Physiological Mechanism of Drought-Resistant Rice Coping With Drought Stress

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Abstract
Drought stress is one of the major threats to rice production. The weakening of leaf photosynthesis due to drought is the main reason for the reduction of grain yield, but its mechanism is still obscure. The objectives of this study were to reveal the physiological mechanism of drought stress affecting photosynthetic capacity and grain yield. Pot experiments were conducted with drought-tolerant cultivars Hanyou113 (HY113) and Zhonghan3 (ZH3) and drought-sensitive cultivar Huanghuazhan (HHZ) under four water management treatments (traditional flooding (CK), mild drought stress (LD), moderate drought stress (MD) and severe drought stress (HD)) at heading stage in 2013 and 2014. Compared with CK, grain yield was significantly reduced by 14.9%, 30.8%, and 12.8% in HY113, HHZ, and ZH3 under LD, 32.9%, 33.7%, and 22.9% in HY113, HHZ, and ZH3 under MD and 53.6%, 45.6%, and 30.7% in HY113, HHZ, and ZH3 under HD, respectively. The photosynthetic rate (Pn) decreased by 49.0% from 20.0 to 10.2 µmol m⁻² s⁻¹ in HY113, and 67.6% from 23.4 to 7.58 µmol m⁻² s⁻¹ in HHZ, and 39.3% from 23.4 to 14.2 µmol m⁻² s⁻¹ in ZH3 under HD. The Pn of HHZ was similar to that of ZH3 under CK conditions. During the drought periods from LD to HD at heading stage, the leaf water potential (LWP) reduced 31.9%, 54.8%, and 15.7% in HY113, HHZ, and ZH3, respectively. The non-photochemical quenching (NPQ) of HY113, HHZ, and ZH3 flag leaves increased by 150%, 97.6%, and 218%, respectively. The effective quantum yield of PSII photochemistry (ΦPSII) of flag leaves reduced by 20.3%, 11.9%, and 22.1% in HY113, HHZ, and ZH3, respectively. The enzymatic activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) increased by 11.4%, 18.0%, and 21.8% in HY113, and 13.2%, 14.3%, and 30.9% in HHZ, and 13.4% 21.7%, and 17.6% in ZH3 under MD on average across two seasons. The yield reduction of drought-resistant cultivars (HY113, ZH3) was smaller than that of conventional cultivars (HHZ). Maintaining leaf water potential (LWP), Pn, photosystem II (PSII) original light energy conversion efficiency, non–photochemical quenching coefficient (NPQ), and increasing in the ratio of photochemical reaction energy in fluorescence and antioxidant enzyme activity is the physiological basis to achieve a relatively high photosynthesis. These traits could be the target for breeder to develop drought-tolerant varieties.

Keywords Rice cultivation · Drought stress · Photosynthesis · Chlorophyll fluorescence · Yield
Introduction

Rice (Oryza sativa L.) is a staple food crop over the world, and more than 65% of the population in China take it as their staple diet (Peng et al. 2010). At present, 95% of rice is produced under traditional puddled transplanted conditions, leading to consumption of large amounts of fresh water. Previous studies suggest that rice production consumes about 65% of total agricultural water consumption (Li et al. 2016). However, with the global climate change, the uneven spatial–temporal distribution of precipitation has caused a severe shortage of freshwater resources, and seasonal drought stress has become a crucial abiotic factor restricting the development of traditional puddled transplanted rice production system in Central China (Wang et al. 2018a, 2019a; Zhuang et al. 2019). If per capita rice consumption is maintained at the current level, with population increasing, rice production need to be increased by about 20% by 2030 (Peng et al. 2009). Water deficit could occur at any stage of crop development, and the magnitude of stress depends on genotypes and soil types (Ji et al. 2012). However, the sensitivity to water deficit shows significant difference at different growth period of rice, many previous studies have shown that reproductive stage is the most susceptible period for rice (Pantuwana et al. 2002; Yang et al. 2019). The photosynthetic physiological activity of rice flag leaves were significantly reduced under drought stress at heading stage, which resulted in a conspicuous decrease in dry matter accumulation. Although the transfer rate and transformation rate of the existing stem sheath have been increased under alternate wet and dry irrigation, it was not enough to prevent the yield declining (Lauteri et al. 2014; Wang et al. 2017a; Park et al. 2011). Therefore, to better understand the physiological mechanism of different genotypes, cultivars coping with drought stress will bring us novel insight for future rice cultivation.

