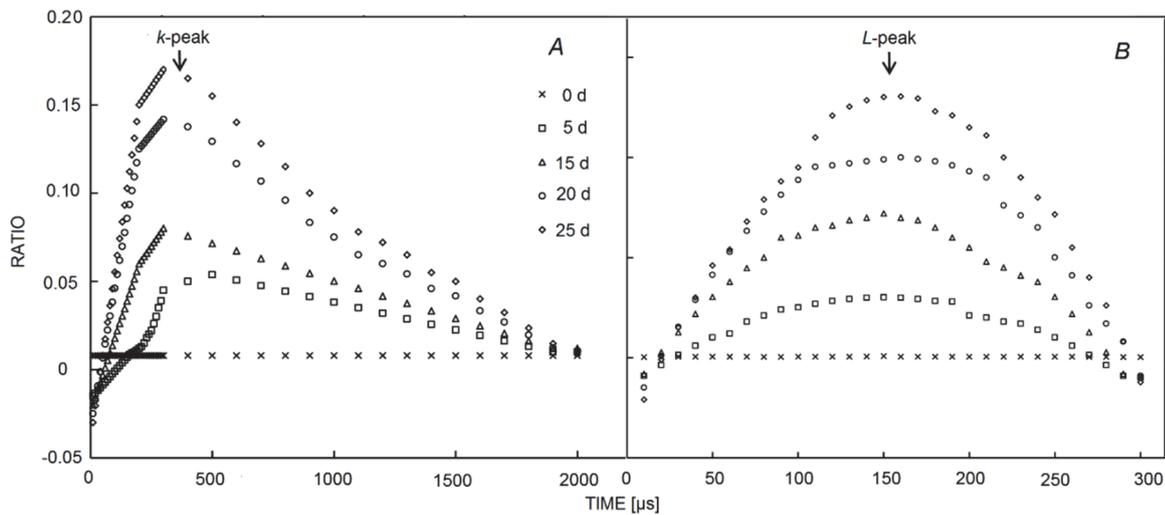


Fig. 3. ΔW_{OJ} (A) and ΔW_{OK} (B) in drought-stressed group at different treatment times. W_{OJ} – relative variable fluorescence for the normalization between F_0 and F_J ; W_{OK} – relative variable fluorescence for the normalization between F_0 and $F_{300 \mu s}$.

could change the characteristic sites of the OJIP transient and reduce fluorescence intensity at the J, I, and P steps (Baker 2008). In the present study, the L peak at about 120–150 μ s became sharp with increasing treatment duration in the DS group, which indicated that the stability and structure of PSII RCs as well as photosynthetic process were influenced. Simultaneously, the appearance of the K peak was observed in the OJIP transient and W_k was found to rise with prolonged treatment duration, which might be induced by OEC inactivation and/or inhibition of electron transport on the donor or acceptor side of PSII (Zhang 1999, Wei *et al.* 2012). The K peak was also found significantly increasing under drought stress, implying OEC of PSII of leaves suffered serious injuries, which was identical with changes in the OEC value (Strasser and Srivastava 1995). Thus, we speculated that the stimulated L and K peaks might be considered as potential indicators for physiological disturbances before appearance of their

visible signs under drought stress.

Additionally, drought stress induced some changes in the JIP parameters. F_v/F_m , as the maximal photochemical efficiency of PSII, was a convenient parameter for reflecting the injury degree of PSII and evaluating its photochemistry (Genty *et al.* 1989). As reported before, the effect of drought stress induced a significant decrease of F_v/F_m only in case of severe drought stress (Souza and Machado 2004). PI_{abs} was a performance index based on the absorption of light energy, which provided useful and quantitative information on the state of plants and their vitality. PI_{abs} was sensitive to changes in the concentration of RC, primary photochemistry, and electron transport. The decrease of PI_{abs} mainly resulted from a reduction of photochemical efficiency or photosynthetic electron transport under drought stress, indicating that the system structure, potential activity of PSII, photoinhibition of photosynthesis, and function of PSII were damaged

