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Photosynthetic and yield responses of rice (*Oryza sativa* L.) to different water management strategies in subtropical China

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Abstract

An experiment was performed to study gas exchange and chlorophyll fluorescence responses of rice (*Oryza sativa* L.) to various regimes, such as flooding–midseason drying–flooding (FDF), flooding–midseason drying–saturation (FDS), and flooding–rain-fed (FR) regimes. Compared to FDF, FR resulted in an obvious decrease in net photosynthetic rate (P_N), due to the decrease in stomatal conductance and the increase in stomatal limitation. In contrast, FDS plants did not suffer stomatal limitation and had comparable P_N with FDF plants. For diurnal light-saturated electron transport rate and saturation irradiance, FDF performed the best, which was followed by FDS and FR successively. FR and FDS plants tended to suffer from midday depression. FDS reduced irrigated water by 17.2% compared to FDF for comparable yields. The results suggested that FDS can be an effective irrigation regime to save water.

Additional key words: rapid light curve; water productivity; water saving.

Introduction

Rice (*Oryza sativa* L.) production takes up about 11% of the global cultivated land (Khush 2005), and consumes about 34–43% of the global irrigation water (Bouman *et al*. 2007). Rice cultivation has shaped the cultures, diets, and economies in Asia, where 90% of rice is grown and consumed (Khush 2005). Rice is mostly cultivated in puddled fields with flooded water, accounting for approximately 50% of the irrigated area in Asia (Barker *et al*. 2004). Water deficit is a major abiotic stress factor limiting crop productivity worldwide, which more or less affects about 50% of the world rice production (Belter *et al*. 2004, Lal *et al*. 2012, Akram *et al*. 2013, Ambavaram *et al*. 2014, Zhou *et al*. 2017). With climate change and rapidly increasing demands for higher valued uses (industry, municipal use, and hydropower), water resource for agriculture sector is becoming increasingly scarce (Barker *et al*. 2004, Wei *et al*. 2010, Elliott *et al*. 2013, Yan *et al*. 2015). At present, the challenge is to produce more rice with less water in order to meet the increasing demand for rice due to growing population.

Water loss in rice cultivation is mainly caused by evaporation, seepage, percolation, and surface runoff (Bouman *et al*. 2007, Alberto *et al*. 2011, Thakur *et al*. 2014). To cut down the unproductive water outflows, researchers have developed a promising water-saving irrigation regime to keep soil saturated without waterlogging, which is called saturated soil culture. Some researchers found that saturated soil culture increased grain yield by 9–15% compared to continuously flooded culture (Pan *et al*. 2009, He 2010, Escasinas and Zamora 2011, He *et al*. 2014). However, some researchers reported no yield increase or small yield reductions (Bouman and Tuong 2001, Tabbal *et al*. 2002, Zain *et al*. 2014). Those previous reports indicate that saturated soil culture has the potential to increase rice

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Abbreviations: C_a – ambient CO_2 concentration; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; E_m – saturation irradiance; ETR – electron transport rate; ETR_{max} – light-saturated ETR; FDF – flooding – midseason drying – flooding water regime; FDS – flooding – midseason drying – saturating water regime; FR – flooding – rain-fed water regime; F_m' – maximal fluorescence yield of the light-adapted state; F_t – instantaneous fluorescence; g_s – stomatal conductance; L_s – stomatal limitation value; P_N – net photosynthetic rate; RLC – rapid light curve; WP – water productivity; Φ_{PSII} – effective quantum yield of PSII photochemistry.
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yield, or at least, it could obtain the comparable yield when compared to continuous flooding culture.