Leaf photosynthesis is the basis of crop yield formation, chloroplasts convert light energy into chemical energy, which is used to form carbohydrates by capturing and assimilating carbon dioxide (CO₂) (Zhu et al. 2010). Photosynthesis has been singled out as an important determinant of grain yield in cereal species. Therefore, many studies advocate breeding for improved photosynthesis as a sustainable means of increasing yields in rice (Liu et al. 2019a, 2020). The depression of leaf photosynthesis under LD might be due to CO₂ diffusion path from atmosphere to site of carboxylation that was narrowed; however, the decrease in leaf photosynthesis MD and HD is considered to be dominant by significant reduction in the quantum efficiency, maximum photochemical efficiency, and carboxylation efficiency (Sarabi et al. 2019; Flexas et al. 2004; Varone et al. 2012; Drake et al. 2017). Leaf as a primary photosynthetic organ in rice, the level of the leaf water potential, and the amount of chlorophyll content have a significant effect on photosynthesis (Meinzer et al. 2017; Takai et al. 2010). Previous studies have shown that leaf water potential participates in the regulation of cellular stomata movement (Zhou et al. 2017). Under drought stress, LWP will decrease, leading to stomatal closure and xylem embolization, which ultimately leads to a significant increase in resistance of water to the soil–plant–atmosphere transport process. If the LWP is kept at low level for too long, it will cause plant carbon starvation and death (Wang et al. 2018b; Johnson et al. 2018). Lack of CO₂ will promote photo-oxidative stress in the chloroplasts, which can lead to the photochemical activity of PSII decrease and the formation of reactive oxygen species (ROS). In addition, the degree of chloroplast structure damage and chlorophyll decomposition will be greatly increased under drought stress (Gholizadeh et al. 2017). However, some studies have found that high chlorophyll content is not a necessary condition for high photosynthetic rate of leaves, and the electron transport chain is not affected by the reduction of chlorophyll content (Gu et al. 2017). Appropriately reducing the chlorophyll content of the leaves can reduce the absorption of excessive light energy and light suppression, which can improve the PSII efficiency. On the other hand, it can reduce the consumption of nitrogen in the chlorophyll synthesis process of the leaves with rubisco enzyme content increase, ultimately increasing Pn of the leaves (Slattery et al. 2017; Wang et al. 2017b).

Chlorophyll fluorescence is generated during the photochemical reaction of chlorophyll molecules in the ground state stimulated by light during the initial reaction of photosynthesis. Chlorophyll fluorescence analysis is widely used to investigate the mechanism of photosynthesis and to identify variation in photosynthetic physiological circumstances (Li et al. 2013; Murchie and Lawson 2013; Meacham et al. 2017). Measuring chlorophyll fluorescence kinetics parameters such as the maximal quantum yield of PSII photochemistry (Fv/Fm), photochemical quenching (qP), ΦPSII, and NPQ can give a better understanding of the mechanism of the change in the activity of PSII under drought stress in different genotypes (Kanazawa and Kramer 2002; Ruban 2016; Zhou et al. 2013). Different genotypes are expected to respond differently to drought stress in chlorophyll fluorescence parameters. The PSII photochemical activities of drought-tolerant species could be maintained at a high level under drought stress (Wang et al. 2017a; Xing et al. 2018). Under drought stress conditions, an excess of light energy absorption leads to efficient photorespiration and excessive energy in the excited state, which may increase the accumulation of chloroplast ROS and oxidative...
damage (Lazár, 2015; Kirst et al. 2017; Dias et al. 2018). Under normal conditions, rice can maintain the balance of chloroplast ROS production and elimination through its own antioxidant enzyme system. Among them, SOD, POD, and CAT are the main roles to eliminate the accumulation of reactive oxygen species. However, the balance of this antioxidant system is broken under drought stress, and membrane lipid peroxidation occurs in the cell membrane, producing a large amount of malondialdehyde (MDA). The massive accumulation of MDA limits the activity of antioxidant enzymes and further accelerates cell death (Miller et al. 2010; Gill and Tuteja 2010; Shukla et al. 2012; Liao et al. 2019; Wang et al. 2019b).

However, the coordination between qP and NPQ in different cultivars and the coordination between them and photosynthetic capacity in response to drought stress still needs further study. Furthermore, these studies attempted to assess the effects of drought stress on photosynthetic physiology in upland rice, and comparison in photosynthetic physiology among different rice ecotypes are still scarce (Lauteri et al. 2014; Yun et al. 2016; Zu et al. 2017). To better understand the physiological mechanism of different genotypes cultivars coping with drought stress, we explored the changes of leaf water potential, chlorophyll content, photosynthesis, chlorophyll fluorescence, ROS, yielding, and their interrelationships using three different genotypes cultivars at heading stage to analyze their responses to different level of drought stress.