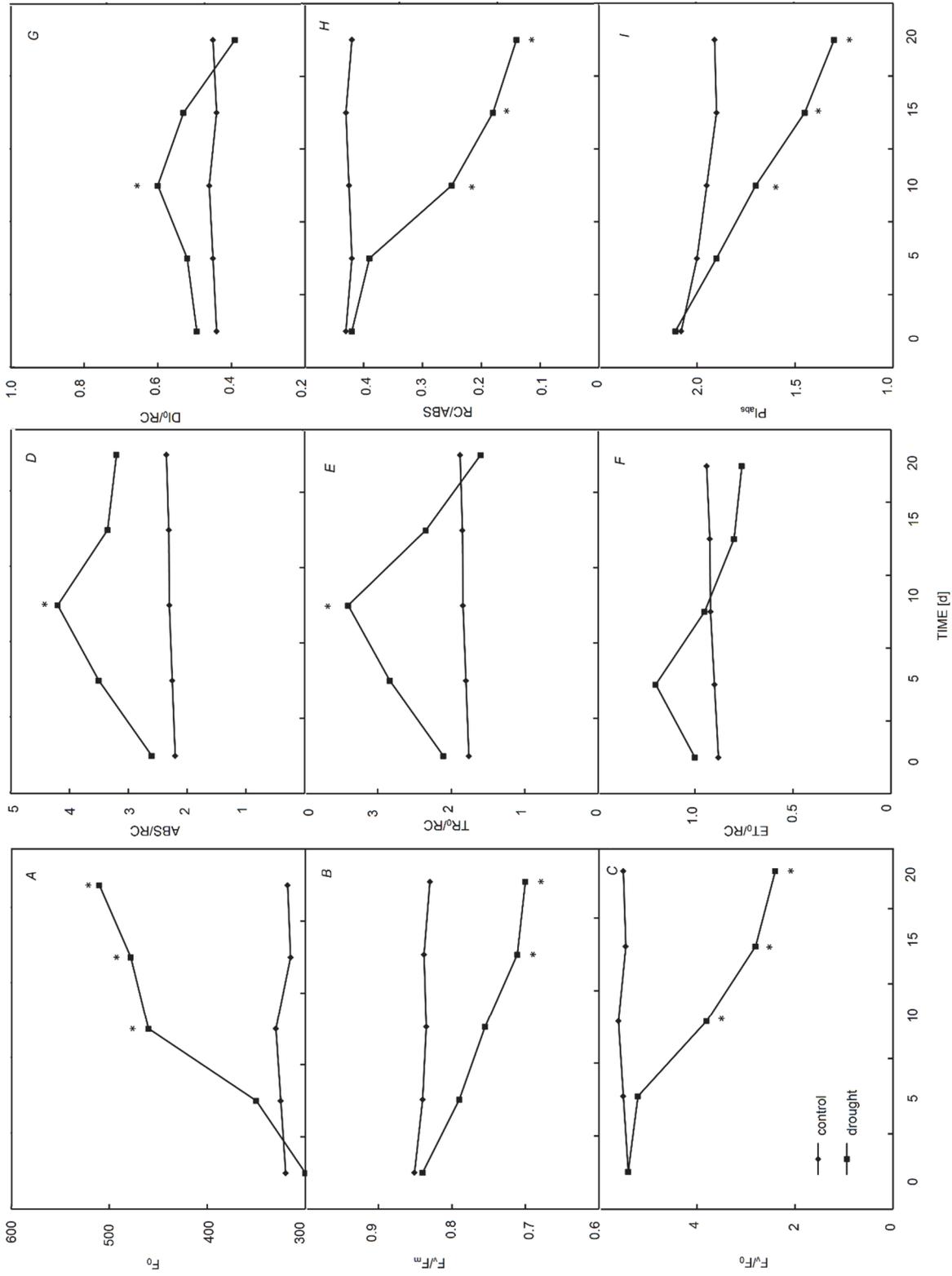


Fig. 4. Chlorophyll *a* fluorescence parameters of F_0 (A), F_v/F_m (B), F_v/F_0 (C), ABS/RC (D), TR_0/RC (E), ET_0/RC (F), Dl_0/RC (G), RC/ABS (H), and Pl_{abs} (I) derived by the JIP-test from OJIP transient in control and drought groups at different treatment times. * - $P < 0.05$ compared with control group. F_0 - minimal fluorescence; F_v/F_m - maximum photochemical efficiency; F_v/F_0 - lateral reactivity; ABS/RC - absorption center per reaction center; TR_0/RC - trapped energy flux per RC; ET_0/RC - electron transport flux per RC; Dl_0/RC - dissipated energy flux per RC; RC/ABS - reaction center per absorption; Pl_{abs} - performance index based on absorption of light energy.

