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Effects of Drought Stress and Rewatering on the Photosynthetic Physiology of Rice Seedlings

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Abstract

To clarify the photosynthetic and physiological responses of rice seedlings to drought stress and subsequent rewatering, four rice cultivars (HHZ, PH34, WGZ, and LD24) were employed as experimental materials. Three water treatments were applied, including a well-watered control (CK), drought stress (DS), and rewatering (RW) following drought exposure. This study focused on leaf chlorophyll content and quantified variations in photosystem II (PSII) functionality using the JIP-test to analyze rapid chlorophyll a fluorescence induction kinetics (OJIP transients). Drought stress significantly reduced leaf chlorophyll content; while rewatering partially restored chlorophyll levels, they remained significantly lower than those in the control group. Distinct treatment-specific differences were observed in the OJIP curves after the J step: in both the DS and RW groups, the ascending trends of the J-I and I-P phases were attenuated, with the fluorescence intensity from the I to P phase being markedly lower than that in the CK group. This reduction was most prominent under drought stress conditions. The occurrence of distinct L-, K-, and J-bands in the differential curves indicated damage to the oxygen-evolving complex (OEC) and impaired electron donation on the donor side of PSII. Furthermore, both drought stress and rewatering decreased V_j and F_v/F_m values, as well as the performance indices reflecting overall PSII activity (PI_{abs}, PI_{total}) and energy distribution per cross-section (TR_o/CS_o, ET_o/CS_o). In contrast, ABS/RC, DI_o/RC, ET_o/RC, and TR_o/RC were elevated, whereas RC/CS_m was reduced. These changes suggested an accumulation of inactivated reaction centers and an increased excitation load on the remaining active reaction centers. Collectively, these results demonstrate that drought stress strongly inhibits the photosynthetic function of rice seedlings by impairing photoprotective mechanisms and damaging PSII reaction centers, thereby restricting seedling growth. Although rewatering triggers partial physiological compensation, the photosynthetic capacity fails to fully recover to the normal level after severe drought stress.

Keywords

Rice, Drought Stress, Rewatering, Photosystem II, OJIP Transient

1. Introduction

Global climate change is increasing both the frequency and intensity of extreme drought events, thereby exacerbating abiotic constraints on crop production systems [1] [2]. Drought disrupts plant water balance, suppresses key metabolic processes and impedes growth and development. It has become one of the major factors limiting crop yield and quality, and a serious threat to global food security. Dissecting the physiological mechanisms by which crops respond to drought stress is therefore critical for designing climate resilient agricultural strategies and ensuring sustainable grain production [3] [4].

Rice is the staple food for more than half of the world's population, and the drought resilience of rice production systems is of paramount importance. However, due to its physiological characteristics, rice is highly sensitive to water deficit [5] [6]. Drought frequently impairs its photosynthetic machinery, reducing assimilate accumulation and ultimately yield. In particular, understanding how the photosynthetic apparatus, especially photosystem II (PSII)—responds dynamically to drought and subsequent rewatering is essential for clarifying the physiological basis of drought tolerance and for guiding drought resilient breeding and cultivation practices.

Photosynthesis provides the material and energy foundation for crop yield formation. PSII is the primary site of photochemical charge separation and the initiation point of the photosynthetic electron transport chain, and is also one of the components most sensitive to environmental stress [7] [8]. Chlorophyll fluorescence techniques, especially rapid chlorophyll a fluorescence induction kinetics (OJIP transients) and the associated JIP-test, allow noninvasive and real-time monitoring of the full sequence of events in PSII reaction centers, from light absorption to electron transport and energy conversion. By analyzing key fluorescence parameters such as the maximum quantum efficiency of PSII (F_v/F_m), the performance index (PI_{abs}) and the energy fluxes per reaction center (e.g. ABS/RC, TR_o/RC, ET_o/RC), the functional status of the donor side, reaction center and acceptor side of PSII can be precisely diagnosed. These tools have become powerful methods for evaluating plant stress physiology and for early detection of environmental constraints [9] [10].

Previous studies have shown that drought stress affects PSII function in rice through multiple mechanisms. It can initially impair the activity of the oxygen evolving complex (OEC), thereby hampering water splitting and electron donation [11] [12]. Drought may also cause reversible inactivation or irreversible damage of PSII reaction centers, leading to blockage of electron transport. In addition, drought disturbs excitation energy allocation, enhances non-photochemical quenching and induces photoinhibition [13] [14]. At the fluorescence level, these lesions are typically manifested as decreases in F_v/F_m and PI_{abs}, accompanied by increases in ABS/RC and TR_o/RC, which often reflect a reduction in the number of active reaction centers and a higher excitation burden on those remaining [15]. Rewatering offers an opportunity to assess the repair capacity of the photosynthetic apparatus; however, part of the drought-induced damage may be irreversible, and the rate and extent of recovery are key indicators of varietal drought tolerance. Although OJIP-based approaches have been applied to evaluate drought tolerance in rice, most studies have focused on single stress levels or specific growth stages and have often been limited to static observations. Systematic investigations of the dynamic responses and recovery patterns of PSII function in rice seedlings under progressive soil drying and subsequent rewatering remain scarce. In particular, a quantitative dissection of the energy fluxes through discrete PSII modules using the JIP-test, integrated with morphological and physiological traits to explain varietal differences in drought tolerance, is still lacking [16]-[19].

In this study, rice cultivars with contrasting drought tolerance were grown in pots under controlled water regimes to simulate progressive soil drought followed by rewatering. By dynamically recording OJIP transients and conducting JIP-test analysis, we aimed to: 1) characterize the temporal dynamics and damage sites of PSII light harvesting, electron transport, and energy conversion under drought stress; 2) evaluate the recovery capacity and limiting factors of PSII function after rewatering; and 3) elucidate the photosynthetic physiological mechanisms underlying cultivar-specific differences in drought responses. This work seeks to deepen our understanding of drought stress and subsequent recovery in rice seedlings from the perspective of photosynthetic energy fluxes, while providing sensitive physiological indicators and theoretical support for drought tolerance assessment and genetic improvement of rice. To further clarify the photosynthetic and physiological responses of rice seedlings to drought stress and rewatering, four rice cultivars (HHZ, PH34, WGZ, and LD24) were employed as experimental materials. Three water treatments were applied, including a well-watered control (CK), drought stress (DS), and rewatering (RW) following drought exposure. This study focused on leaf chlorophyll content and quantified variations in photosystem II (PSII) functionality using the JIP-test to analyze rapid chlorophyll a fluorescence induction kinetics (OJIP transients).