Materials and Methods

Site Description

Pot experiments were conducted in glass greenhouse at Huazhong Agricultural University, Hubei Province, China (30°28′N, 114°21′E) during rice growing season of 2013 and 2014 (May to October). The soils were taken at 0–30 cm depth from a paddy field, then air-dried and 2-mm sieved. The sieved soil was mixed with sand at a mass ratio of 4:1, and then 18 kg soil filled in plastic pots (30 cm × 30 cm × 25 cm) to 1.50 g cm−3 of bulk density. The pH, total nitrogen (N), available phosphorus, potassium, and organic matter of soil were 5.99, 0.21 g kg−1, 22.3 mg kg−1, 167 mg kg−1, and 1.20 g kg−1, respectively, in 2013 and 6.00, 0.18 g kg−1, 19.2 mg kg−1, 188 mg kg−1, and 1.04 g kg−1, respectively, in 2014. The glass greenhouse equipped with irrigation and cooling system, which is convenient for precise quantitative irrigation of each pot, while reducing the impact of high temperatures.

Experiment Design and Management

In this study, the experiments were laid out in a randomized complete block design using 12 replicates. Four drought stress levels traditional flooding (CK), mild drought stress (LD), moderate drought stress (MD), and severe drought stress (HD) were compared at heading stage with three different genotype rice cultivars Hanyou113 (HY113), Huangguazhan (HHZ), and Zhonghan3 (ZH3) in both 2013 and 2014. Among them, HHZ was a traditional cultivar, HY113 was a water-saving and drought resistance cultivar, and ZH3 was an aerobic cultivar. These three cultivars were mega varieties widely planted in Central China; drought resistance level is expressed as ZH3 > HY113 > HHZ. In addition, these three varieties have the same growth period performance. To better control soil water status, 3 cm water level were kept during the whole growth season for CK, while soil drought stress was monitored by soil moisture tensiometer (Procheck, Decagon Devices, Pullman, WA, USA) at 9:00, 14:00, and 17:00, maintain 85%, 70%, and 55% of saturated soil moisture for LD, MD, and HD, respectively. From then on, 3 cm of water level was kept in the pots until 1 week before harvest. Except for rainfall, other meteorological data (daily average temperature) were collected through weather monitor (TPi-20, Tuopu Instruments Ltd, Zhejiang, China), installed close to the experimental site.

Twenty-day-old seedlings were manually transplanted into well prepared soil with two seedings per pot on 15 May in both 2013 and 2014. A commercial compound fertilizer (N:P2O5:K2O = 15:15:15) dose of 12 g per pot was applied at soil preparation. In addition, 4.48 g N was applied at tillering and panicle initiation following the ratio of 5:5 in the form of urea. Weeds, diseases, and insects were intensively controlled throughout the whole growing season in both years to avoid yield loss.

Sampling and Analysis

Chlorophyll was extracted from uppermost fully expanded leaves with 80% acetone, and chl a, chl b, Car were determined throughout UV-1900 spectrophotometer (Shimadzu, Japan) as described (Dinc et al. 2012). Leaf vein were removed, then soaking with anhydrous ethanol, dark treatment at 4°C for 48. Chlorophyll content were estimated on the basis of the absorbance at 470 nm, 649 nm and 665 nm. Leaf water potential (LWP) was determined according to the method used by Zhou, six fully expanded leaves (those for which gas exchange measurements) were sampled and cut into small pieces and mixed immediately (< 20 s) at midday (12:00–14:00). A WP4 Dew-point potential meter (WP4C, Decagon Devices Inc., USA) was used for LWP measurement (Zhou et al. 2017).
chlorophyll fluorescence was determined at heading stage using a portable FMS–2 Pulse Modulated Fluorometer (Hansatech, England) (Ruban 2016). The minimal fluorescence level (F$_0$), variable fluorescence (F$_v$) and maximal fluorescence level (F$_m$) was measured after dark adaption for 20 min. The minimal fluorescence parameters level in light adapted state (F'$_0$) was observed by illumination the leaf with far-red light. The parameters were calculated following the method of Gauthami et al. (2014). The maximal (dark–adapted) quantum yield of PSII photochemistry, photochemical quenching coefficient, non–photochemical quenching coefficient, and effective (light–adapted) photochemical efficiency were calculated as F$′_v$/F$′_m$ = (F$'_m$–F$'_0$)/F$'_m$, q$′$ = (F$'_m$–F$'_0$)/(F$'_m$–F$'_0$), NPQ = (F$'_m$–F$'_0$)/F$'_m$, and Φ$_{ph}$ = (F$'_m$–F$'_0$)/F$'_m$, respectively.

