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# Response of photosynthesis and chlorophyll fluorescence to drought stress in two maize cultivars

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This study investigated the changes of leaf photosynthetic characteristic and chlorophyll fluorescence parameter responding to drought stress (DS) in two species of maize at elongating stage. The results of net photosynthesis rate ( $P_n$ ) and light intensity response curve indicated that  $P_n$  reduced with enhanced light intensity. Photoinhibition in varying degrees appeared in different genotype varieties, and DS intensified the extent of photoinhibition. Results showed that for DS at elongating stage,  $P_n$  of the cultivar JD28 was insensitive to highlight.  $P_{max}$  and  $R_d$  decreased, and physiological activity reduced obviously. Compared with JD28, JD261 decreased more. Moreover, DS resulted in decreased light compensation point (LCP) and light saturation point (LSP). And it caused highlight utilization ratio reduced but weak light use efficiency increased. JD28 had higher light use efficiency. Diurnal variation curve of  $F_v/F_m$  changed greatly in DS and there was no significant difference between the two species. DS treatments decreased photochemical quenching (qP), PhiPS2 and  $F_v'/F_m'$ , while it increased non-photochemical quenching (NPQ). The reduction of PhiPS2 was caused by the decrease of qP and  $F_v'/F_m'$ . DS treatments weakened maize leaves' capability of assimilation, transformation and light energy utilization. JD28 could use more light than JD261 in photosynthesis. While JD261's light use efficiency was lower, the less light used for photosynthesis and the excessive photon flux energy was dissipated in form of heat.

**Key words:** Elongating stage, maize, drought-tolerance, photosynthesis.

## INTRODUCTION

Agro-meteorological hazard is the major limiting factor for plant growth and food production in many regions of the world. Among agro-meteorological hazards, drought has the greatest effect on yield stability (Vinocur and Altman, 2005; Li et al., 2000). It can seriously affect the grain quality and grain output reducing average yields by 50% or even more (Wang et al., 2003). With the increase of the world population and decrease of crop water resources, it is significant to develop crops with a high utilization of water as well as a good drought tolerance (Barnabas et al., 2008). Maize, a water-intensive crop, is vulnerable to water stress, especially during early growth

stage (Bartels and Nelson, 1994; Edmeades et al., 1993; Farre et al., 2000). Northeast China is an important rainfed corn-producing region which usually experience limited and irregular precipitation during growing season. Northeast China has a large region of dryland farming, which accounts for about 55% of the nation's total cultivated land area. Drought tends to occur more often, and its degrees of damage on maize production have increased recently owing to global climate change (Zhang, 2004).

Previous studies have showed that different genotypes of maize have different growing responses to drought stress (Li and Van Staden, 1998; Efeoğlu, 2009; Bohnert et al., 1995). Chaves (2003) and Mahajan (2005) have suggested that as the earliest responses to drought, stomatal closure and a decrease in the rate of

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photosynthesis can reduce vegetative growth. The productivity of crops is directly related to their ability to obtain resources such as water and light, and then convert these physical resources into biological materials (Azam-Ali et al., 1994). Photosynthesis, as a significant physiological process to yield is sensitive to water stress. The photosynthetic rate keeps decreasing while the intensification of stress increases, which is the main reason for the reduction of yield by drought (Boyer, 1970; Ephraïm, 1991).

Moreover, it is possible to determine if there is damage to light reaction systems in photosynthetic machinery during drought (Jones, 2005). Photosynthetic light-response curve can reflect the relationship between photosynthetic rate and illumination intensity. This curve is very important to judge the photosynthetic capacity of plant (Jiang and He, 1999). Measuring chlorophyll fluorescence has become a very useful technique in obtaining rapid qualitative and quantitative information on photosynthesis (Roháček, 1999), and it can provide information on the relationship between structure and function of photosystem II (PSII) reaction center (Rosenqvist and Van Kooten, 2003). Chlorophyll fluorescence analysis is a useful, non-invasive, powerful, and reliable technique to assess the changes in function of PSII under different environments (Schreiber et al., 1994; Sayed, 2003; Colom, 2003; Mauchamp and Methy, 2004). It can check the composition and organization of photosystems, the excitation energy transfer, the photochemistry, and the effects of various stresses on plants (Yang, 2009). Chlorophyll fluorescence provides useful information about leaf photosynthetic performance of many plants under drought stress (Baker and Rosenqvist, 2004). Furthermore, chlorophyll fluorescence can tell the extent to which PSII is using the energy absorbed by chlorophyll and the extent to which it is being damaged by excessive light (Maxwell and Johnson, 2000).