2. Materials and Methods

2.1. Experimental Materials and Design

The experiment was carried out in the Smart Crop Factory of the College of Agriculture, Fujian Agriculture and Forestry University, under controlled environmental conditions with an average temperature of 28˚C and relative humidity of 70%. Four rice cultivars, namely HHZ, PH34, WGZ, and LD24, were provided by the Fujian Provincial Engineering Technology Research Center for Special Crop Breeding and Utilization. Paddy soil (moisture content: 31.00%, pH ≈ 5.6) was used as the base substrate, and a mixture of paddy soil and commercial nutrient soil at a ratio of 3:1 was prepared for seedling transplantation. To clarify the photosynthetic and physiological responses of rice seedlings to drought stress and subsequent rewatering, these four cultivars were employed as experimental materials. Three water treatments were applied, including a well-watered control (CK), drought stress (DS), and rewatering (RW) following drought exposure. This study focused on leaf chlorophyll content and quantified variations in photosystem II (PSII) functionality using the JIP-test to analyze rapid chlorophyll a fluorescence induction kinetics (OJIP transients).

Three water treatments were imposed: well watered control (normal, moisture content is maintained at 80% ± 5% of the field water-holding capacity), drought stress (DS, moisture content is maintained at 40% ± 5% of the field water-holding capacity) and rewatering. For the drought treatment, irrigation was stopped when the seedlings had recovered from transplanting and reached the four leaf one heart stage. Plants were monitored daily between 11:00 and 12:00. When a portion of leaves exhibited visible drought symptoms yellowing, wilting and curling the plants were considered to have reached the drought stress point. At this time, measurements were taken, after which the pots were thoroughly irrigated to initiate the rewatering treatment, and no further water was supplied thereafter. Morphological indices were measured again 5 days after rewatering.

2.2. Measurements and Methods

2.2.1. Determination of Morphological Parameters

From each treatment, three pots were randomly sampled, and three uniformly growing seedlings with similar vitality were measured per pot. Plant height, leaf length and leaf width were recorded, and leaf area was estimated by applying the leaf area coefficient.

2.2.2. SPAD Readings and Chlorophyll Content

Relative chlorophyll content was assessed using a SPAD 502 chlorophyll meter (Konica Minolta, Japan). For each treatment, three plants with uniform growth were selected per pot. On each plant, four leaves were chosen, and three positions per leaf were measured three times; the mean SPAD value was recorded.

For total chlorophyll, 0.2 g of functional leaf tissue was rapidly sampled and placed into a 10 mL centrifuge tube. An appropriate volume of 95% ethanol was added to fully immerse the leaves. Samples were extracted in darkness at 4˚C for 48 h, with intermittent shaking to ensure complete pigment extraction. Absorbance of the extracts was determined at 665 nm and 649 nm using a spectrophotometer. Each sample was measured in triplicate, and mean values were used to calculate total chlorophyll content according to standard equations.

2.2.3. OJIP Transients and Chlorophyll Fluorescence Parameters

Chlorophyll fluorescence was measured using a Handy PEA portable plant efficiency analyzer (Hansatech Instruments, UK). Prior to measurement, leaves were dark-adapted for 30 min. For each treatment, three uniformly growing plants were selected per pot, and four leaves per plant were measured. On each leaf, three positions were selected and measured three times.

OJIP transients were recorded, and the following fluorescence parameters were obtained via JIP-test: initial fluorescence (F_o), maximum fluorescence (F_m), variable fluorescence (F_v) and derived ratios F_o/F_m, F_v/F_m and F_v/F_o; V_j and S_m, which reflect electron transport characteristics; energy fluxes per reaction center (ABS/RC, TR_o/RC, ET_o/RC, DI_o/RC); energy fluxes per cross-section (TR_o/CS_o, ET_o/CS_o, DI_o/CS_o, RE_o/CS_o); and comprehensive performance indices (PI_{abs}, PI_{total}). These parameters include both directly measured raw fluorescence values and physiological parameters calculated from them.

To further dissect PSII behavior at different phases of the fluorescence induction, the OJIP curves were normalized at multiple time points: 50 μs (O step), 300 μs (K step), 2 ms (J step), 30 ms (I step) and the time of maximum fluorescence (P step). This multi-time-point normalization was used to analyze PSII light energy utilization and electron transport characteristics at distinct stages.

2.3. Data Processing and Statistical Analysis

Data were analyzed using IBM SPSS Statistics 27. One way ANOVA was performed followed by LSD tests to assess significant differences among treatments. Figures were generated using Microsoft Excel 2016 and Origin 2025.

3. Results and Analysis

3.1. Effects of Drought Stress and Rewatering on Morphological Parameters of Rice Seedlings

The dynamic changes of morphological indexes of rice after CK (normal), drought and rehydration treatment are shown in Table 1.

Drought treatment caused declines in leaf length, leaf width, leaf area, and plant height across all rice materials, which recovered after rehydration. As shown in Table 1, the drought tolerance varied significantly among materials. Compared to the control group (CK), all four rice materials exhibited reduced leaf length, width, and plant height post-drought. Following rehydration, all four materials showed rebounding increases in leaf length, width, plant height, and leaf area, with the experimental material WGZ demonstrating the most pronounced recovery in leaf length and width. Overall, drought treatment significantly affected leaf dimensions and plant height, but rehydration restored all morphological traits, though the recovery varied among drought-tolerant rice types.

Table 1. Effects of drought stress and rewatering on morphological parameters of rice seedlings.

Material	Treatment	Morphological indices ($\overline{X} \pm SD$)			
		Leaf length	Leaf width	Leaf area	Plant height
HHZ	CK	25.68 ± 3.63a	0.64 ± 0.02a	13.70 ± 2.82a	35.47 ± 4.39a