China has the world's second largest planting area with the highest rice production, accounting for 18.8% of the world rice area and 28.1% of the global rice production (FAO 2014). The south of China is the major rice-producing region, where midseason drying (FDF) is prevailing. The most representative saturated soil culture is flooding–midseason drying–saturation (FDS) cycle. After midseason drying, irrigation is applied to make the soil saturated without ponded water. Traditionally, rice is also grown under rain-fed conditions (FR), mainly due to the lack of irrigation. Rain-fed lowland rice is grown in 54 million out of 163 million ha of world rice area (Bouman *et al*. 2007, FAO 2014). Photosynthesis is the basis of crop growth and yield formation (Ambavaram *et al*. 2014). However, there is little information on the physiological basis of rice photosynthesis, which leads to yield gap between saturated soil culture and conventional irrigation (FDF and FR). Photosynthesis is an important physiological process that is sensitive to water deficit (Pieters and Nùñez 2008, Akram *et al*. 2013, Perdomo *et al*. 2015, 2017). Photosynthetic capacity, especially during the reproductive stage, is crucial for grain formation (Akram *et al*. 2013, Ambavaram *et al*. 2014). In rice, more than 60% of the carbon content of grains originates from CO_2 assimilation during the grain-filling stage, and flag leaves are the primary contributors to the accumulation of dry matter in grains (Yoshida 1981). The objective of the research is to investigate the responses of photosynthetic gas exchange, chlorophyll (Chl) fluorescence, grain yield, and water-use efficiency of rice to different water management strategies under the climatic conditions of southern China. The results can give insight into understanding of photosynthetic physiology underlying water-saving cultivation of rice.

Materials and methods

Experimental site: The experiment was carried out at Taoyuan Station of Agro-ecology Research (111°27′E, 28°55′N) from June to October in 2011. The region is characterized by subtropical humid monsoon climate, with an average annual air temperature of 16.5°C, precipitation of 1,448 mm, sunshine of 1,513 h, and frost-free period of 283 d. The soil is developed from Quaternary red clay. Characteristics of the soil were as follows: soil organic carbon (SOC) 17.1 g kg^{-1}, total nitrogen of 1.79 g(N) kg^{-1}, total phosphorus of 0.58 g(P) kg^{-1}, total potassium of 12.1 g(K) kg^{-1}. Precipitation and air temperature were measured at a meteorological station nearby the experiment field, which was within 100 m. Specific precipitation and air temperature are shown in Fig. 1, with an average annual air temperature of 24.8ºC and precipitation of 234 mm from rice transplanting to harvest.

Experimental design: The water regimes were: flooding–midseason drying–flooding (FDF), flooding–midseason drying–saturating (FDS), and flooding–rain-fed (FR). Each treatment had three replicates. In all the treatments, fields were flooded with about 10-cm water layer for land preparation and seedling transplanting. Midseason drying was carried out at the end of the tillering stage, and it lasted for about one week. In the FDF plots, 2–10-cm water layer was kept after midseason drying. In the FDS plots, intermittent irrigation was adopted after midseason drying to keep water table at 0–3 cm below soil surface so that the soil was saturated without obvious standing water. In the FR plots, there was no more irrigation since 15 d after transplanting, so the soil moisture was mainly below saturation from the shooting stage to harvest. Specific field water conditions are shown in Fig. 2. A local popular hybrid rice cv. Fengyuanyou 299 was used in this study. Seedlings were raised in the seedbed with the sowing date being 20 June, and transplanted on 19 July at a hill spacing of 0.20 by 0.20 m with two seedlings per hill. The heading date (50% of the panicles fully emerged from the boot) started from 6 September. After heading and flowering, the grains entered the filling stage. Plants were harvested by hand on 10 October. The fertilizers applied were urea for N, calcium superphosphate for P, and potassium chloride for K, at the rates of 101 kg(N) ha^{-1}, 20 kg(P) ha^{-1}, and 110 kg(K) ha^{-1}, respectively. Urea was applied with three splits, with 50% as a basal fertilizer, 33.3% as tillering fertilizer, and 16.7% as panicle fertilizer. The calcium superphosphate and potassium chloride were applied as basal fertilizers. Weeds, pests, and diseases were controlled as required to avoid a yield loss.