Drought stress plants show a reduction of the photochemical chlorophyll fluorescence quenching, photosystem II quantum yield and electron transport rate and more heat dissipation as compared to controls (Dias and Bruggemann, 2010). Light energy absorbed by chlorophyll molecules in a leaf can undergo one of three fates: it can be used to drive photosynthesis (photochemistry), excessive energy can be dissipated as heat or it can be re-emitted as light-chlorophyll fluorescence. These three processes occur in competition, that is - any increase in the efficiency of one will result in a decrease in the yield of the other two (Maxwell and Johnson, 2000). Therefore, the objectives of the present study were to investigate (i) the fates of light energy absorbed by chlorophyll molecules in maize leaf, (ii) the change of photosynthesis, (iii) chlorophyll fluorescence quantum yield and consumption of excessive light energy in DS. This information would be valuable in determining whether these traits can be used for selecting drought-tolerance genotypes at early stage of maize growth.

## MATERIALS AND METHODS

### Experimental design

The pot incubation test took place at Shenyang Agricultural University (SAU)'s experimental station in Shenyang, Liaoning Province, China (123°4' E, 41°8' N, 49 m above sea level) under greenhouse conditions in 2010. The pot was 33 cm in diameter and 28 cm in height, filled with 16 kg Brunisolic soil obtained from the experimental field of SAU in May 2011. Relevant soil properties were as follows: pH 5.76, organic matter 6.76 g·kg<sup>-1</sup>, total nitrogen (N) 1.26 g·kg<sup>-1</sup>, total phosphorus (P; P<sub>2</sub>O<sub>5</sub>) 1.17 g·kg<sup>-1</sup> and total potassium (K; K<sub>2</sub>O) 24.36 g·kg<sup>-1</sup>. Before sowing, a compound fertilizer consisting of 2.5 - 4.2 - 15.4 g·pot<sup>-1</sup> of N-P<sub>2</sub>O<sub>5</sub>-K<sub>2</sub>O was incorporated into the soil. An additional 5 g (N) per pot of solution fertilizer was added during elongating stage.

Two maize (*Zea mays* L.) cultivars, JD28 and JD261, were used in present study based on their relatively similar date of anthesis and clear differences in yield under drought and in absence of stress. For each cultivar, two treatments including well-irrigated (CK) and drought stress (DS) were applied. We obtained a field water capacity of ca. 45% (DS) and 65% (CK) (Bączek-Kwinta and Seidler-Lozykowska, 2011). All pots were arranged in randomized block design with three replications. Five seeds were planted in one pot and then thinned to one plant per pot two weeks after emergence. The pots were placed in a greenhouse under natural light from May to October, 2011. Drought stress was imposed on the plants 50 days after sowing by withholding irrigation for 7 days and then re-watering as CK.

### Plant photosynthesis

Net photosynthesis rate (P<sub>n</sub>), stomatal resistance (G<sub>s</sub>), intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) and transpiration (T<sub>r</sub>) of single leaves were measured on the middle of first young fully mature healthy leaf on the elongating stage in 2011, with a portable photosynthesis system (LI-6400, LI-COR Inc., Lincoln, NE, USA). The CO<sub>2</sub> concentration, temperature and relative air humidity in leaf chamber were respectively kept at 400 μmol mol<sup>-1</sup>, 25 ± 0.5°C and 60 ± 1%. During the measurements of light response curves of photosynthetic characteristics, photosynthetic photon flux density (PPFD) was 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 80, 60, 40, 20, 10 and 0 μmolm<sup>-2</sup>s<sup>-1</sup>, adjusted automatically by a red-blue light-emitting diode (LED) light source (LI-6400-02B LED; LI-COR). All parameters were measured from 09:00 to 17:00h on a clear, cloudless day. Measurements were repeated five times with three plants each time.