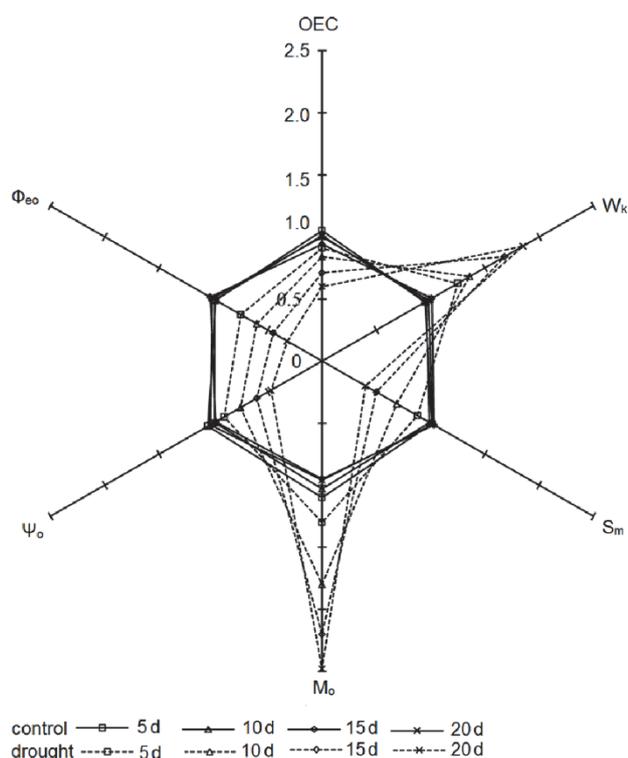


Fig. 5. Radar plot of chlorophyll *a* fluorescence parameters at different treatment times. Each parameter was normalized with a value of control on the day 0. OEC – oxygen evolving complex; S_m – normalized total complementary area above the OJIP transient; M_0 – approximated initial slope of the fluorescence transient; Ψ_0 – probability that a trapped excitation transfers an electron into the electron transport chain beyond Q_A ; Φ_{E0} – quantum yield of electron transport; W_k – ratio of variable fluorescence at K-step to the amplitude $F_J - F_0$.

(Appenroth *et al.* 2003, Ouakroum and Schansker 2009). In accordance with the conclusion of previous studies (Ouakroum *et al.* 2007, van Heerden *et al.* 2004), drought stress-induced changes in PI_{abs} were found to be significant, although a slight decrease of F_v/F_m was observed under drought stress. Thus, we inferred that the decrease of F_v/F_m

References

- Akhkha A.: The effect of water stress on photosynthesis, respiration and relative chlorophyll index of the desert plant *Calotropis procera*. – *Asian Biosci. Biotechnol. Res.* **6**: 653-658, 2009.
- Akhkha A., Boutraa T., Alhejely A.: The rates of photosynthesis, chlorophyll content, dark respiration, proline and abscisic acid (ABA) in wheat (*Triticum durum*) under water deficit conditions. – *Int. J. Agric. Biol.* **13**: 215-221, 2011.
- Appenroth K.J., Keresztes A., Sárvári E. *et al.*: Multiple effects of chromate on *Spirodela polyrhiza*: electron microscopy and biochemical investigations. – *Plant. Biol.* **5**: 315-323, 2003.
- Ashraf M., Foolad M.: Roles of glycine betaine and proline in improving plant abiotic stress resistance. – *Environ. Exp. Bot.* **59**: 206-216, 2007.
- Baker N.R.: Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. – *Annu. Rev. Plant. Biol.* **59**: 89-113, 2008.
- Centritto M., Loreto F., Chartzoulakis K.: The use of low $[CO_2]$ to estimate diffusional and non-diffusional limitations of photosynthetic capacity of salt-stressed olive saplings. – *Plant. Cell. Environ.* **26**: 585-594, 2003.
- Daie J.: C4 grasses and cereals: Growth, development, and stress response. – *Soil Sci.* **142**: 242, 1986.
- Ekmekci Y., Bohms A., Thomson J.A. *et al.*: Photochemical and antioxidant responses in the leaves of *Xerophyta viscosa* Baker and *Digitaria sanguinalis* L. under water deficit. – *Z. Naturforsch.* **60**: 435-443, 2005.