Gas exchange: Photosynthetic gas-exchange parameters were measured on fully expanded flag leaves using a portable photosynthesis measuring system (*LI-6400, Li-Cor Inc*., Lincoln, NE, USA) during 09:30–11:30 h on cloudless days, 6 September during the heading stage, and 24 September during the filling stage. PPFD of 1,500 μmol m^{-2} s^{-1} was provided by light-emitting diode (model *6400-02B Red-Blue*, *Li-Cor Inc*.). Temperature of a leaf chamber was controlled for all measurements at 30ºC. CO_2 concentration was provided and controlled by the CO_2 injector system at 400 μmol mol^{-1}. Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i), and ambient CO_2 concentration (C_a) were obtained directly. Stomatal limitation value (L_s) was calculated using the following formula: $L_s = 1 - C_i/C_a$

Chl fluorescence parameters were measured on fully expanded flag leaves using a *Mini-PAM* fluorometer (*Walz*, Germany). *Mini-PAM* fluorometer uses three different lights to manipulate the photosynthetic apparatus, measuring light to excite fluorescence, saturating pulse

[3,000 μmol(photon) m^{-2} s^{-1}, 0.8 s] to close all PSII reaction centers to determine maximum fluorescence, and actinic light to induce photosynthesis (electron transport). Minimal fluorescence yield (F_0) and maximal fluorescence yield (F_m) were measured before dawn. Diurnal rapid light curves (RLCs) were recorded at 08:00, 10:00, 12:00, 14:00, 16:00, and 18:00 h on a cloudless day, 24 September, during the filling stage. RLCs were measured using the "light curve" routine at nine levels of actinic light [0, 105, 215, 340, 510, 720; 1,050; 1,420; and 2,180 μmol(photon) m^{-2} s^{-1}] in an increasing order. Each actinic light lasted for 10 s. At the end of each actinic light, a saturating pulse was applied to measure instantaneous fluorescence (F_t) and maximum fluorescence yield at the corresponding actinic light (F_m'). The following parameters were calculated: effective quantum yield of PSII photochemistry, $\Phi_{PSII} = (F_m' - F_t)/F_m$, and electron transport rate, $ETR = 0.5 \times \Phi_{PSII} \times PPFD \times 0.84$, where 0.5 is a multiplication factor for two quanta of light required for the transport of one electron, and 0.84 is the species-specific fraction of incident quanta absorbed by the leaf. To determine the cardinal points of RLCs, the ETR *vs*. PPFD data were fitted using a double exponential decay function: $P = Ps(1 - e^{-(\beta E/Ps)})$. Light-saturated ETR ($ETR_{max}$) and saturation irradiance (E_m) were estimated using the following equations: $ETR_{max} = Ps\,[\alpha/(\alpha+\beta)]\,[\beta/(\alpha+\beta)]^{\beta/\alpha}$ and $E_m = Ps/\alpha \log_e^{(\alpha+\beta)/\beta}$. The definitions of the parameters can be found in Platt *et al*. (1980) and Ralph and Gademann (2005).

Rice yield: Rice was harvested manually from each plot at maturity stage. Grain samples were oven-dried at 70°C and weighed to calculate grain yields assuming the water content of 14%.

Water productivity: A water flow meter was installed in the irrigation pipeline in each plot to monitor the amount of irrigated water. Water productivity (WP) was calculated as grain yield divided by total amount of irrigated water as follows: WP = grain yield/gross irrigation.

Statistical analysis: The data were analyzed statistically with analysis of variance (*ANOVA*) using *Statistical Package for the Social Sciences 16.0* software. The mean values were compared with the *Duncan*'s post-hoc test with $p<0.05$ considered significant.

