The Long-Term Changes in Midday Photoinhibition in Rice (Oryza sativa L.) Growing under Fluctuating Soil Water Conditions

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Abstract: Rice crops growing under fluctuating soil water conditions in a rainfed field frequently experience severe photoinhibition at midday, potentially decreasing their biomass production. In this study, the long-term changes in midday photoinhibition in five rice cultivars growing under variable soil water conditions in a rainfed field were evaluated by determining the maximum quantum yield of photosystem II (Fv/Fm). Fv/Fm was generally lower under rainfed conditions than under flooded conditions at 65 – 75 days after sowing (DAS), but was similar under both conditions at 109 – 124 DAS. This mitigation of photoinhibition over time is likely an up-regulation of mechanisms to dissipate excess electrons, and an analysis of covariance showed that the degree of mitigation under the rainfed condition varied among the cultivars. Such genotypic differences in the long-term changes in Fv/Fm might be determined by the capacity of the cultivar to adapt to drought conditions.

Key words: Acclimation, Chlorophyll fluorescence, Photoinhibition, Rainfed, Rice.

Photosystem II (PSII) plays a crucial role in photosynthetic electron transport but is sensitive to photooxidative damage (Keren and Krieger-Liszkay, 2011), termed photoinhibition, and is typically estimated by the maximum quantum yield of PSII (Fv/Fm, a parameter of chlorophyll fluorescence). Photoinhibition, which is caused by an excess of light energy that is neither used for photosynthetic electron transport nor dissipated as heat, increases with the light intensity (Kato et al., 2003). Hikosaka et al. (2004) examined the effect of photoinhibition on photosynthesis and concluded that photoinhibition at any level of light intensity decreases the photosynthetic rate, and the photoinhibitory reduction of photosynthesis causes a significant reduction in the daily carbon gain (Werner et al., 2001).

On the other hand, photoinhibition is thought to be an energy control mechanism, whereby energy quenching in the photoinhibited PSII reaction centers contributes to the dissipation of excess energy (Horton and Ruban, 2005). This photoinhibitory energy dissipation in PSII limits the linear electron flow and helps maintain the downstream oxidation state, preventing more severe oxidative damage to photosystem I (Keren and Krieger-Liszkay, 2011).

The effect of photoinhibition with regard to plant productivity is still controversial. Some highly productive rice genotypes exhibit less photoinhibition (Wang et al., 2005; Kumagai et al., 2009), resulting in a high photosynthetic rate under favorable environmental conditions. In contrast, there is no evidence of the advantage of increased photoinhibition for higher productivity under field conditions.

Drought stress is one of the major constraints on rice production in rainfed cultivation systems. Under fluctuating soil water conditions, the stability of photosynthesis to a changing environment is important for biomass production. Under conditions of drought stress, decrease in the photosynthetic rate decreases the linear electron flow in the electron transport chain (ETC), causing an increase in excess light energy and accelerating the rate of photoinhibition (Murata et al., 2007). Many of the electron dissipation mechanisms that mitigate photoinhibition, such as photorespiration, cyclic electron flow, the water-water cycle and other alternative electron flow pathways, are up-regulated under drought stress (Biehler and Fock, 1996; Wingler et al., 1999; Golding and Johnson, 2003; Bartoli et al., 2005; Kohzuma et al., 2009). In addition, the dissipation of excess light energy as heat might also be up-regulated by structural changes in the light-harvesting complex (Horton and Ruban, 2005). Because field-grown crops are often exposed to long-term
drought that progresses slowly and is highly variable, photoinhibition under such drought conditions could be substantially altered by the long-term responses of the electron dissipation mechanisms to drought stress. Thus, the changes in photoinhibition in field settings must be analyzed quantitatively to examine the effects of long-term drought on photoinhibition.

In this study, five rice cultivars were grown under flooded and rainfed conditions, and the midday values of $F_v/F_m$ were measured as an indicator of midday photoinhibition. The aim of this study was to assess the long-term changes in midday photoinhibition under the rainfed condition. As drought stress increased, we observed a mitigation response to photoinhibition, which we discuss in relation to the mechanism of adaptation to drought conditions.