The full expanded leaves without vein (0.5 g) were crushed into powder in a mortar with pestle under liquid nitrogen. In addition, a small amount of quartz sand also needs to be added during grinding. A reaction mixture was prepared by adding 50 mM phosphate buffer (pH 7.0) and 1% (w/v) polyvinyl pyrrolidone at 0 °C for extracting crude enzyme of the powder. The homogenate was centrifuged at 15,000 g for 20 min, and the supernatant was taken for enzyme activity measurement. The SOD activity was assayed as well as other antioxidative enzymes by CANOCO 5.0 (Microcomputer Power Ithaca, USA; Braak and Smilauer, 2012).

**Results**

**Effects of Drought Stress on Grain Yield and Yield Components**

Drought stress at heading stage reduced grain yield across cultivars, and yield decline increased with the increase of drought intensity. The grain yield reduced by 14.9%, 30.8%, and 12.8% in HY113, HHZ, and ZH3 under LD, respectively, 32.9%, 33.7%, and 22.9% in HY113, HHZ, and ZH3 under MD, respectively, and 53.6%, 45.6%, and 30.8%, 12.8% in HY113, HHZ, and ZH3 under LD, respectively. Which can account for the yield loss under the LD. With the increase of drought stress, especially under the HD, the reduction of effective spikes, number of spikelets per panicle, and 1000-grain weight contributed to the reduction of grain yield. In addition, the average grain yield in 2014 was lower about 32.9%, 39.7%, and 41.7% than in 2013, respectively. The results of the analysis of variance show
that there is a significant interaction between the treatment and the year.

**Chlorophyll Content and Ratio of Chlorophyll a (Chla) and Chlorophyll b (Chlb)**

Except for carotenoids, the content of Chla and Chlb of flag leaves were significantly decreased under drought stress at heading stage and the chlorophyll content reduce along with the increase of drought intensity. However, changes in chlorophyll content under drought conditions showed differences among rice varieties, for HY113 and HHZ, they were reduced by 16.1% and 17.8%, respectively, under severe drought stress, while ZH3 was reduced by 9.85%, and the variation tendency is accordant in 2013 and 2014 (Table 2). As shown in Fig. 1, the ratio of Chla to Chlb was increased significantly with the increase of drought stress level at heading stage, the ratio was increased by 13.8% in HY113, 10.7% in HHZ, and 16.0% in ZH3 on average across two seasons, respectively.

**Response of LWP to Drought Stress**

The drought stress treatment to these tress cultivars (HY113, HHZ and ZH3) resulted in water deficit. The response of flag leaves toward water deficit were compared by analyzing LWP. During the drought periods from LD to HD at heading stage, the LWP reduced 31.9% from −0.94 Mpa to −1.24 Mpa, and 54.8% from −0.97 Mpa to −1.50 Mpa, and 15.7% from −0.89 Mpa to −1.03 Mpa in HY113, HHZ and ZH3, respectively (Fig. 2). Maintain of leaf water relations parameters to that CK was more stable in drought-tolerant
cultivar ZH3 than HY113 and HHZ, the differences between these cultivars were more pronounced at severe drought conditions.

### Changes of Photosynthetic Parameters Under Drought Stress

Figure 3a shows that the $P_n$ of flag leaves decreased gradually as compared to CK during the drought stress periods at heading stage and the magnitude of decline was greater for all cultivars under severe drought stress. The $P_n$ decreased 49.0% from 20.0 to 10.2 µmol m$^{-2}$ s$^{-1}$ in HY113, and 67.6% from 23.4 to 7.58 µmol m$^{-2}$ s$^{-1}$ in HHZ, and 39.3% from 23.4 to 14.2 in ZH3. The $P_n$ of HHZ was similar to that of ZH3 under CK conditions. However, it is found in Fig. 3b that the intercellular carbon dioxide concentration ($C_i$) decreases at first and then increases as the degree of drought stress increases. Figure 3c and d show that the stomatal conductance ($G_s$) and transpiration rate ($T_r$) variable tendency of flag leaves is identical to the $P_n$. The $G_s$ decreased 64.0% from 0.50 to 0.18 mol m$^{-2}$ s$^{-1}$ in HY113, and 68.8% from 0.61 to 0.19 mol m$^{-2}$ s$^{-1}$ in HHZ, and 54.3% from 0.35 to 0.16 mol m$^{-2}$ s$^{-1}$ in ZH3. The $T_r$ decreased 71.7% from 12.7 to 3.60 mmol m$^{-2}$ s$^{-1}$ in HY113, and 73.6% from 13.8 to 3.65 mmol m$^{-2}$ s$^{-1}$ in HHZ, and 71.2% from 12.5 to 3.60 mmol m$^{-2}$ s$^{-1}$ in ZH3.