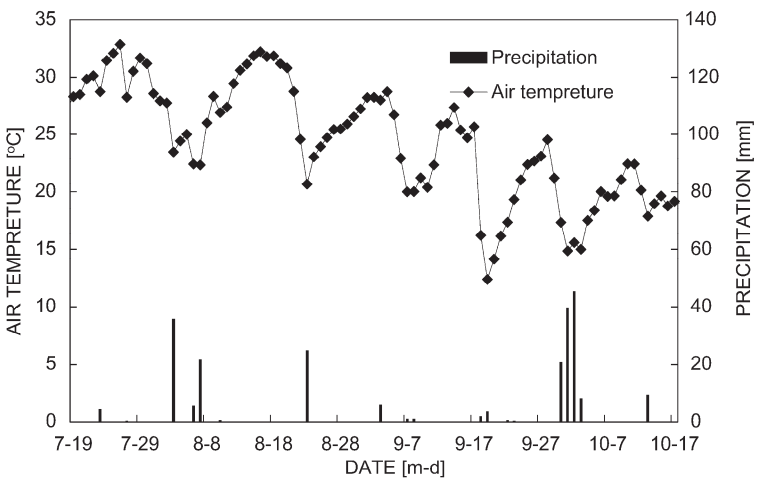

Fig. 1. Dynamics of daily rainfall and daily average air temperature throughout the experimental period.

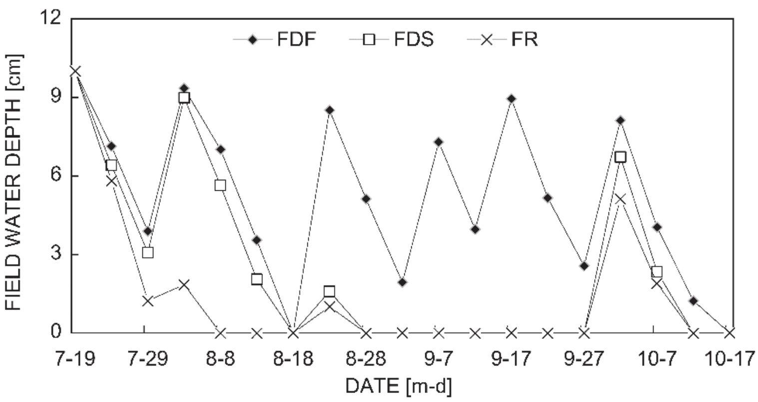

Fig. 2. Dynamics of water table throughout the experimental period. FDF, flooding–midseason drying–flooding water regime; FDS, flooding–midseason drying–saturating water regime; FR, flooding–rainfed water regime.

Results

Gas exchange: The gas-exchange parameters at the heading and filling stage are listed in Table 1. FDS plants were comparable to FDF plants in P_N, g_s, E, and L_s at the heading stage. FDS resulted in a small decrease in P_N, g_s, and E, and a small increase in L_s at the filling stage. In contrast, FR resulted in an obvious decrease in P_N, g_s, and E compared to FDF and FDS at both the heading and filling stage. L_s of FR plants was significantly higher than that of the FDF and FDS plants. The decrease in P_N and E of FR plants was due to the increase in L_s and the decrease in g_s. Stomata plays a dominant role in the response to leaf water vapor emission loss and carbon dioxide assimilation. The stomatal factor-limited P_N was associated with decreased g_s. The FDS plants, however, were not obviously limited by stomata, leading to comparable P_N between FDS and FDF.

Chl fluorescence: RLCs provide important ecophysiological information for understanding potential photosynthesis capacity of leaves. Diurnal changes of RLCs under different water conditions are presented in Figs. 3 and 4. ETR increased with the increase of actinic light. ETR under various water conditions differed in performance, especially during 10:00–16:00 h when air temperature was relatively high and sunlight relatively strong. Diurnal variation curve of ETR under FDF treatment reached the highest values around 12:00 h, while ETR under FDS and FR reached the highest values around 10:00 h. The order of ETR under different treatments was as follows: FDF > FDS > FR.