### Plant chlorophyll fluorescence

Chlorophyll fluorescence was measured with an auxiliary equipment of LI-6400 (LI-6400-40LCF; LI-COR). Leaves were dark-adapted for 30 min prior to the measurement of the minimal fluorescence (F<sub>0</sub>), maximum fluorescence (F<sub>m</sub>), variable fluorescence (F<sub>v</sub>) and maximum photochemical efficiency of photosystem II (F<sub>v</sub>/F<sub>m</sub>). F<sub>v</sub>/F<sub>m</sub> was calculated through (F<sub>m</sub>-F<sub>0</sub>)/F<sub>m</sub>. Light-adapted for about 10 min before the quantum efficiency of photosystem II (PSII), photochemical quenching (qP) and non-photochemical quenching (NPQ) of chlorophyll fluorescence were measured. Then PPFD values were obtained over a range of between 0 and 2000 μmolm<sup>-2</sup>s<sup>-1</sup>. The relative effective quantum yield of photochemical energy conversion at steady-state photosynthesis was calculated as: Φ<sub>PS2</sub> = (F<sub>m</sub>'-F<sub>s</sub>)/F<sub>m</sub>', where F<sub>s</sub> and F<sub>m</sub>' are respectively the fluorescence at steady-state photosynthesis and the maximum fluorescence in the light. qP was calculated as: (F<sub>m</sub>-F<sub>m</sub>')/(F<sub>m</sub>'-F<sub>0</sub>). NPQ quenching was calculated

as  $(F_m - F_m')/F_m'$  (Genty et al., 1989). The measurement of diurnal  $F_v/F_m$  change was conducted from 6:00 to 18:00 at one-hour intervals.

### Modeled photosynthetic parameters

The relationship between the light response curves  $P_n$  and PPFD was fitted with a Michaelis-Menten model (Thornley, 1976) as shown in Equation 1. SPSS 11.0 was employed to simulate the photosynthetic parameters.

$$P_n = \frac{\alpha PPFD P_{\max}}{\alpha PPFD + P_{\max}} - R_d \quad (1)$$

Light compensation point (LCP) and light saturation point (LSP) can be calculated according to equation (2) and (3):

$$LCP = \frac{P_{\max} R_d}{\alpha(P_{\max} - R_d)} \quad (2)$$

$$LSP = \frac{P_{\max} (0.75 P_{\max} + R_d)}{\alpha(0.25 P_{\max} - R_d)} \quad (3)$$

The light use efficiency (LUE) was calculated using equation (4):

$$LUE = \frac{P_n}{PPFD} \quad (\text{Long, 1993}) \quad (4)$$

Where  $\alpha$  is the estimated apparent quantum yield ( $\mu\text{mol CO}_2 \mu\text{mol PPFD}^{-1}$ ). The maximum net photosynthetic rate ( $P_{\max}$ ) is the estimated maximum net photosynthetic rate of  $P_n$  at saturating PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and apparent dark respiration rate ( $R_d$ ) is the estimated apparent dark respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Ruimy et al., 1995).

### Data analysis

The experimental data were analyzed with SPSS (Version.11.0) statistical programme (Chicago, USA). Probabilities of significance were used to test the significance among treatments and LSD ( $P < 0.05$ ) was used to compare the means. All measurements were recorded five times repeatedly for each sampling data.

## RESULTS AND ANALYSIS

### The light response curves of $P_n$

The relationship between  $P_n$  and PPFD corresponds with a rectangular hyperbolic curve, and can be described by Model Michaelis-Menten, through which parameters  $\alpha$ ,  $P_{\max}$  and  $R_d$  were worked out.  $P_n$  of all test maize cultivars during their elongating stage fitted the rectangular hyperbolic equation well under CK and DS, ( $R^2$  values being above 0.98), and there were differences among cultivars. Figure 1 shows the light-response curve for  $P_n$  using the estimated value calculated by the

parameters in Table 1. Regardless of DS, the  $P_n$  value increased rapidly as PPFD increased to  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  and then increased slowly to a maximum, followed by a slow decrease as PPFD increased to  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . On the whole, at low irradiance (below  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), JD261 had similar shapes of photosynthetic light-response curve with JD28 counterparts. However, the difference between CK and DS in the shape of photosynthetic light-response curve broadened with the increase in irradiance (Figure 1). The net photosynthetic rate in JD261 was lower than that in JD28 under DS.

Compared with the ones under CK, the value of  $R_d$  (apparent dark respiration rate) declined significantly ( $P < 0.05$ ) in DS plants (Table 1).  $R_d$  of JD28 and JD261 was respectively decreased by 30.79 and 54.39% in DS plant.  $P_{\max}$  at saturating light intensities and  $\alpha$  of photosynthetic light response were also decreased in DS plant (Table 1). The value of  $P_{\max}$  in JD28 and JD261 were decreased by 33.86 and 49.04% by DS. The reduction of  $R_d$  in JD261 was beneficial to accumulate dry matter and enhance biological yield. However, the  $P_{\max}$  was significantly decreased ( $P < 0.05$ ) in DS. The decreased rate of  $R_d$  was greater than  $P_{\max}$  in JD261. Therefore, the physiological activity of JD261 was dropped under DS. JD261 was very sensitive to DS and its drought resistance or ability to tolerate drought was rather poor.