Materials and Methods

1. Plant materials and growth conditions

Five rice (*Oryza sativa* L.) cultivars, including different germplasm groups, were used in the experiment. Asu is an indica-type landrace, B6144-MR-6-0-0 and Milyang23 are indica-type improved cultivars, and Khau-tan-chiem and Tima are tropical japonica-type landraces. Two adjacent paddy fields at the experimental field of Kyoto University in Japan were used in the experiment. Because the fields were carefully managed, differences in the chemical and physical properties between the two fields were expected to be negligible. One field was subjected to flooded conditions and the other to rainfed conditions. Seeds of each cultivar were sown on 30 April 2009 and transplanted at 20 and 28 days after sowing (DAS) into $2 \times 2$ m plots in each field at a density of 22.2 plants m$^{-2}$. Fertilizer was applied at a rate of 5-5-5 g m$^{-2}$ (N-P$_2$O$_5$-K$_2$O) to each field prior to transplanting. The flooded field was submerged in water throughout the experiment, whereas the rainfed field was irrigated immediately after transplanting to avoid transplanting damage but was not irrigated after that.

The volumetric soil water content (SWC) was measured using time-domain reflectometry (TDR) method described by Topp et al. (1980). Three parallel metal rods as the TDR probes (rod length of 30 cm) were vertically inserted into the soil, and the measurements were retrieved twice a week using a Tektronix 1502B cable tester (Tektronix Inc., Beaverton, OR, USA). The SWC value of the rainfed field remained relatively high (approximately 0.25 m$^3$ m$^{-3}$) until approximately 100 DAS because of constant rainfall. However, precipitation was low after 100 DAS, and SWC decreased to 0.09 m$^3$ m$^{-3}$ by 124 DAS (Fig. 1a). At approximately 120 DAS, leaf wilting and rolling were partially observed in some cultivars under the rainfed condition; and such damaged leaves were not used for any of the measurements described the following section.

The integral of incident solar radiation (MJ m$^{-2}$) was measured once an hour using a silicon pyranometer (LI200X-L, LI-COR Inc., Lincoln, NE, USA). Because photoinhibition is known to be severest at midday, the sum of radiation values from 1000 to 1400 was recorded as the midday solar radiation ($S_m$). There was a large day-to-day variation in $S_m$ during the experimental period, as shown in Fig. 1b.

2. Chlorophyll fluorescence

$F_v/F_m$ of the topmost fully expanded leaf of plants exposed to sunlight was measured using a portable Mini-PAM fluorometer (Heinz Walz GmbH, Effeltrich, Germany); five plants were randomly selected for replications of the measurement for each cultivar under both water conditions. The leaves were dark-adapted for 10 min prior to the measurement of $F_v/F_m$; the duration was decided according to previous studies (Murchie et al., 1999; Chen et al., 2003; Iseki et al., 2013) in which photoinhibition was evaluated for field-grown rice. The data collection was performed at midday (from 1000 to

![Fig. 1. Soil volumetric water content under the rainfed condition (a) and the midday solar radiation ($S_m$) (b) during the experimental period. The soil volumetric water content data represent the averages of six measurements in the rainfed field. The midday solar radiation is the daily integral of incident solar radiation at midday (from 1000 to 1400).](image-url)
1400) for a total of 15 days from 65 to 124 DAS. At 95 and 124 DAS, the light-adapted quantum yield of PSII ($\Phi_{PSII}$) was also measured at a photosynthetic photon flux density (PPFD) of 1200 $\mu$mol m$^{-2}$ s$^{-1}$.

3. Photosynthetic rate and stomatal conductance
The net CO$_2$ gas exchange rate and stomatal conductance of the topmost fully expanded leaf of plants exposed to sunlight were measured using a portable photosynthesis system (LI-6400, LI-COR Inc., Lincoln, NE, USA); three plants were randomly selected from each cultivar under both water conditions for replications of the measurement. The measurements were performed at midday (from 1000 to 1400) on sunny days at approximately 100 and 120 DAS at 1200 $\mu$mol m$^{-2}$ s$^{-1}$ PPFD under the ambient air temperature and CO$_2$ conditions.

4. SPAD measurement
The chlorophyll content of the topmost fully expanded leaf of the plants was evaluated by using a hand-held chlorophyll meter (SPAD-502, Konica Minolta, Tokyo, Japan); five plants were randomly selected from each cultivar under both water conditions for replications of the measurement. The measurements were performed at the same time as the measurements of the photosynthetic rate at approximately 100 and 120 DAS.