Table 1. Net photosynthetic rate (P_N), stomatal conductance (g_s), and stomatal limitation value (L_s) under different water conditions. [PPFD: 1,500 μmol(photon) m^{-2} s^{-1}] P_N – net photosynthetic rate; E – transpiration rate; g_s – stomatal conductance; L_s – stomatal limitation value. FDF – flooding–midseason drying–flooding water regime; FDS – flooding–midseason drying–saturating water regime; FR – flooding–rain-fed water regime. Data within the same column and same stage followed by *different letters* are significantly different at p<0.05 (mean ± SE, n = 3).

Stage	Treatment	P_N [μmol(CO_2) m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]	L_s
Heading	FDF	20.9 ± 0.5^a	0.89 ± 0.03^a	5.5 ± 0.1^a	0.14 ± 0.00^b
	FDS	20.2 ± 0.5^a	0.84 ± 0.02^a	5.5 ± 0.1^a	0.14 ± 0.01^b
	FR	16.7 ± 0.4^b	0.47 ± 0.05^b	4.2 ± 0.2^b	0.19 ± 0.01^a
Filling	FDF	20.7 ± 0.5^a	0.93 ± 0.04^a	8.6 ± 0.3^a	0.14 ± 0.01^b
	FDS	19.1 ± 0.3^b	0.75 ± 0.02^b	7.8 ± 0.3^a	0.16 ± 0.01^b
	FR	16.6 ± 0.6^c	0.59 ± 0.06^c	5.2 ± 0.3^b	0.19 ± 0.01^a

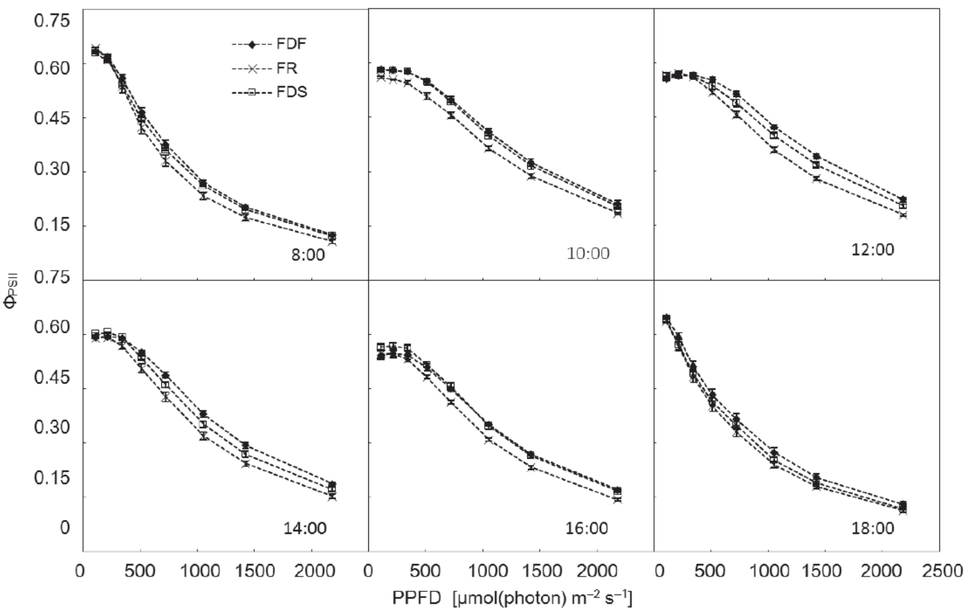

Fig. 3. Diurnal changes of rapid light curves under different water conditions at the filling stage (mean ± SE, n = 3). Φ_{PSII} – effective quantum yield of PSII photochemistry; FDF – flooding–midseason drying–flooding water regime; FDS – flooding–midseason drying –saturating water regime; FR – flooding–rain-fed water regime.