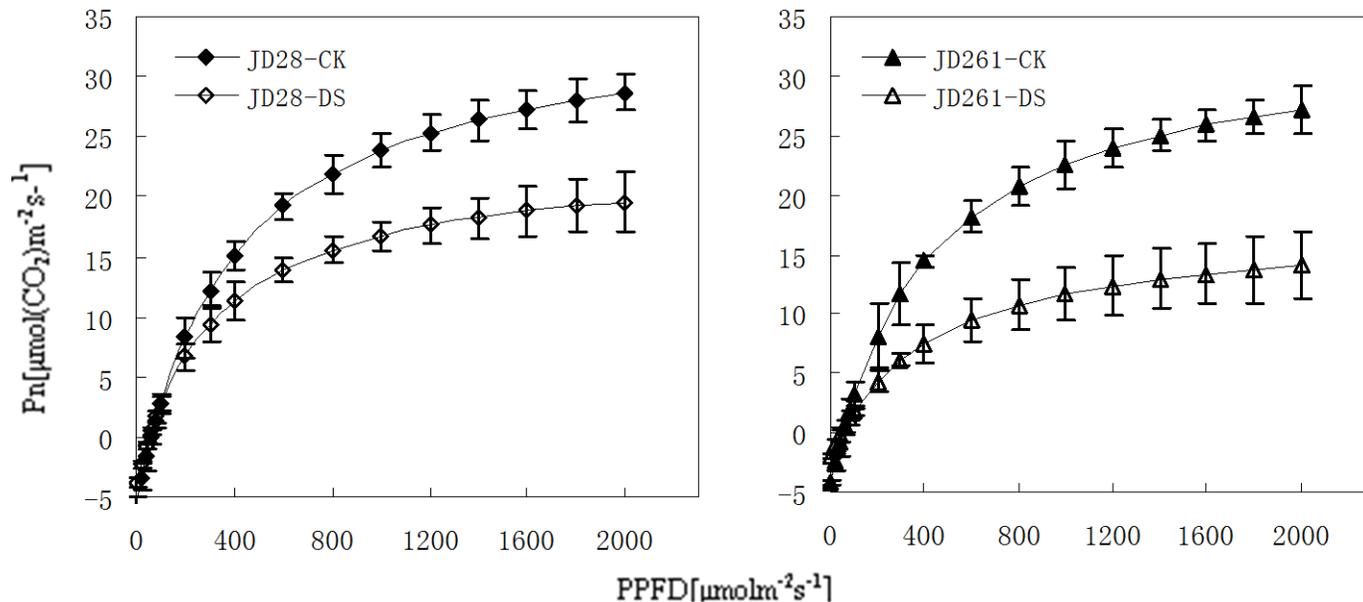
In addition, the light compensation point (LCP) in DS plants were significantly lower ( $0.01 < P < 0.05$ ) than the ones in CK. The low irradiance using scope was expended under DS. LCP of JD28 and JD261 was respectively decreased by 15.22 and 10.38% in DS plant. The value of LSP was also declined in DS. The LSP in JD28 was higher than JD261 after DS.

### Light use efficiency (LUE)

The light-response curves of LUE in CK for maize studied in our research presented two distinct phases; a rapid increase to maximum at low irradiance from 100 to  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a period of linear decline to negligible LUE at high irradiance (Figure 2). Within certain range of irradiance, LUE of DS reached a maximum, which was lower than that in CK. Overall, JD261 had a lower LUE than JD28, while irradiance changed from low to high in DS.

### Diurnal variation of chlorophyll fluorescence

$F_v/F_m$  presented different diurnal patterns in CK and DS.  $F_v/F_m$  in CK of the two maize cultivars did not significantly decline diurnally and averaged at 0.79 during the day. The value of  $F_v/F_m$  declined from 06:00 to 12:00 and reached the first minimum at 12:00 and second minimum at 14:00, after which it increased slowly and recovered 99.08% of the value measured at 06:00. The shape



**Figure 1.** Response of Pn to PPFD of the first mature leaves between JD28 and JD261 under CK (◆ JD28, ▲ JD261) and DS (◇ JD28, △ JD261) treatment in elongating stage. Each parameter point represents estimated value using Michaelis-Menten model, with the adopted value of  $\alpha$ ,  $P_{max}$  and  $R_d$  are shown in Table 1.