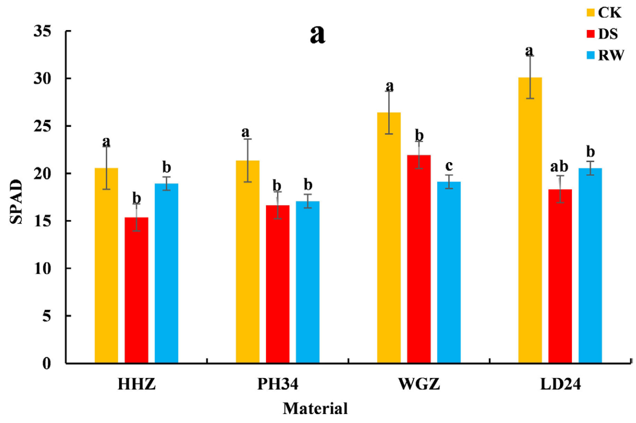
Continued

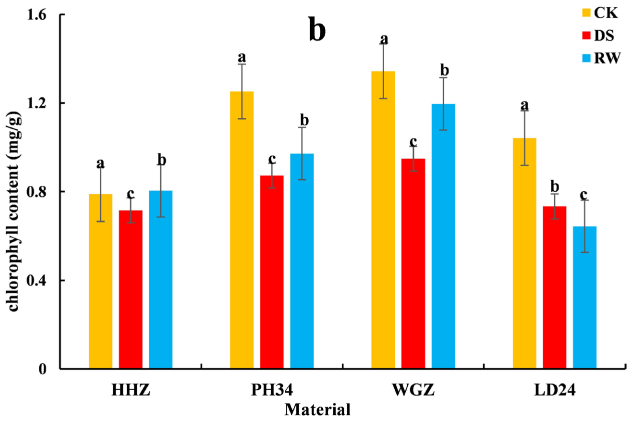
	Drought stress	13.23 ± 1.58c	0.36 ± 0.04c	4.36 ± 1.22c	27.63 ± 3.11b
	Rewatering	19.34 ± 5.67b	0.38 ± 0.05b	7.82 ± 2.11b	30.05 ± 3.15b
PH34	CK	25.86 ± 1.97a	0.61 ± 0.02a	13.25 ± 1.75a	35.59 ± 2.12a
	Drought stress	14.34 ± 2.08b	0.36 ± 0.01c	4.63 ± 0.87c	27.78 ± 3.00ab
	Rewatering	20.49 ± 5.13c	0.46 ± 0.04b	8.05 ± 1.41b	30.34 ± 2.13b
WGZ	CK	16.51 ± 2.17b	0.52 ± 0.02ab	7.49 ± 0.92b	28.79 ± 1.33a
	Drought stress	14.28 ± 2.11b	0.49 ± 0.03b	6.36 ± 1.11b	25.96 ± 2.03a
	Rewatering	21.60 ± 2.97a	0.56 ± 0.03a	10.32 ± 1.35a	27.30 ± 2.36a
LD24	CK	22.99 ± 1.45a	0.55 ± 0.08a	10.89 ± 2.66a	27.96 ± 3.55a
	Drought stress	17.54 ± 2.43b	0.28 ± 0.09c	4.53 ± 2.16b	25.55 ± 1.58b
	Rewatering	17.58 ± 1.45b	0.42 ± 0.02b	6.52 ± 1.01b	26.70 ± 1.44b

Note: In the same column, different lowercase letters denote statistically significant disparities among various treatment groups at the identical time point ($P < 0.05$). All data are expressed as mean ± standard error with three replicates ($n = 3$); The letters used for comparison are not applicable across distinct test materials. Abbreviations: CK: control group, DS: drought stress treatment, RW: rewatering treatment.

3.2. Effects of Drought and Rewatering on Relative and Absolute Chlorophyll Content in Rice Leaves

As shown in **Figure 1**, chlorophyll content declined after drought treatment in all cultivars, with WGZ exhibiting the smallest reduction. Rewatering led to partial recovery of chlorophyll content, but in none of the cultivars did levels return to those of the well watered control. Among the cultivars, HHZ showed the greatest recovery after rewatering, with chlorophyll content increasing by 28.75% relative to the drought-stressed level. LD24 was more strongly affected by drought, and its chlorophyll content after rewatering remained lower than under drought alone. Compared with CK, SPAD values in the four cultivars decreased by 17.09%, 12.52%, 11.61% and 15.85%, respectively, following drought stress. After rewatering, SPAD values partially recovered but remained below the control in all cases. These results indicate that drought stress causes substantial damage to leaf chlorophyll apparatus in rice, as reflected by reduced SPAD readings.





Note: Different lowercase letters above the bars in the bar charts indicate significant differences ($P < 0.05$) among treatment combinations based on Duncan's test. Values are presented as mean ± SE (n = 3). The error bars denote standard deviation. CK: Control. DS: Drought stress. RW: Rewatering.

Figure 1. Effects of drought stress and rewatering on relative and absolute chlorophyll content in rice leaves.

3.3. Effects of Drought Stress and Rewatering on OJIP Transients in Rice

The dynamic changes in OJIP transients of rice leaves under CK, drought and rewatering treatments are shown in Figure 2. Rapid chlorophyll fluorescence represents the time-dependent changes in fluorescence intensity emitted by chlorophyll a molecules after dark adapted leaves are exposed to strong actinic light, and serves as an effective probe of PSII reaction center activity and electron transport efficiency.

In this study, OJIP transients were recorded from fully dark-adapted leaves and the corresponding parameters were analyzed. All treatments displayed typical OJIP induction curves. Fluorescence intensity at the O step (50 μs) was similar among treatments, with negligible differences. As induction progressed to the J step (2 ms), fluorescence in CK, drought and rewatering groups increased, and intensities at the I and P steps were substantially higher than at the O and J steps. Overall, the rise in the O-J segment was more gradual than in the I-P segment. Relative to CK, however, the J-I and I-P phases in the drought and rewatering groups exhibited a markedly slower increase and a reduced amplitude. For all four cultivars, fluorescence intensity from the I to P steps was significantly lower under drought and rewatering than in CK, with the overall decline in the OJIP curves being most pronounced under drought stress. These observations indicate that drought stress causes pronounced damage to the photosynthetic system of rice, reducing light energy conversion efficiency and suppressing photosynthesis. Although rewatering partially alleviated the effects of drought, photosynthetic function did not fully recover to control levels. Notably, in PH34 and WGZ, the rise from O to J was higher under rewatering than in CK, likely reflecting a transient photosynthetic compensation effect once favorable water conditions were restored.