5. Shoot dry weight
The total shoot was sampled at 70 DAS and at the heading stage of each cultivar (approximately 120 DAS); four typical plants were sampled for each cultivar under both water conditions. The shoot materials were dried at 80°C for 72 hr, and the total shoot biomass was calculated by multiplying the biomass per plant by planting density and expressed as g m$^{-2}$.

6. Analysis of covariance (ANCOVA)
A dataset of 75 measurements of midday $F_v/F_m$ values (5 cultivars for 15 d), each of which was an average of 5 replications, was analyzed. The effects of cultivar, DAS and Sm on the long-term changes in the midday $F_v/F_m$ value in each field treatment (flooded or rainfed) were estimated by an ANCOVA using the model below (Equation 1); DAS and Sm are covariance components. The ANCOVA was performed using the statistical software SAS version 9.3 (SAS Institute Inc., Cary, NC, USA).

\[
\text{Midday } F_v/F_m = \text{Cultivar} + \text{DAS} + S_m + \text{Cultivar} \times \text{DAS} + \text{Cultivar} \times S_m
\]  

Results
The leaf chlorophyll content (SPAD value) and total shoot biomass during the experiment are shown in Table 1. The average values of SPAD under the rainfed condition were higher than under the flooded condition at both 100 and 120 DAS (Table 1), but the differences were not significant. Only the B6144-MR-6-0-0 cultivar showed a lower SPAD value under the rainfed condition than the flooded condition. The values of the SPAD value were not much different between 100 and 120 DAS in all of the cultivars. The average values of the shoot biomass at 70 DAS and the heading stage were not significantly changed by the soil water conditions, but they tended to be slightly higher under the rainfed condition than the flooded condition, where the cultivar B6144-MR-6-0-0 exhibited larger shoot biomass under the rainfed condition than the flooded condition throughout the experimental period.

At approximately 100 DAS, stomatal conductance (Fig. 2a) and photosynthetic rate (Fig. 2b) were lower under the rainfed condition than the flooded condition, even though SWC was relatively high (more than 20%) (Fig. 1a). The values of $\Phi_{PSII}$ in the same period were similar in both field conditions, except for genotype

| Cultivar           | SPAD 100 DAS | SPAD 120 DAS | Total shoot biomass 70 DAS | Total shoot biomass Heading stage |
|-------------------|--------------|--------------|---------------------------|----------------------------------|
|                   | Flooded      | Rainfed      | Flooded                   | Rainfed                          |
| Asu               | 315.9        | 336.8        | 1101.3                    | 1012.8                           |
| B6144-MR-6-0-0    | 174.2        | 290.7        | 916.8                     | 1171.3                           |
| Khau tan chiem     | 251.1        | 182.2        | 803.3                     | 952.3                            |
| Milyang23         | 181.8        | 124.2        | 814.5                     | 852.6                            |
| Tima              | 197.3        | 211.7        | 1112.4                    | 1171.3                           |
| Average           | 224.1        | 229.1        | 949.7                     | 1080.7                           |

ANOVA Cultivar ** ns ns ns ns ns
Water condition ns ns ns ns ns

1) The panicles did not emerge in Tima under the rainfed conditions. The total shoot biomass of Tima at 188 DAS was 1414.7 g m$^{-2}$.

** indicates significant difference at $P < 0.01$, and ns indicates not significant.
B6144-MR-6-0-0 in which $\Phi_{\text{PSII}}$ decreased under the rainfed condition (Fig. 2c). At approximately 120 DAS, SWC decreased greatly (less than 10%) (Fig. 1a), and the stomatal conductance (Fig. 2d) and photosynthetic rate (Fig. 2e) also decreased markedly under the rainfed condition. The values of $\Phi_{\text{PSII}}$ tended to decrease under the rainfed condition, but the difference was small and not significant (Fig. 2f). In comparison with the other cultivars, Khau-tan-chiem showed the lowest $\Phi_{\text{PSII}}$ values under both field conditions at approximately 120 DAS.