### Effects of Drought Stress on the Photosynthetic Response Curve Parameters

Photosynthesis light response curve is useful to estimate the adaptation of plants to adversity stress. The photosynthetic rate increases with the increase of photosynthetically active radiation within a certain range, but the increase amplitude was different. However, the photosynthetic curve was separated with different drought stress degree, and the greater the stress degree was, the smaller the increase amplitude of the light response curve was (Fig. 4). Drought stress at the heading stage resulted in a significant decrease in maximum photosynthetic rate ($P_{\text{max}}$), apparent quantum yield ($\Phi$) and light saturation point ($L_{\text{SP}}$), and a significant increase in light compensation point ($L_{\text{CP}}$), but it had no significant effect on dark respiration ($R_d$) (Table 3). The $P_{\text{max}}$ decreased 53.8% from 26.4 to 12.2 µmol m$^{-2}$ s$^{-1}$ in HY113, and 58.2 from 26.1 to 10.9 µmol m$^{-2}$ s$^{-1}$ in HHZ, and 45.3% from 25.6 to 14.0 µmol m$^{-2}$ s$^{-1}$ in ZH3. The $\Phi$ decreased 50.8% from 0.063 to 0.031 mol µmol$^{-1}$ in HY113, and 70.4% from 0.071 to 0.021 mol µmol$^{-1}$ in HHZ, and 47.5% from 0.061 to 0.032 mol µmol$^{-1}$ in ZH3. The $L_{\text{SP}}$ decreased 33.6% from 1840 to 1221 µmol m$^{-2}$ s$^{-1}$ in HY113, and 33.0% from 1862 to 1247 µmol m$^{-2}$ s$^{-1}$ in HHZ, and 32.0% from 1874 to 1274 µmol m$^{-2}$ s$^{-1}$ in ZH3. While the $L_{\text{CP}}$ increased 48.4% from 38.6 µmol m$^{-2}$ s$^{-1}$ in HY113, and 56.9% from 33.9 to 53.2 µmol m$^{-2}$ s$^{-1}$ in HHZ, and 25.8% from 32.2 to 40.5 µmol m$^{-2}$ s$^{-1}$ in ZH3.

### Effects of Drought Stress on Chlorophyll Fluorescence Characteristics

Chlorophyll fluorescence technology is an important means to reflect the interaction between plant leaf photosynthesis and survival environment. The chlorophyll fluorescence characteristics including $F_v/F_m$, $\Phi_{\text{PSII}}$, and $q_p$ of flag leaves all significantly decreased under MD and HD at heading stage, except for NPQ (Fig. 5). The $F_v/F_m$ of flag leaves reduced by 15.2%, 19.7%, and 21.3% in HY113, HHZ, and ZH3, respectively (Fig. 5a). The NPQ of HY113, HHZ, and ZH3 flag
leaves increased by 150%, 97.6%, and 218%, respectively (Fig. 5b). The ΦPSII of flag leaves reduced by 20.3%, 11.9%, and 22.1% in HY113, HHZ, and ZH3, respectively (Fig. 5c). The qP of flag leaves reduced by 19.3%, 21.7%, and 19.7% in HY113, HHZ, and ZH3, respectively (Fig. 5d).

Monitoring the light energy conversion, electron transfer, distribution and heat dissipation parameters absorbed by the leaf through chlorophyll fluorescence technology can better reflect the true situation of photosynthesis. In the distribution and transformation of light energy

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**Fig. 1** Different response of the ratio of Cha and Chb to HD at heading stage in 2013 and 2014. CK indicates traditional flooding and HD is severe drought stress at heading stage. Different letters indicate statistical significance in variables mean among treatment according to LSD (P ≤ 0.05), vertical bars represent standard errors

**Fig. 2** Effects on LWP under different drought stress levels at heading stage in 2013 and 2014. CK indicates traditional flooding, LD is mild drought stress, MD is moderate drought stress, and HD is severe drought stress at heading stage. Vertical bars represent standard errors
absorbed by flag leaves, the PSII photochemistry (P) decreased significantly under drought stress, while excess energy (E) and antennas heat dissipation (D) increased significantly (Table 4). The P reduced by 24.6% in HY113, 27.0% in HHZ, and 13.4% in ZH3, while the E and D was increased by 66.7% and 48.0% in HY113, 57.1% and 34.8% in HHZ, and 25.0% and 47.8% in ZH3.