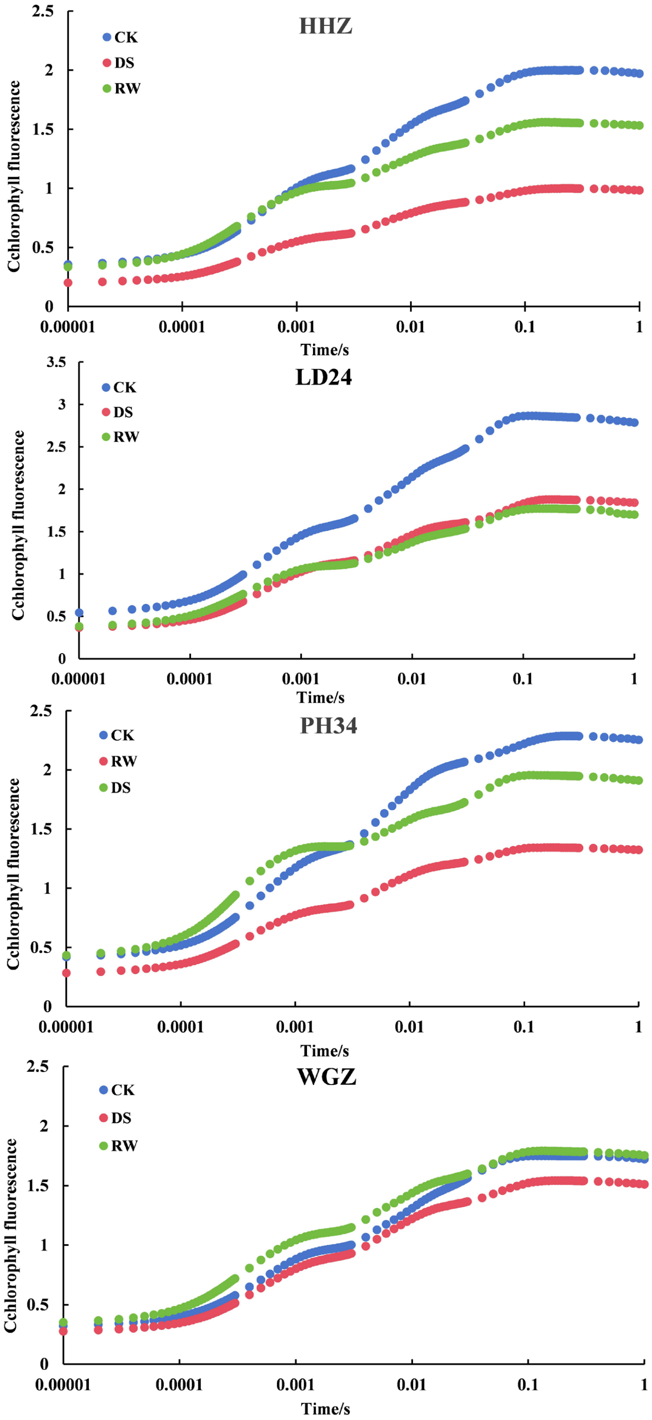


Figure 2. Changes in rapid chlorophyll fluorescence induction kinetics (OJIP transients) in rice under drought stress and rewatering.

To further elucidate the mechanisms underlying treatment-dependent differences in fluorescence dynamics and to compare responses among phases of the OJIP transient, we performed differential analyses of the OJIP curves for two contrasting cultivars, HHZ and LD24. This approach facilitates detection of subtle changes in transition regions of the curve and provides a basis for evaluating the effects of drought stress and rewatering on photosynthetic function.

In OJIP based studies, the L-, K- and J-bands in differential curves are widely used to infer structural and functional changes in PSII. The L-band primarily reflects the structural integrity of thylakoid membranes and the degree of energetic connectivity among PSII units. The K-band is closely associated with the functional status of the OEC, while the J-band indicates the efficiency of electron transport from the primary quinone acceptor Q_A to the secondary acceptor Q_B on the PSII acceptor side. Together, these indices provide important tools for assessing drought tolerance and recovery potential in rice.

As shown in **Figure 3**, ΔWL (L-band), ΔWK (K-band) and ΔWJ (J-band) all increased to varying degrees in HHZ and LD24 following drought and rewatering, indicating disrupted energy transfer across thylakoid membranes and impaired connectivity among PSII reaction centers. The K-band increased more strongly in HHZ than in LD24, suggesting more severe OEC damage and more pronounced restriction of electron donation from water. Both cultivars exhibited a pronounced J-band, implying that under drought and rewatering, reduced Q_A (Q_{A-}) was not efficiently re-oxidized by Q_B, leading to accumulation of Q_{A-} and decreased electron transport efficiency on the PSII acceptor side.