Under the flooded condition, the values of the midday $F_v/F_m$ were nearly the same until approximately 100 DAS, but decreased slightly at approximately 120 DAS in all cultivars (Fig. 3a). In contrast, under the rainfed condition, the midday $F_v/F_m$ tended to increase with increasing DAS from 65 to 97 DAS, and reached the same level under the flooded condition approximately 120 DAS in all cultivars (Fig. 3b), even though SWC was markedly decreased. Because changes in $F_v/F_m$ are mainly driven by solar radiation, the relationship between the midday $F_v/F_m$ and $S_m$ values was examined for three temporal periods. The midday $F_v/F_m$ in the five cultivars were analyzed separately for three periods: early (65 – 75 DAS), middle (84 – 97 DAS) and late (109 – 124 DAS). As expected, the relationship between $S_m$ and midday $F_v/F_m$ did not vary with the period under the flooded condition (Fig. 4a). In contrast, the midday $F_v/F_m$ relative to $S_m$ under the rainfed condition tended to be higher in the late period compared with the early and middle periods (Fig. 4b).

The effect of DAS on the midday $F_v/F_m$ was analyzed using an ANCOVA (Table 2). The statistical model expressed in Equation (1) was significant for both field treatments, and the effects of cultivar and $S_m$ on the midday $F_v/F_m$ were all significant at the probability level of
0.05 in both field treatments, while the effect of DAS was significant only under the rainfed condition. Remarkably, a higher F value was observed for the S_m parameter under the flooded condition, whereas the S_m and DAS parameters under the rainfed condition both exhibited higher F values than the other parameters. The significant interaction between cultivar and DAS under the rainfed condition indicated that there was genotypic variation in the effect of DAS on the midday F_v/F_m. The DAS parameter was positive in all cultivars in the model for the estimation of midday F_v/F_m under the rainfed condition (Table 3), indicating that increasing DAS increased the midday F_v/F_m under the rainfed condition, regardless of cultivar. In contrast, the DAS parameter showed both positive and negative values in the model for the flooded condition, but the absolute values were smaller than those obtained under the rainfed condition. Among the five cultivars, the value of the DAS parameter under the rainfed condition was the highest in the cultivar Khau-tan-chiem, indicating that this cultivar displayed the largest DAS-dependent increase in midday F_v/F_m. Khau-tan-chiem also showed the highest value of the DAS parameter under

![Fig. 3. Long-term changes in the midday F_v/F_m in five rice cultivars under flooded (a) and rainfed (b) conditions. Each data point represents a day value in each cultivar and is an average of five replications (n = 5).](image)

![Fig. 4. Relationships between the midday F_v/F_m and midday solar radiation under flooded (a) and rainfed (b) conditions. Each data point represents a day value in each cultivar and is an average of five replications (n = 5). All the data for the midday F_v/F_m are divided into the early (65 – 75 DAS), middle (84 – 97 DAS) and late (109 – 124 DAS) periods of the experiment. Each period included between 3 and 6 measurement days.](image)

| Model | Flooded F value | Probability | Rainfed F value | Probability |
|-------|-----------------|-------------|-----------------|-------------|
| Model | 5.3             | < 0.001     | 8.1             | < 0.001     |
| Cultivar | 4.6             | 0.003       | 3.2             | 0.020       |
| DAS | 2.7             | ns           | 40.4            | < 0.001     |
| S_m | 46.6            | < 0.001     | 38.3            | < 0.001     |
| Cultivar × DAS | 1.7            | ns           | 2.6             | 0.043       |
| Cultivar × S_m | 0.1            | ns           | 0.5             | ns          |

The total number of data points is 75 (n = 75) for each field treatment.
The days after sowing (DAS) and the midday solar radiation (S_m) were covariate components.
ns indicates not significant.
In this study, the midday $F_v/F_m$ during the early period was lower under the rainfed condition than under the flooded condition (Figs. 3 and 4). A decrease in the photosynthetic rate caused by the lower stomatal conductance might induce an increase in excess light energy and photoinhibition and cause a decrease in midday $F_v/F_m$. The higher SPAD value under the rainfed condition (Table 1) might be another reason for the lower $F_v/F_m$, since a high ratio of chlorophyll content to Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) content induces excess energy, thus increasing photoinhibition (Kumagai et al., 2007).

Although photoinhibition was severer under the rainfed condition than under the flooded condition (Figs. 3 and 4), it tended to decrease slightly in the late period (Figs. 3a and 4a). The high vapor pressure deficit caused by the low precipitation and high solar radiation might decrease stomatal conductance and photosynthesis (Figs. 2d and 2e), thus increasing photoinhibition. The midday $F_v/F_m$ under the rainfed condition increased with increasing DAS (Figs. 3b and 4b), even though the soil water deficiency increased during the same period (Fig. 1a). The positive effect of DAS on $F_v/F_m$ in all 5 cultivars under the rainfed condition was confirmed by the ANCOVA results (Table 3). The increase in the midday $F_v/F_m$ was observed only under the rainfed condition, suggesting that the increased midday $F_v/F_m$ was an effect of long-term soil water deficiency.