and PI_{abs} , especially PI_{abs} , may be also considered as a potential indicator for effects of drought stress before appearance of visible physiological disturbances.

Electron transport and energy transformation were influenced owing to damage to PSII RCs under drought stress. Some JIP parameters were calculated in order to identify the damage site on the acceptor side of PSII, such as energy absorption, energy trapping, and electron transport (Strasser *et al.* 2004). For example, among the specific fluxes per RC, ABS/RC , TR_0/RC , and DI_0/RC were higher under drought stress than that of control. These results indicated some RCs were inactive and the efficiency per RC was enhanced. The increase of absorbed and trapped energy did not result in the increase of electron transport energy ET_0/RC , but a sharp increase in DI_0/RC , implying most energy was dissipated in a heat form. It was also a self-protection mechanism of plant leaves under drought conditions (Monneveux *et al.* 2003). M_0 significantly increased and Ψ_0 and Φ_{E0} declined steadily at the later phase of the treatment, induced by inhibition of electron transport of $Q_A - Q_B$ and Q_A accumulation, which may explain why the proportion of opened PSII RCs and the number of electron used to carbon fixation was reduced and why the energy dissipated by heat increased. Interestingly, ABS/RC , TR_0/RC , DI_0/RC , and even ET_0/RC in the DS plants were also increasing at the first stage of the treatment, reaching the peak after 10 DAT, and then decreased. Therefore, we speculate that *P. scutellarioides* might resist drought stress in order to maintain the growth state *via* inhibition of electron transport and decrease of PSII photochemical activity during the earlier stage of stress.

From these results we concluded that drought stress considerably decreased the fluorescence characteristics of PSII in leaves. *P. scutellarioides* responded to the drought stress *via* inhibition of electron transport and decrease of PSII photochemical activity. Findings of this study might contribute to our understanding of the drought stress effect on PSII in leaves of *P. scutellarioides*, as well as the underlying mechanisms.