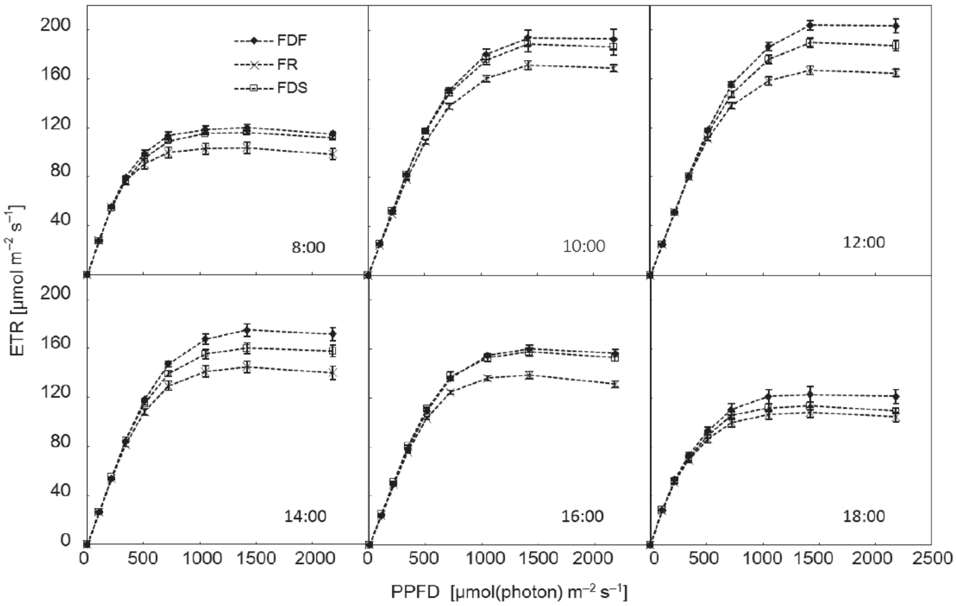

Fig. 4. Diurnal changes of rapid light curves under different water conditions at the filling stage (mean ± SE, n = 3). ETR – electron transport rate; FDF – flooding–midseason drying–flooding water regime; FDS – flooding–midseason drying–saturating water regime; FR – flooding–rain-fed water regime.

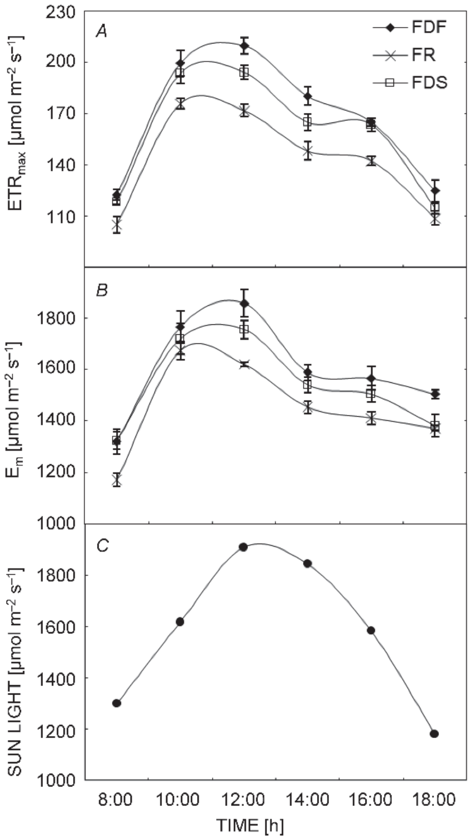

Fig. 5. Diurnal changes of ETR_{max} (*A*), E_m (*B*), and sun light (*C*) under different water conditions at the filling stage (mean ± SE, n = 3). E_m – saturation irradiance; ETR_{max} – light-saturated electron transport rate; FDF – flooding–midseason drying–flooding water regime; FDS – flooding–midseason drying–saturating water regime; FR – flooding–rain-fed water regime.