Fig. 3 (a) $P_n$; (b) $C_i$; (c) $G_s$; and (d) $T_r$ in photosynthetic traits changes under different drought stress levels at heading stage in 2013 and 2014. CK indicates traditional flooding, LD is mild drought stress, MD is moderate drought stress, and HD is severe drought stress at heading stage. Vertical bars represent standard errors.

Fig. 4 Effects on photosynthetic light response curve under different drought stress levels at heading stage. CK indicates traditional flooding, LD is mild drought stress, MD is moderate drought stress, and HD is severe drought stress at heading stage.
Effects of Drought Stress on Antioxidant Enzyme Activity and MDA

The enzymatic activities of SOD, POD, CAT was gradually increased under LD and MD, but decreased significantly under HD at heading stage (Table 5). The enzymatic activities of SOD, POD, CAT increased by 11.4%, 18.0% and 21.8% in HY113, and 13.2%, 14.3% and 30.9% in HHZ, 13.4% 21.7% and 17.6% in ZH3 under MD on average across two seasons. Compared with MD, the activity of SOD, POD, CAT is significantly reduced by 16.1%, 24.1% and 14.7% in HY113, and 17.2% 20.1% and 7.6% in HHZ, and 9.8%, 26.5% and 7.7% in ZH3. The MDA content of HY113, HHZ and ZH3 had an increasing trend under LD at the heading stage, but there was no statistical difference. Moreover, the MDA content increased significantly by 14.7%, 15.3%, and 9.8% in HY113, HHZ and ZH3, respectively.

Fig. 5 (a) Fv/Fm; (b) NPQ; (c) ΦPSII; and (d) qP changes of chlorophyll fluorescence parameters under different drought stress levels at heading stage in 2013 and 2014. CK indicates traditional flooding, LD is mild drought stress, MD is moderate drought stress, and HD is severe drought stress at heading stage.
and 35.3% under HD, respectively (Table 5). It shows that under HD, the cell membrane is seriously damaged due to the accumulation of peroxides.

Path Analysis of Photosynthetic

Path analysis of photosynthetic rate and pigment, chlorophyll fluorescence, antioxidative enzymes in drought-resistant-type (HY113, ZH3) and non-drought-resistant-type HHZ in Fig. 6a and b, which could be useful for understanding the true relationship between photosynthesis and related parameters. The results showed that for the drought-resistant varieties, the order of the magnitude of the impact on photosynthesis is $G_s > \Phi_{PSII} > SOD > NPQ > Caro$, when it comes to no-drought-resistant varieties, the order turns to be $\Phi_{PSII} > C_i > CAT > F_v/F_m$.

Discussion

In this experiment, different levels of drought stress were treated at the heading stage of rice through pot experiments. Our results showed that drought at the heading stage significantly reduced the grain yield, and the yield was negatively correlated with the degree of drought stress (Table 1), which was consistent with the previous studies (Yang et al. 2019; Chang et al. 2016). Due to the high temperature in 2014, the reduction in yield was greater than in 2013. Compared with HY113 and HHZ, the yield of ZH3 decreases slightly under the same drought stress conditions. ZH3 can maintain relatively high LWP and $P_n$ should be the basis for maintaining yield under drought stress. Yield components are the basis for the formation of rice output and the changes in yield components caused by drought stress at different growth stages of rice was the key to determine the final grain yield. The accumulation of photosynthetic products from heading stage to maturity stage is crucial for yield formation. Drought stress at heading stage has an effect on number of spikelet per panicle and 1000-grain weight, but the significant reduction in seeding rate is an important factor led to the reduction of rice yield (Table 1). This study shows that the LWP reduced 31.9%, 54.8%, and 15.7% in HY113, HHZ, and ZH3, respectively (Fig. 2). Studies have shown that reduction in LWP led to panicle birth defect and a negative correlation was found between LWP and spikelet sterility under drought stress at flowering stage. The lower LWP with higher leaf temperature may be an important cause of spikelet sterility in rice (Liu et al. 2006).

The dry matter accumulated through photosynthesis is the basis of plant growth and yield, and improving photosynthetic production efficiency is the goal of crops to cope with drought stress. Photosynthetic rate decline is affected by stomatal limitation and non-stomatal limitation (Drake et al. 2017). Studies have found that the main factor leading to the decrease of $P_n$ under LD and MD is stomatal limitation, while under HD, non-stomata limitation takes the lead (Li et al. 2017). In this experiment, under LD and MD at heading stage, $G_s$ and $P_n$ of leaf decreased almost simultaneously, indicating that the decrease in $P_n$ was mainly due to stomatal limitation. Nevertheless, we still need to explain the changes in rice leaf photosynthesis under drought conditions from the perspective of chloroplast microstructure and key enzymes of photosynthetic metabolism in the future.