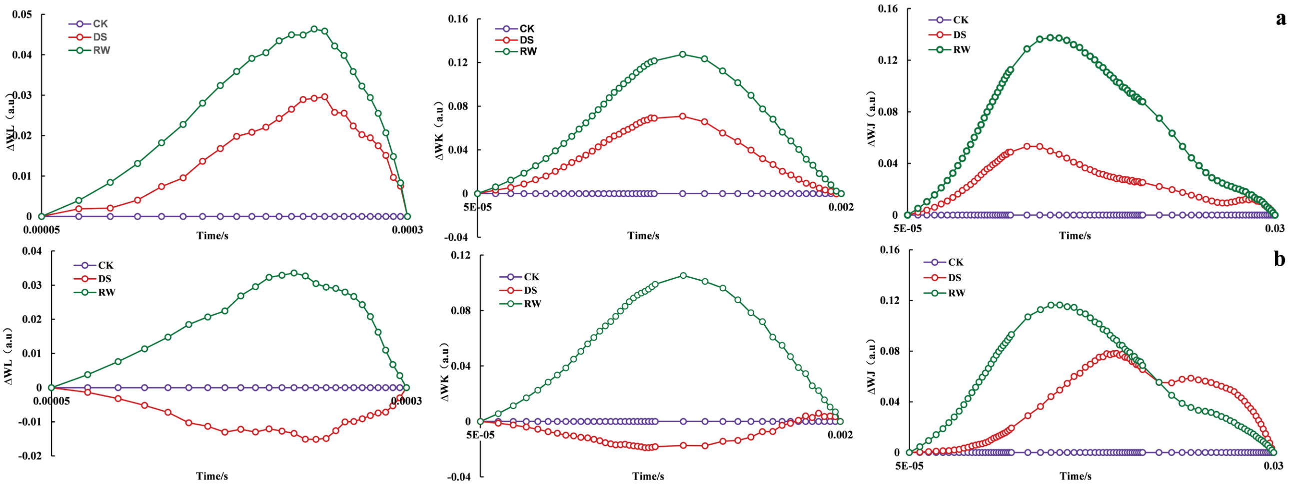
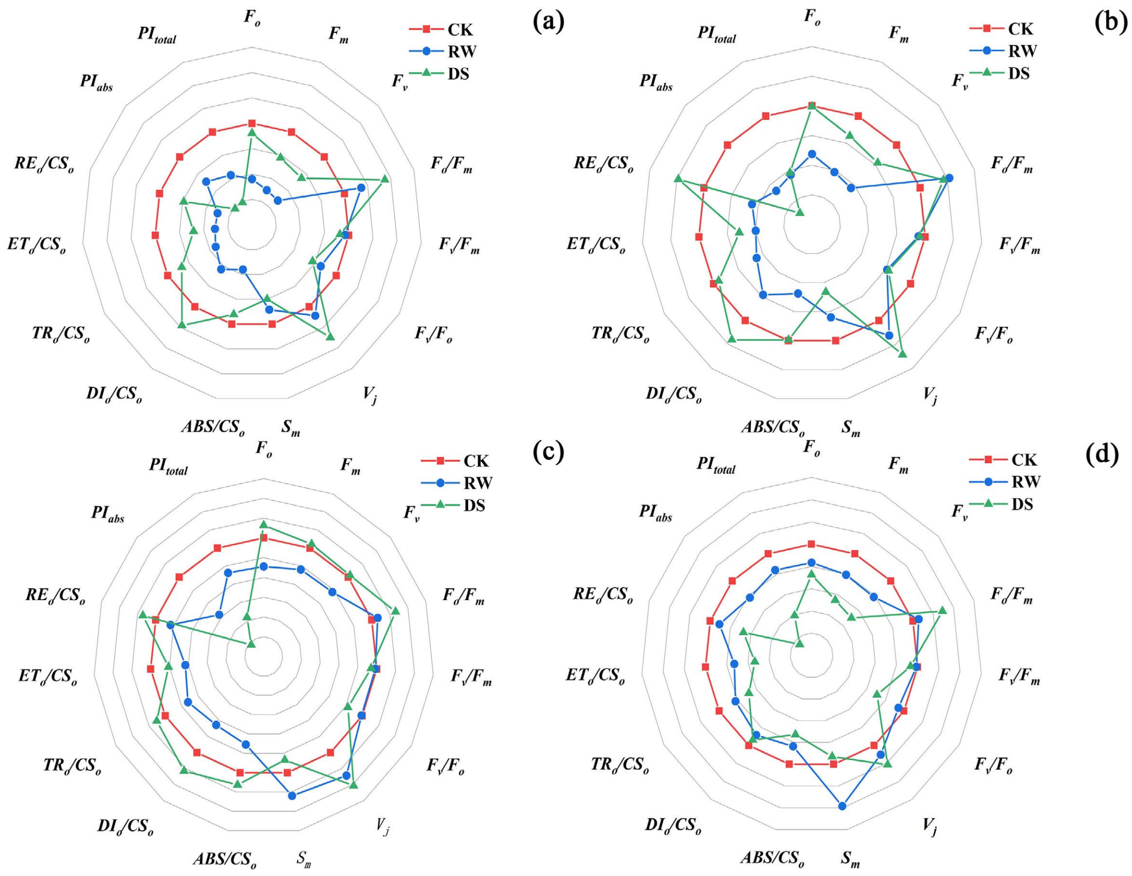


Figure 3. Differential changes in ΔWL (L-band), ΔWK (K-band) and ΔWJ (J-band) in rice leaves under drought stress and rewatering.

3.4. Effects of Drought Stress and Rewatering on Chlorophyll Fluorescence Kinetic Parameters

To gain deeper insight into how drought and rewatering affect the photosynthetic electron transport chain, we applied JIP-test analysis to derive fluorescence kinetic parameters, including F_v/F_m, V_J, S_m, PI_{abs}, PI_{total}, TR_o/CS_o, ET_o/CS_o, DI_o/CS_o and RE_o/CS_o. These parameters provide a comprehensive view of PSII electron transport under different treatments. As shown in **Figure 4**, the relative variable fluorescence at the J step (V_J) tended to decrease under drought and rewatering. This pattern reflects perturbations in PSII reaction center function, likely involving impaired electron transfer from Q_A to Q_B and consequent closure of reaction centers. Drought stress may also compromise OEC activity, suppressing water photolysis and limiting electron supply, so that Q_{A-} cannot be re-oxidized efficiently.

Across drought-related treatments, the four cultivars exhibited significantly lower F_v/F_m, PI_{abs} and PI_{total} compared with the control. F_v/F_m is a widely used indicator of stress severity; its decline indicates that drought strongly inhibits the normal operation of the photosynthetic apparatus, reducing the overall accumulation of photosynthates. Analysis of the energy flux parameters reflecting PSII reaction center activity (TR_o/CS_o, ET_o/CS_o, DI_o/CS_o, RE_o/CS_o) showed that TR_o/CS_o and ET_o/CS_o decreased in all four cultivars under drought, demonstrating reduced efficiency of light energy capture and conversion into electron transport, as well as impaired electron flow from PSII to PSI. These changes likely disrupt ATP and NADPH production and lead to structural damage in the photosynthetic reaction centers. The decline in the comprehensive performance index PI_{total} further supports this conclusion. Overall, drought stress exerts multi-faceted damage on PSII structure and function, substrate supply and electron transport. Although rewatering partially restored photosynthetic activity, PSII function did not fully return to the control state, indicating that some drought-induced lesions are persistent.