ETR_{max} and E_m curves under different water conditions are presented in Fig. 5. Compared to FDF, FR decreased ETR_{max} and saturating irradiance obviously. However, FDS showed a lesser decrease. The decreases in saturating irradiance would reduce light-utilization efficiency, especially on cloudless days. ETR_{max} curve of FDF tended to have a single peak and peak at about 12:00 h, while ETR_{max} curves of FR and FDS tended to have double peaks and get the first peak before noon. In addition, the differences of E_m curves under different treatments were similar with that of ETR_{max} curves. During the measuring day, the sunlight obviously exceeded the E_m at 14:00 h (Fig. 5*B*,*C*). The orders of ETR_{max} and E_m under different treatments were consistent (FDF > FDS > FR). The results indicate that photosynthesis of FR and FDS plants tended to suffer midday depression.

Rice yield and water productivity: Rice yield, irrigation amount, and water productivity (WP) are listed in Table 2. Rice yields under FDF and FDS were comparable, and they were significantly higher than that under FR. Compared to FDF, FDS resulted in 2.8% of a yield decline. In contrast, FR decreased rice yield by 22%. Compared to FDF, FDS and FR saved 17.2 and 53.5% of irrigation water, respectively. Correspondingly, WP was enhanced by 17.2 and 67.5% under FDS and FR, respectively. FDS not only maintained the grain yield, but also saved irrigation water. With a combination of rainfall (234 mm) and irrigation, the WP were 0.66, 0.73, and 0.84 kg m^{-3} for FDF, FDS, and FR, respectively.

Discussion

Rice can survive under a range of water conditions. Its photosynthesis, however, is affected if the soil water content is insufficient. As this study showed, P_N, g_s, E, and L_s of rice plants were influenced by field water conditions. Photosynthesis is the primary drive for rice production, which is closely correlated with stomatal conductance (Ohsumi *et al*. 2008, Pieters and Nùñez 2008, Ambavaram *et al*. 2014, Stuerz *et al*. 2014). In the present study, low P_N and E under non-flooding conditions were caused by high L_s and low g_s, which prevented losing too much water and increased water-use efficiency, showing a strong self-regulatory and adaptive capacity. Nguyen *et al*. (2009) concluded that g_s under saturated soil conditions was reduced by 13–27% compared to that under conventional flooding system, whereas other physiological parameters were not affected much by water treatments, particularly when the water table was maintained at around 10 cm below soil surface. In the present study, plants under FDS showed little differences compared to plants under FDF in P_N, g_s, E, and L_s, indicating that it was feasible to reduce irrigation by switching from FDF to FDS.

RLCs can provide detailed information on saturation characteristics of electron transport as well as overall photosynthetic performance of a plant (Ralph and Gademann 2005). Drought could decrease effective quantum yield of PSII photochemistry (Φ_{PSII}) and is main regulatory mechanisms in rice (Pieters and El Souki 2005). Similarly, in the present study, diurnal courses of ETR corresponding diurnal courses of Φ_{PSII} varied greatly under different water conditions (Figs. 3, 4). Diurnal changes of RLCs occurred mainly due to diurnal changes in the microclimate, *i.e.* radiation, temperature, relative humidity, *etc.* Photosynthesis cannot proceed without photons, but not all the absorbed photons can be utilized in the process of photosynthesis (Kumagai *et al*. 2009). Excessive radiation loads in canopy leaves can produce reactive oxygen species, which can damage the photosynthetic apparatus, particularly PSII, resulting in photoinhibition due to an imbalance in the photosynthetic redox signaling pathways and the inhibition of PSII repair (Foyer and Noctor 1999, Gururani *et al*. 2015). Drought-induced inhibition of photosynthesis appeared gradually with growing radiation (Fig. 5). High temperature and low relative humidity could aggravate photodepression, especially under non-flooding conditions (Perdomo *et al*. 2015, 2017). Non-flooded rice fields had higher sensible heat flux and lower latent heat flux compared to flooded fields, indicating that a large proportion of available net radiation was used for sensible heat transfer or for the warming of the surrounding air (Alberto *et al*. 2009, 2011), which resulted in a higher canopy temperature and lower relative humidity (Yan *et al*. 2012, Stuerz *et al*. 2014). In the present study, compared to FDF, the FR and FDS plants were more likely subjects to midday photodepression (Fig. 5), indicating that photosynthetic performance at midday may allow more precise estimate of water stress.