We interpreted the DAS parameter as representing the response of midday photoinhibition to the long-term drought in the rainfed field. One cause of this response is thought to be drought acclimation: stress-induced osmotic adjustment mitigates leaf dehydration as drought acclimation, helping to sustain photosynthetic rates and PSII activity (Conroy et al., 1988; Chaves et al., 2009). However, in the late period of the experiment, the midday $F_v/F_m$ under the rainfed condition was as high as that under the flooded condition (Figs. 3 and 4), even though the stomatal conductance and photosynthetic rate had greatly decreased (Figs. 2d and 2e). Furthermore, the values of SPAD under the rainfed condition at approximately 120 DAS were not largely different from that under the flooded condition (Table 1). Accordingly, we suggest that the mitigation of midday photoinhibition was caused not only by mechanisms of dehydration tolerance, such as osmotic adjustment, but also by an acclimation response of electron dissipation mechanisms in the electron transport chain (ETC).

| Cultivar (a$_c$) | DAS (a$_{D}$) | $S_m$ (a$_{S}$) |
|-----------------|---------------|-----------------|
| Flooded (× 10$^{-3}$) | Rainfed (× 10$^{-3}$) | Flooded (× 10$^{-3}$) | Rainfed (× 10$^{-3}$) |
| Asu | 0.79 | 0.62 | −0.1 | 1.4 |
| B6144-MR-6-0-0 | 0.78 | 0.66 | 0.1 | 1.0 |
| Khau tan chiem | 0.76 | 0.58 | 0.4 | 2.2 |
| Milyang23 | 0.84 | 0.70 | −0.4 | 0.9 |
| Tima | 0.80 | 0.70 | −0.1 | 0.9 |

The total number of data points is 75 (n = 75) for each field condition. The days after sowing (DAS) and the midday solar radiation (S$_m$) were covariate components. Midday $F_v/F_m$ is expressed by the following equation with parameters a$_c$, a$_D$, and a$_S$, for each cultivar under each condition: Midday $F_v/F_m$ = a$_c$ + a$_D$ DAS + a$_S$ S$_m$.
sink occurred through which excess light energy was mitigated, such that the midday photoinhibition was also mitigated. The activation of electron dissipation mechanisms is affected by the redox status of ETC (Walters, 2005; Oelze et al., 2008). The reductive state of ETC under the flooded condition in the early period, which caused lower Fv/Fm, may have induced the mitigation of photoinhibition in the late period.

In the ANCOVA model for the flooded condition, no interaction was found between the cultivar parameter and DAS or Sm, suggesting that the cultivar parameter represents genotypic differences in physiological traits that can influence Fv/Fm but is not affected by DAS or Sm. In previous studies, the genotypic variation in photoinhibition sensitivity in rice was explained by differences in antioxidant capacity and electron dissipation (Jiao and Ji, 2001; Kumagai et al., 2010). These antioxidant and electron dissipation mechanisms compete with carbon fixation processes for absorbed light energy and can potentially decrease plant growth (Raven, 2011). The cultivar parameter for Khau-tan-chiem exhibited the lowest value among the five cultivars under the flooded condition, but the DAS parameter under the flooded condition was the highest in this cultivar. The adaptive change to the midday Fv/Fm may have contributed to the small differences in shoot biomass between the two field conditions at the heading stage (Table 1).

Khau-tan-chiem also showed a positive value for the DAS parameter under the flooded condition, and an increase in the midday Fv/Fm under this condition may have been caused by the increase in heat dissipation via such a mechanism as non-photochemical quenching. The lower values of Fv/Fm in Khau-tan-chiem at approximately 120 DAS (Fig. 2f) might be the result of the increase in heat dissipation due to the decrease in photosynthetic rate under the flooded condition during the late period. Therefore, regardless of the water condition, photoinhibitory energy dissipation is likely partially replaced by other energy and electron control mechanisms as a response to the long-term condition of photosynthesis reduction. The long-term response of Fv/Fm under the flooded condition may be determined by the drought adaptation capacity of the plant.

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