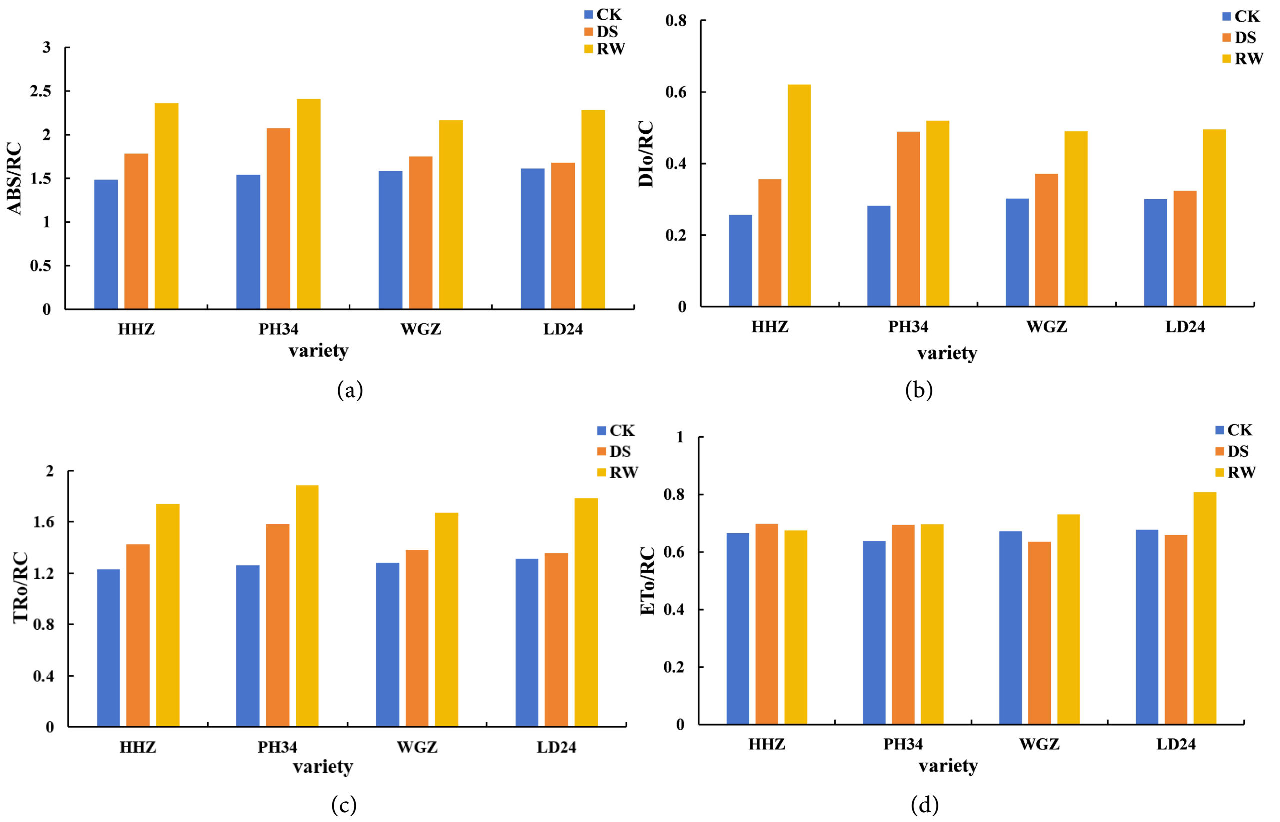


Note: (a) represent rice materials HHZ; (b) represent rice materials PH34; (c) represent rice materials WGZ; (d) represent rice materials LD24.

Figure 4. Dynamic changes in chlorophyll fluorescence kinetic parameters in rice leaves under drought stress and rewatering.

3.5. Effects of Drought Stress and Rewatering on the Status of PSII Reaction Centers

As shown in **Figure 5**, the parameters the energy absorbed per reaction center (ABS/RC), the energy dissipated per reaction center (DI_o/RC), the energy used for electron transport (ET_o/RC), and the energy trapped per reaction center (TR_o/RC) describe the energy partitioning per PSII reaction center. With increasing drought severity, all four cultivars showed rising trends in ABS/RC, TR_o/RC, ET_o/RC and especially DI_o/RC. This indicates that the absorbed light energy, trapped energy, electron transport and dissipated energy per active reaction center increased under drought and rewatering.



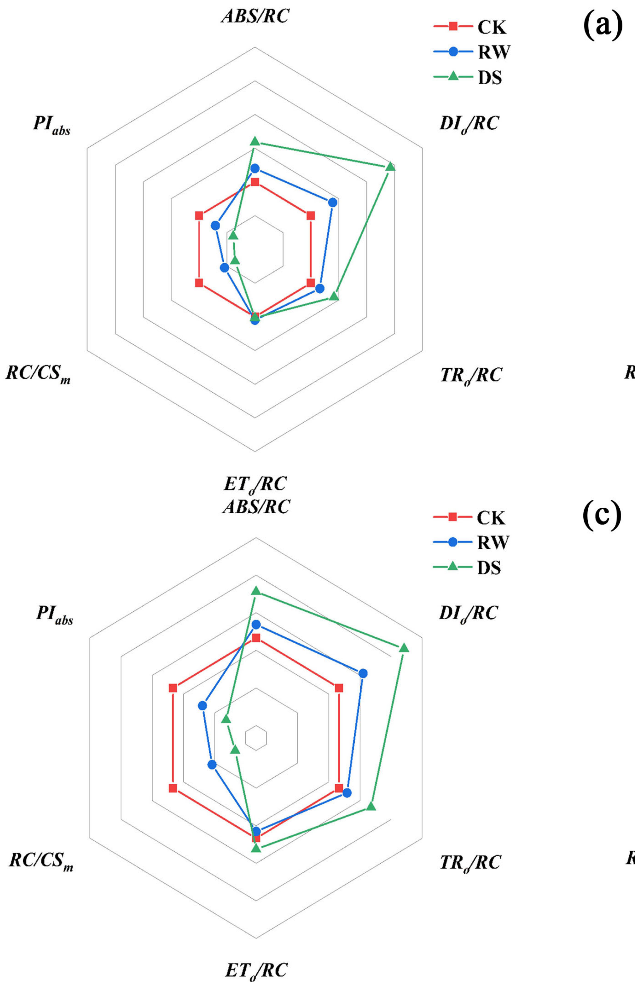
(a) (b)

(c) (d)

Note: (a) Representing rice materials HHZ; (b) Representing rice materials PH34; (c) Representing rice materials WGZ; (d) Representing rice materials LD24.

Figure 5. Changes in PSII reaction center energy fluxes in rice leaves under drought stress and rewatering.

In combination with **Figure 6**, which shows specific activity parameters and RC/CS_m (the density of active PSII reaction centers per excited thylakoid cross-section), it is evident that RC/CS_m decreased under drought. Concomitant increases in ABS/RC, TR_o/RC, ET_o/RC and DI_o/RC, together with decreases in RC/CS_m and PI_{abs}, indicate an increase in the proportion of inactivated reaction centers and a higher excitation load on the remaining active centers on a thylakoid cross-section basis. In other words, drought stress reduces the number of functional PSII units, forcing the surviving centers to process more energy, which enhances the risk of photodamage. Rewatering partially alleviated these effects but did not fully restore PSII reaction center function.



Note: (a) Representing rice materials HHZ; (b) Representing rice materials PH34; (c) Representing rice materials WGZ; (d) Representing rice materials LD24.

Figure 6. Specific activity parameters, reaction center density RC/CS_m and performance index based on absorbed energy in rice leaves under different drought treatments.