However, under HD, $C_i$ increased significantly, and $P_n$ was still falling, indicating that stomatal limitation became the main reason for restricting $P_n$, which is consistent with the results of previous studies. (Fig. 3a). In addition, the $P_n$ of ZH3 and HY113 under different drought stress levels are higher than that of HHZ, indicating that drought-resistant cultivar could show better performance in $P_n$ after suffer drought stress. Analysis of the light response curve shows that HHZ will cause photoinhibition when the light intensity reaches 1000 $\mu$mol m$^{-2}$ s$^{-1}$ under drought stress. For ZH3 and HY113, the light intensity needs to reach 1500 $\mu$mol m$^{-2}$ s$^{-1}$ photoinhibition will occur, and the maximum photosynthetic potential of ZH3 and HY113 is significantly higher than HHZ.

The photosynthetic rate depends on the Rubisco activity and the electron transfer rate. By monitoring the process of light energy conversion, electron transfer, distribution, and heat dissipation absorbed by the leaves, our research found that the chlorophyll fluorescence characteristics including $F_v/F_m$, $\Phi_{PSII}$, $q_p$ of flag leaves all significantly decreased under moderate and HD at heading stage, except for NPQ, and the magnitude of decline and increase was greater for

| Varieties | Treatments | $P$ (%) | $E$ (%) | $D$ (%) |
|-----------|------------|---------|---------|---------|
| HY113     | CK         | 0.69 a  | 0.06 c  | 0.25 d  |
|           | LD         | 0.65 ab | 0.06 c  | 0.29 c  |
|           | MD         | 0.63 b  | 0.07 b  | 0.31 b  |
|           | HD         | 0.52 c  | 0.10 a  | 0.37 a  |
| HHZ       | CK         | 0.63 a  | 0.14 b  | 0.23 c  |
|           | LD         | 0.55 b  | 0.20 a  | 0.25 c  |
|           | MD         | 0.49 c  | 0.23 a  | 0.28 b  |
|           | HD         | 0.46 c  | 0.22 a  | 0.31 a  |
| ZH3       | CK         | 0.67 a  | 0.08 b  | 0.23 c  |
|           | LD         | 0.64 ab | 0.08 b  | 0.28 b  |
|           | MD         | 0.62 b  | 0.08 b  | 0.29 b  |
|           | HD         | 0.58 c  | 0.10 a  | 0.34 a  |

CK: Traditional flooding; LD: Mild drought stress; MD: Moderate drought stress; HD severe drought stress. Lowercase letters indicate significant differences ($P \leq 0.05$) among means across water treatments within varieties for each year according to an ANOVA.
all cultivars under HD (Fig. 5). Which indicates that drought stress reduced the open ratio of PSII reaction centers in the leaves and reduced the ability of PSII to transfer electrons, resulting in a significant decrease in PSII's original light energy conversion efficiency, and ultimately leading to insufficient ATP and NADPH energy required for CO₂ assimilation in the photosynthetic system. The decrease of PSII reaction center activity under HD is the main reason for the decrease of photosynthetic rate (Liu et al. 2019b).

The generation of residual light energy leads to an increase in active oxygen, which led the enzymatic activities of SOD, POD, CAT was gradually increased under mild and MD, and decreased significantly under HD at heading stage (Table 5). Plants activates the antioxidant enzyme system to remove the superoxide anion O₂⁻ formed under strong light due to carbon assimilation hindered by SOD, and the generated H₂O₂ can be further

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**Table 5** Effects of antioxidant enzyme activity and malondialdehyde content in leaves of different types of rice under drought stress