Table 2. Rice grain yield, irrigation amount, and water productivity (WP) under different treatments. FDF – flooding–midseason drying–flooding water regime; FDS – flooding–midseason drying–saturating water regime; FR – flooding–rainfed water regime. Data within the same column followed by *different letters* are significantly different at $p<0.05$ (mean ± SE, $n = 3$).

Treatment	Yield [kg ha^{-1}]	Irrigation [m^3 ha^{-1}]	WP [kg m^{-3}]
FDF	5,647 ± 161^a	6,221 ± 169^a	0.91 ± 0.05^c
FDS	5,490 ± 188^a	5,149 ± 87^b	1.07 ± 0.04^b
FR	4,403 ± 110^b	2,890 ± 70^c	1.52 ± 0.04^a

With rapid population growth and increasing water scarcity, it is critically important to sustain high grain yields through improved water productivity. In paddy fields, irrigation without standing water would lead to lesser water loss from evaporation, percolation, seepage, and surface runoff (Bouman *et al*. 2007, Alberto *et al*. 2011). In the present study, the highest water productivity (WP) was observed in FR treatment, which showed the lowest grain yield. High yield production with relatively high WP was observed in FDS treatment, with an increase of 17.2% in WP and a reduction of only 2.8% in yield in comparison with FDF treatment (Table 2). The result was consistent with previous studies (*e.g.,* Bouman and Tuong 2001, Tabbal *et al*. 2002, Zain *et al*. 2014). It indicates that FDS could provide sufficient moisture for a high rice yield. Such association of high (or moderate) WP values with high (or moderate) yield has an important implication for water-saving irrigation management. Also, saturated soil culture increased grain yields in some studies (*e.g.*, Pan *et al*. 2009, He 2010, Escasinas and Zamora 2011, He *et al*. 2014). The dispute could be attributed to differences in climates, soil properties, and varieties (Belder *et al*. 2004, Nguyen *et al*. 2009, Matsuo *et al*. 2010, Akram *et al*. 2013, Chu *et al*. 2014, Fong *et al*. 2016). It indicates that FDS system could guarantee yield, as long as minimum soil moisture was controlled reasonably according to local climates, soil properties, and varieties.

Continuous flooding was widely adopted before 1980s and gradually replaced by midseason drying (FDF). To cope with water scarcity, people have adopted partly non-flooded management strategies, such as alternate wetting and drying culture and FDS described in the present study. With efficient alternate wetting and drying irrigation, soil was dried out to a reasonable threshold between irrigation events, which could greatly reduce water input without reducing the rice yield (Thakur *et al*. 2014, Lampayan *et al*. 2015, Kumar *et al*. 2017). In contrast, no standing water existed in saturated soil culture, which would reduce more water loss. In practice, irrigation is adopted not only for crop growth but also as a management tool during rice cultivation. Soil flooding provides favorable conditions for soil pounding, seedling transplanting, and weed control (Nguyen *et al*. 2009). There was usually abundant rainfall during early-middle periods of single-season rice and late-season rice, which made it easy to implement soil flooding during early-middle periods. Therefore, FDS in the present study also conformed to integrative field management and precipitation distribution.

Conclusion: In this study, RF significantly inhibited rice photosynthesis and yield, as compared to FDF. However, FDS substantially alleviated these reductions, and their values were not significantly different from those of FDF. Therefore, we concluded that FDS (water table was 0–3 cm below soil surface after midseason drying) could be considered as an effective irrigation regime to increase water productivity without obvious adverse effects on photosynthetic capacity and grain yield in rice cultivation. With increasing water scarcity, lower water input in rice cultivation is inevitable. This study would be instructive for determining water-saving cultivation method and exploring relations between water management and photosynthetic physiology.

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