4. Discussion

Current rice cultivation practices predominantly rely on continuous flooding, which confers relatively poor drought tolerance, high water consumption and high vulnerability to drought and heat extremes [20] [21]. Numerous studies have demonstrated that drought stress causes pronounced physiological damage in rice, affecting morphological development, chlorophyll biosynthesis and reaction center activity, thereby markedly suppressing photosynthesis [22]. These physiological perturbations are ultimately reflected in plant morphology. Under drought, rice leaves typically curl and yellow. Moderate leaf rolling can help reduce transpiration and excessive light interception, representing an adaptive self-protection strategy. Traits such as leaf size, trichome density, stomatal density and stomatal aperture are also important indicators of drought tolerance. In this study, drought stress significantly inhibited increases in plant height, leaf length, leaf width and leaf area. After rewatering, these morphological traits partially recovered, but the extent of recovery differed among cultivars.

Photosynthesis is a central metabolic process underpinning plant survival, growth, reproduction and ecosystem functioning. Under drought stress, photosynthesis is often the earliest and most strongly suppressed physiological process [23]. Chlorophyll, the key pigment for light harvesting and energy conversion, directly drives the light reactions that generate ATP and NADPH [24]. Under water deficit, chlorophyll content typically declines due to inhibited biosynthesis and accelerated degradation. Consistent with this general pattern, our results showed reduced chlorophyll content after drought, with only partial recovery after rewatering and chlorophyll levels remaining below those of well-watered plants.

Photosynthesis comprises light reactions and carbon fixation reactions. In the light reactions, PSI and PSII cooperate to convert light energy into chemical energy and evolve oxygen [25]. OJIP transients sensitively reflect changes in the primary photochemical reactions of PSII reaction centers. The characteristic phases of the OJIP curve are closely related to the functional status of reaction centers, the activity of the electron transport chain and the integrity of the photosynthetic apparatus as a whole. Drought stress often first targets PSII, disrupting both the donor and acceptor sides and causing imbalances in electron transport. In this study, the amplitude of the OJIP rise under drought was lower than that of the control, indicating restricted electron transport. Under stress, characteristic L-, K- and J-band frequently appear, reflecting OEC damage, interruption of donor-side electron flow, excess excitation energy and imbalances in the electron transport chain. These conditions enhance non-photochemical energy dissipation, and PSI may also be secondarily impaired, leading to global inhibition of photosynthesis. The appearance of these characteristic bands after drought in our experiment indicates that drought disturbed electron flow on both sides of the PSII reaction center, causing structural damage.

Chlorophyll fluorescence parameters provide quantitative measures of energy partitioning and electron transport efficiency in the photosynthetic apparatus and are widely used to evaluate stress damage and tolerance mechanisms [26] [27]. Drought-induced damage to the photosynthetic system is often concentrated on the PSII acceptor side, where electron transport is hindered, key components are inactivated and reactive oxygen species accumulate, causing oxidative damage and leading to declines in F_v/F_m, F_v/F_o and related parameters， among which HHZ showed the most significant decreasing trend. In our study, drought increased V_j and decreased F_v/F_m in rice, indicating elevated reduction pressure in the plastoquinone (PQ) pool on the PSII acceptor side and restricted electron transfer from Q_A to Q_B. The performance index based on absorption (PI_{abs}) is a comprehensive indicator of the functional status of the photosynthetic apparatus; its reduction signifies structural or functional damage. Under drought stress, both *PI*-

$_{total}$ and PI_{abs} showed a decreasing trend across the four varieties, among which the decreasing trend of WGZ was the least significant. However, the extent of recovery is constrained by the severity and duration of prior stress. Here, severe drought markedly impaired the photosynthetic machinery and reaction centers of rice. Although leaf morphology partially recovered after rewatering, chlorophyll fluorescence traits indicated that the photosynthetic system retained persistent functional impairment.

5. Conclusion

In summary, drought stress suppresses photosynthesis in rice by reducing chlorophyll content, damaging PSII donor and acceptor sides, decreasing reaction center density and disturbing energy distribution, which together impair growth and development. Rewatering elicits partial compensatory responses but cannot fully reverse structural or severe functional damage to the photosynthetic apparatus. These findings provide a physiological basis for improving water use efficiency and drought resilience in rice under water-limited conditions. Given the complexity of natural environments and the diversity of plant stress responses, further work is needed to refine our understanding of the underlying mechanisms and to translate these insights into robust agronomic and breeding strategies.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

[1] Faiz, M.A., Wang, Q., Muneer, S., Zhang, Y., Baig, F. and Naz, F. (2025) Probabilistic Approach to Monitoring Vegetation Water Stress Using Solar-Induced Chlorophyll Fluorescence Data. *Agricultural Water Management*, **315**, Article ID: 109559. https://doi.org/10.1016/j.agwat.2025.109559

[2] Saini, D.K., Bardhan, K., Somayanda, I., Bahuguna, R.N. and Jagadish, S.V.K. (2025) Translational Research Progress and Challenges for Developing Drought Resilient Rice. *Plant Stress*, **15**, Article ID: 100751. https://doi.org/10.1016/j.stress.2025.100751

[3] Saha, S. and Johnson, G.N. (2025) Divergent Effects of Successive Drought and Flooding on Photosynthesis in Wheat and Barley. *Frontiers in Plant Science*, **16**, Article 1603355. https://doi.org/10.3389/fpls.2025.1603355

[4] Damalas, C.A. and Koutroubas, S.D. (2024) Potassium Supply for Improvement of Cereals Growth under Drought: A Review. *Agronomy Journal*, **116**, 3368-3382. https://doi.org/10.1002/agj2.21703

[5] Wang, H., Ye, T., Guo, Z., Yao, Y., Tu, H., Wang, P., *et al.* (2024) A Double-Stranded RNA Binding Protein Enhances Drought Resistance via Protein Phase Separation in Rice. *Nature Communications*, **15**, Article No. 2514. https://doi.org/10.1038/s41467-024-46754-2

[6] Lou, Q., Chen, Y., Wang, X., Zhang, Y., Gao, T., Shi, J., *et al.* (2025) Phenomics-Assisted Genetic Dissection and Molecular Design of Drought Resistance in Rice. *Plant Communications*, **6**, Article ID: 101218. https://doi.org/10.1016/j.xplc.2024.101218

[7] Li, Y., Xue, Y., Guan, Z., Wang, Z., Hou, D., Zhao, T., *et al.* (2025) Salt Stress Responses of Different Rice Varieties at Panicle Initiation: Agronomic Traits, Photo-

synthesis, and Antioxidants. *Plants*, **14**, Article 2278. https://doi.org/10.3390/plants14152278

[8] Liu, X., Zheng, J., Feng, X., Zhuang, J., Fang, Y., Qiu, Z., *et al.* (2025) Impact of Low Canopy, Root Temperature, and Drought at the Booting Stage on Yield, Grain Quality, Photosynthesis, and Antioxidant Responses in Rice. *Physiologia Plantarum*, **177**, e70268. https://doi.org/10.1111/ppl.70268