- Flower D., Ludlow M.: Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeon pea (*Cajanus cajan* (L.) millsp.) leaves. – *Plant. Cell. Environ.* **9**: 33-40, 1986.
- Genty B., Briantais J.M., Baker N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – *Biochim. Biophys. Acta* **990**: 87-92, 1989.
- Komura M., Yamagishi A., Shibata Y. *et al.*: Mechanism of strong quenching of photosystem II chlorophyll fluorescence under drought stress in a lichen, *Physciella melanchla*, studied by subpicosecond fluorescence spectroscopy. – *BBA-Bioenergetics* **1797**: 331-338, 2010.
- Lawlor D., Cornic G.: Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. – *Plant Cell Environ.* **25**: 275-294, 2002.
- Lazár D., Nauš J.: Statistical properties of chlorophyll fluorescence induction parameters. – *Photosynthetica* **35**: 121-127, 1998.
- Logan B.A.: Chlorophyll *a* fluorescence: a signature of photosynthesis. – *J. Torrey. Bot. Soc.* **132**: 650-652, 2005.
- Longenberger P.S., Smith C., Duke S. *et al.*: Evaluation of chlorophyll fluorescence as a tool for the identification of drought tolerance in upland cotton. – *Euphytica* **166**: 25-33, 2009.
- Monneveux P., Pastenes C., Reynolds M.P.: Limitations to photosynthesis under light and heat stress in three high-yielding wheat genotypes. – *J. Plant Physiol.* **160**: 657-666, 2003.
- Oukarroum A., Schansker G., Strasser R.J.: Drought stress effects on photosystem I content and photosystem II thermotolerance analyzed using Chl *a* fluorescence kinetics in barley varieties differing in their drought tolerance. – *Physiol. Plantarum* **137**: 188-199, 2009.
- Oukarroum A., Madidi S.E., Schansker G. *et al.*: Probing the responses of barley cultivars (*Hordeum vulgare* L.) by chlorophyll *a* fluorescence OLKJIP under drought stress and re-watering. – *Environ. Exp. Bot.* **60**: 438-446, 2007.
- Ranjbarfordoei A., Samson R., Lemeur R. *et al.*: Effects of osmotic drought stress induced by a combination of NaCl and polyethylene glycol on leaf water status, photosynthetic gas exchange, and water use efficiency of *Pistacia khinjuk* and *P. mutica*. – *Photosynthetica* **40**: 165-169, 2002.
- Shao H.B., Chu L.Y., Jaleel C.A. *et al.*: Understanding water deficit stress-induced changes in the basic metabolism of higher plants-biotechnologically and sustainably improving agriculture and the environment in arid regions of the globe. – *Crit. Rev. Biotechnol.* **29**: 131-151, 2009.
- Souza R., Machado E., Silva J. *et al.*: Photosynthetic gas exchange, chlorophyll fluorescence and some associated metabolic changes in cowpea (*Vigna unguiculata*) during water stress and recovery. – *Environ. Exp. Bot.* **51**: 45-56, 2004.
- Sperdoui I., Moustakas M.: Interaction of proline, sugars, and anthocyanins during photosynthetic acclimation of *Arabidopsis thaliana* to drought stress. – *J. Plant Physiol.* **169**: 577-585, 2012.
- Strasser B.J., Strasser R.J.: Measuring fast fluorescence transients to address environmental questions: the JIP-test. – In: Mathis P. (ed.): *Photosynthesis: From Light to Biosphere*. Pp. 977-980. Kluwer Academic Publishers, Dordrecht 1995.
- Strasser R.J., Tsimilli-Michael M., Srivastava A.: Analysis of the chlorophyll *a* fluorescence transient. – In: Papageorgiou G.C., Govindjee (ed.): *Chlorophyll *a* Fluorescence. Advances in Photosynthesis and Respiration*. Pp. 321-362. Springer, Dordrecht 2004.
- Strasser R.J., Srivastava A.: Polyphasic chlorophyll *a* fluorescence transient in plants and cyanobacteria. – *Photochem. Photobiol.* **61**: 32-42, 1995.
- Terzi R., Saglam A., Kutlu N. *et al.*: Impact of soil drought stress on photochemical efficiency of photosystem II and antioxidant enzyme activities of *Phaseolus vulgaris* cultivars. – *Turk. J. Bot.* **34**: 1-10, 2010.
- van Heerden P.D., Strasser R.J., Krüger G.H.: Reduction of dark chilling stress in N₂-fixing soybean by nitrate as indicated by chlorophyll *a* fluorescence kinetics. – *Physiol. Plantarum* **121**: 239-249, 2004.
- Wei X., Chen G., Shi D. *et al.*: Effects of drought on fluorescence characteristics of photosystem II in leaves of *Ginkgo biloba*. – *Acta Ecol. Sinica* **32**: 7492-7500, 2012.
- Zhang S.R.: [A discussion on chlorophyll fluorescence kinetics parameters and their significance.] – *Chinese B. Bot.* **16**: 444-448, 1999. [In Chinese]
- Zhou H.G., Wang W.T.: [Classification of *Coleus* cultivars and their application in landscape.] – *Guangdong Landsc. Arch.* **3**: 57-61, 2011. [In Chinese]
- Zushi K., Matsuzoe N., Kitano M.: Developmental and tissue-specific changes in oxidative parameters and antioxidant systems in tomato fruits grown under salt stress. – *Sci. Hortic.-Amsterdam* **122**: 362-368, 2009.