| Year | Varieties | Treatments | SOD (U/g) | POD (U/g) | CAT (U/g) | MDA (nmol/g) |
|------|-----------|------------|-----------|-----------|-----------|--------------|
| 2013 | HY113     | CK         | 340 b     | 19.4 b    | 29.4 b    | 15.2 b       |
|      |           | LD         | 367 a     | 21.3 a    | 33.2 a    | 15.5 b       |
|      |           | MD         | 383 a     | 23.0 a    | 34.2 a    | 16.9 ab      |
|      |           | HD         | 313 c     | 18.1 b    | 26.4 b    | 17.7 a       |
|      | HHZ       | CK         | 457 c     | 32.7 b    | 17.1 c    | 14.7 b       |
|      |           | LD         | 473 b     | 33.0 ab   | 20.9 b    | 15.0 b       |
|      |           | MD         | 512 a     | 35.9 a    | 24.9 a    | 16.3 ab      |
|      |           | HD         | 448 c     | 27.3 c    | 22.5 ab   | 17.7 a       |
|      | ZH3       | CK         | 265 c     | 20.9 b    | 23.9 c    | 25.0 c       |
|      |           | LD         | 273 b     | 25.4 a    | 25.6 b    | 27.7 bc      |
|      |           | MD         | 316 a     | 24.6 a    | 28.4 a    | 29.7 b       |
|      |           | HD         | 284 b     | 18.0 b    | 26.5 b    | 31.5 a       |
| 2014 | HY113     | CK         | 433 bc    | 42.0 c    | 30.0 c    | 14.0 b       |
|      |           | LD         | 459 b     | 45.5 b    | 32.3 b    | 15.1 a       |
|      |           | MD         | 477 a     | 49.3 a    | 38.2 a    | 15.0 a       |
|      |           | HD         | 411 c     | 40.7 c    | 36.1 ab   | 15.8 a       |
|      | HHZ       | CK         | 427 b     | 50.3 b    | 30.6 c    | 17.6 b       |
|      |           | LD         | 428 b     | 50.5 b    | 32.6 bc   | 17.6 b       |
|      |           | MD         | 488 a     | 59.8 a    | 38.7 a    | 18.3 ab      |
|      |           | HD         | 381 c     | 39.0 c    | 33.6 b    | 19.4 a       |
|      | ZH3       | CK         | 399 b     | 36.2 bc   | 25.4 d    | 23.8 c       |
|      |           | LD         | 391 b     | 39.6 b    | 54.4 c    | 27.2 bc      |
|      |           | MD         | 429 a     | 45.5 a    | 83.0 a    | 30.9 b       |
|      |           | HD         | 388 c     | 33.6 c    | 75.7 b    | 34.4 a       |

**Source of variation**

| Year (Y) |  *  |  *  | ns | ns |
| Treatment (T) |  *  |  *  |  *  |  *  |
| Y×T      |  *  |  *  | ns | ns |

CK: Traditional flooding; LD: Mild drought stress; MD: Moderate drought stress; HD severe drought stress. Lowercase letters indicate significant differences ($P \leq 0.05$) among means across water treatments within varieties for each year according to an ANOVA. * Significant at $p \leq 0.05$; ** Significant at $p \leq 0.01$; ns, non-significant.
detoxified by POD and CAT to form H2O to reduce the damage of free radicals to plants. The reduced activity of PSII reaction center leads to insufficient carbon assimilation capacity in leaves. The excess energy is consumed in the form of heat dissipation NPQ, and the unconsumed part of the energy causes damage to photosynthetic organelles such as cell chloroplasts, which will be produced in plants. A large amount of reactive oxygen species breaks the balance of the ROS scavenging system (Rejeb et al. 2014). At the same time, due to the accumulation of a large amount of reactive oxygen species, the permeability of the cell membrane and the accumulation of MDA content increase, all of which ultimately lead to a significant decline in the photosynthetic capacity of the leaves.

## Conclusion

Drought-resistant cultivars ZH3 showed good yield advantage relative to other two varieties (HY113, HHZ) under drought stress at heading stage, especially under HD. Maintain high photosynthetic capacity and photosynthetic efficiency to promote the formation and accumulation of assimilation under drought stress is the key to achieving stable yield under drought stress for drought-resistant cultivars. Photosynthetic capacity is regulated by chlorophyll and LWP. photosynthetic efficiency is affected by the interaction between qP and NPQ and the activity of PSII, and the protective enzymes in the leaves can ensure the activity of PSII, avoid chlorophyll degradation, and ensure photochemical energy conversion efficiency. Therefore, maintaining higher LWP, PSII primary light energy conversion efficiency, NPQ after being exposed to drought stress, and higher photochemical reaction energy ratio are the main physiological parameters for drought-resistant cultivars to maintain relatively high photosynthesis under drought conditions. These traits could be the target for breeder to develop drought-tolerant varieties.

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## Author Contributions

CC and PL conceived the experiments. XY, LC, HB and YJ conducted the experiments and collected the data. BW and YJ analyzed the data and BW wrote the manuscript. All authors revised the manuscript.

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## Data Availability

All data supporting the conclusions of this manuscript are provided within the manuscript.

## Declarations

### Conflict of interest

The authors declare that they have no competing interests.

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