[9] Xia, Q., Tang, H., Fu, L., Tan, J. and Guo, Y. (2023) A Drought Stress-Sensing Technique Based on Wavelet Entropy of Chlorophyll Fluorescence Excited with Pseudo-Random Binary Sequence. *Computers and Electronics in Agriculture*, **210**, Article ID: 107933. https://doi.org/10.1016/j.compag.2023.107933

[10] Javornik, T., Carović-Stanko, K., Gunjača, J., Vidak, M. and Lazarević, B. (2023) Monitoring Drought Stress in Common Bean Using Chlorophyll Fluorescence and Multispectral Imaging. *Plants*, **12**, Article 1386. https://doi.org/10.3390/plants12061386

[11] Wada, S., Takagi, D., Miyake, C., Makino, A. and Suzuki, Y. (2019) Responses of the Photosynthetic Electron Transport Reactions Stimulate the Oxidation of the Reaction Center Chlorophyll of Photosystem I, P700, under Drought and High Temperatures in Rice. *International Journal of Molecular Sciences*, **20**, Article 2068. https://doi.org/10.3390/ijms20092068

[12] Zhang, J., Li, M., Penuelas, J., Sardans, J., Du, L., Yuan, Z., *et al.* (2025) Leaf Area Modulates the Chlorophyll Fluorescence of Leymus Chinensis in Response to Different Drought Scenarios. *Environmental and Experimental Botany*, **237**, Article ID: 106175. https://doi.org/10.1016/j.envexpbot.2025.106175

[13] Ikram, S., Bhattarai, S. and Walsh, K.B. (2024) Screening New Mungbean Varieties for Terminal Drought Tolerance. *Agriculture*, **14**, Article 1328. https://doi.org/10.3390/agriculture14081328

[14] Giuliani, N., Wegher, M., Asensio, D., Zanotelli, D., Andreotti, C. and Tagliavini, M. (2025) Impact of Soil Water Availability on Apple Tree Physiology during Heatwaves and on Post-Stress Recovery. *Environmental and Experimental Botany*, **235**, Article ID: 106161. https://doi.org/10.1016/j.envexpbot.2025.106161

[15] Yan, W., Lu, Y., Guo, L., Liu, Y., Li, M., Zhang, B., *et al.* (2024) Effects of Drought Stress on Photosynthesis and Chlorophyll Fluorescence in Blue Honeysuckle. *Plants*, **13**, Article 2115. https://doi.org/10.3390/plants13152115

[16] Lyu, H. and Lazár, D. (2024) Assessing Key Parameters in Simultaneous Simulation of Rapid Kinetics of Chlorophyll A Fluorescence and Trans-thylakoid Electric Potential Difference. *Physiologia Plantarum*, **176**, e14517. https://doi.org/10.1111/ppl.14517

[17] Küpper, H., Benedikty, Z., Morina, F., Andresen, E., Mishra, A. and Trtílek, M. (2018) Analysis of OJIP Chlorophyll Fluorescence Kinetics and Q_a Reoxidation Kinetics by Direct Fast Imaging. *Plant Physiology*, **179**, 369-381. https://doi.org/10.1104/pp.18.00953

[18] Spanic, V., Mlinaric, S., Zdunic, Z. and Katanic, Z. (2021) Field Study of the Effects of Two Different Environmental Conditions on Wheat Productivity and Chlorophyll Fluorescence Induction (OJIP) Parameters. *Agriculture*, **11**, Article 1154. https://doi.org/10.3390/agriculture11111154

[19] Xu, Y., Jiang, L., Gao, J., Zhang, W., Zhang, M., Liu, C., *et al.* (2024) Molecular Regulation of Photosynthetic Carbon Assimilation in Oat Leaves under Drought Stress. *Plants*, **13**, Article 3317. https://doi.org/10.3390/plants13233317

[20] Fischer, K.S., Fukai, S., Kumar, A., Leung, H. and Jongdee, B. (2012) Field Phenotyping Strategies and Breeding for Adaptation of Rice to Drought. *Frontiers in Physiol-*

ogy, **3**, Article 282. https://doi.org/10.3389/fphys.2012.00282

[21] Yu, J., Du, T., Zhang, P., Ma, Z., Chen, X., Cao, J., *et al.* (2024) Impacts of High Temperatures on the Growth and Development of Rice and Measures for Heat Tolerance Regulation: A Review. *Agronomy*, **14**, Article 2811. https://doi.org/10.3390/agronomy14122811

[22] Takahashi, Y., Noguchi, K., Ifuku, K., Sohtome, T., Nishimoto, T., Wada, S., *et al.* (2023) Effects of Drought Stress on the Oxidation of the Reaction Center Chlorophyll of Photosystem I and Grain Yield in Paddy-Field Grown Rice Plants. *Soil Science and Plant Nutrition*, **69**, 215-220. https://doi.org/10.1080/00380768.2023.2214579

[23] Vialet-Chabrand, S., Matthews, J.S.A., Simkin, A.J., Raines, C.A. and Lawson, T. (2017) Importance of Fluctuations in Light on Plant Photosynthetic Acclimation. *Plant Physiology*, **173**, 2163-2179. https://doi.org/10.1104/pp.16.01767

[24] Dmitrieva, V.A., Domashkina, V.V., Ivanova, A.N., Sukhov, V.S., Tyutereva, E.V. and Voitsekhovskaja, O.V. (2021) Regulation of Plasmodesmata in Arabidopsis Leaves: ATP, NADPH and Chlorophyll *b* Levels Matter. *Journal of Experimental Botany*, **72**, 5534-5552. https://doi.org/10.1093/jxb/erab205

[25] Leister, D. (2023) Enhancing the Light Reactions of Photosynthesis: Strategies, Controversies, and Perspectives. *Molecular Plant*, **16**, 4-22. https://doi.org/10.1016/j.molp.2022.08.005

[26] Itam, M., Hall, D., Kramer, D. and Merewitz, E. (2024) Early Detection of Kentucky Bluegrass and Perennial Ryegrass Responses to Drought Stress by Measuring Chlorophyll Fluorescence Parameters. *Crop Science*, **64**, 1015-1026. https://doi.org/10.1002/csc2.21173

[27] Liu, J., Huang, D., Cheng, Z. and Wu, R. (2024) Impact of Pulse Electric Field Stimulation on Negative Air Ion Release Capacity of Snake Plants. *Agronomy*, **14**, Article 2248. https://doi.org/10.3390/agronomy14102248