**Table 1.** Parameters of photosynthesis in response to light intensity between JD28 and JD261 in CK and DS treatment in elongating stage.

Variety	Treatment	$\alpha$ ( $\mu\text{molm}^{-2}\text{s}^{-1}$ )	$P_{max}$ ( $\mu\text{molm}^{-2}\text{s}^{-1}$ )	$R_d$ ( $\mu\text{molm}^{-2}\text{s}^{-1}$ )	LCP ( $\mu\text{molm}^{-2}\text{s}^{-1}$ )	LSP ( $\mu\text{molm}^{-2}\text{s}^{-1}$ )	$R^2$ (n=16)
JD28	CK	0.103 <sup>a</sup>	40.844 <sup>a</sup>	5.430 <sup>a</sup>	60.546 <sup>a</sup>	2978.555 <sup>a</sup>	0.991
	DS	0.085 <sup>b</sup>	27.016 <sup>b</sup>	3.758 <sup>b</sup>	51.329 <sup>b</sup>	2546.947 <sup>b</sup>	0.988
JD261	CK	0.091 <sup>a</sup>	37.872 <sup>a</sup>	4.214 <sup>a</sup>	51.815 <sup>a</sup>	2569.368 <sup>a</sup>	0.95
	DS	0.046 <sup>b</sup>	19.301 <sup>b</sup>	1.922 <sup>b</sup>	46.437 <sup>a</sup>	2371.626 <sup>b</sup>	0.991

Values in each row followed by the same letters are not significantly different ( $P < 0.05$ ) according to LSD's multiple range test.  $\alpha$  – The apparent quantum yield;  $P_{max}$  – the maximum net photosynthetic rate;  $R_d$  – the apparent dark respiration rate; LCP – light compensation points; LSP – light saturation point. These parameters were estimated by using nonlinear regression in SPSS 11.0 based on Michaelis-Menten model.

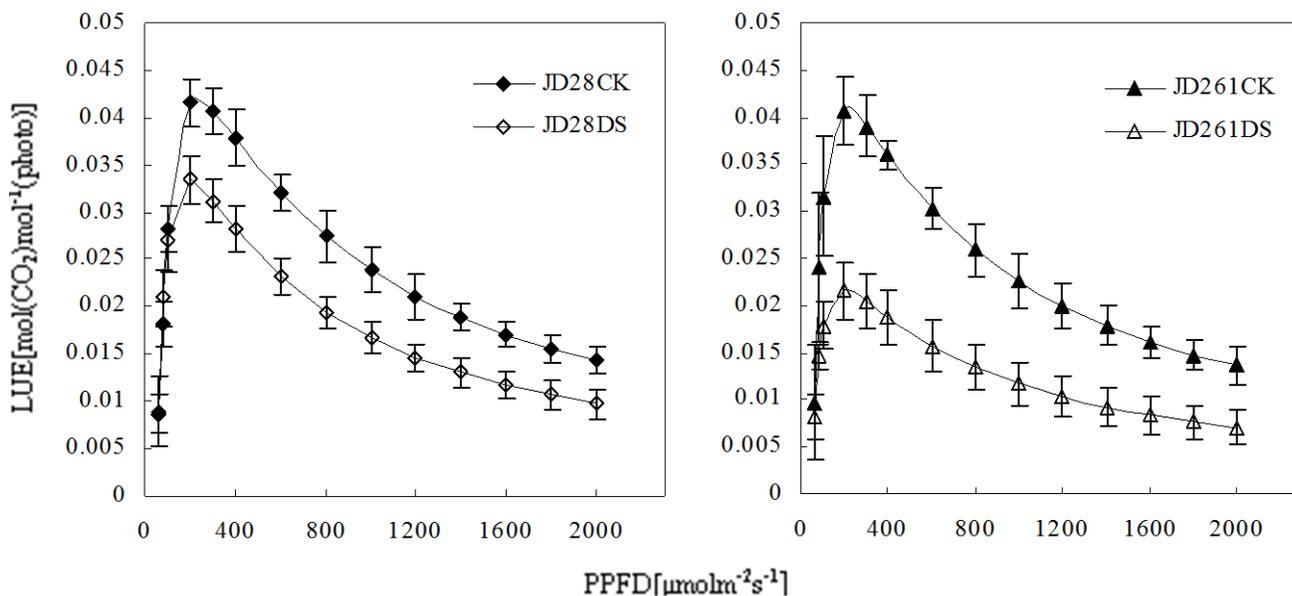
varied as a “W” curve. However,  $F_v/F_m$  of the two maize cultivars significantly decline diurnally and averaged at 0.73 during the day in DS.  $F_v/F_m$  of DS declined from 06:00 to 14:00 and reached the minimum at 14:00 after which it tended to recover to 86.34 % of the value measured at 06:00. The shape varied as a “V” curve. The diurnal  $F_v/F_m$  of JD28 and JD261 decreased to minimum values of 0.626 and 0.612 at 14:00 and then recovered to 12.78 and 11.93% of the value measured at 06:00, respectively (Figure 3).

#### Chlorophyll fluorescence responses to different PPFD in DS

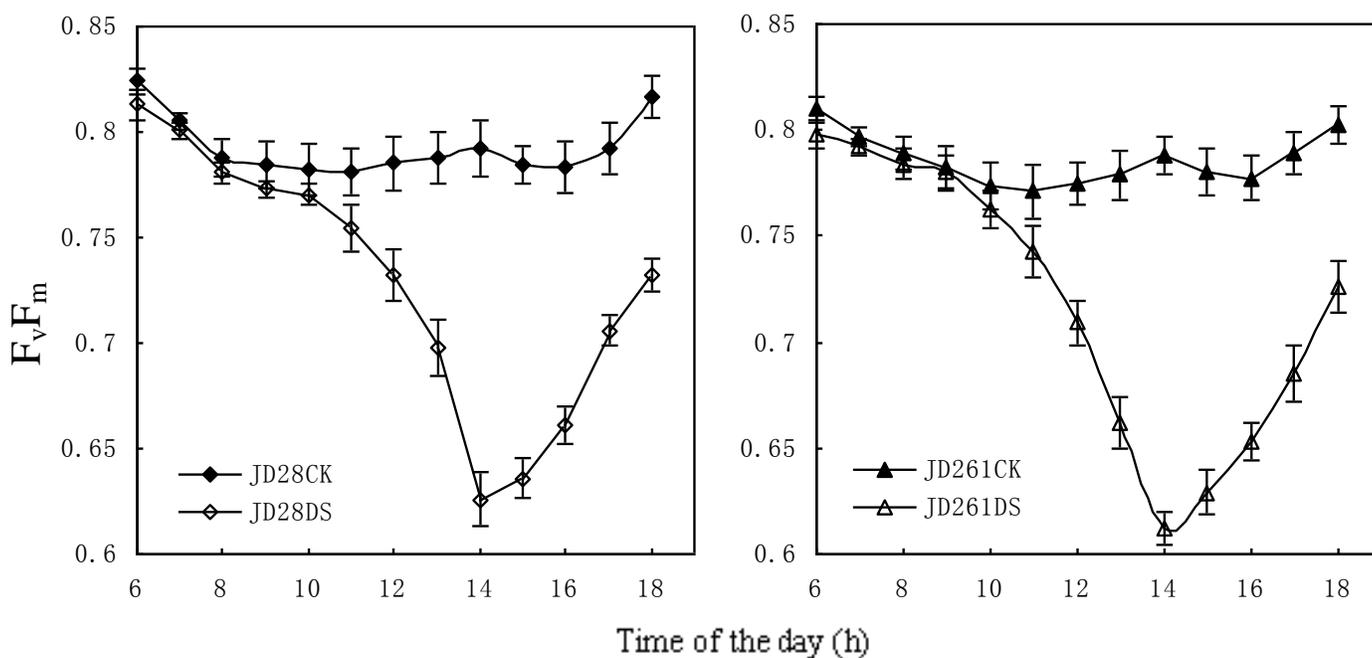
Quenching coefficients plotted as a function of PPFD showed a steady decline in qP and a clear increase in

NPQ with increasing irradiance (Figure 4). The values qP and NPQ of the two maize cultivars had significantly negative correlation and the correlation coefficient generally exceeded 0.99 in CK and 0.94 in DS.  $F_v'/F_m'$  and PhiPS2 declined with the increasing irradiation in CK and DS. In CK, the related coefficient of the two cultivars between  $F_v'/F_m'$  and PhiPS2 were 0.994 in JD28 and 0.997 in JD261, and they were 0.989 and 0.988 severally in DS.

In DS, the qP, PhiPS2 and  $F_v'/F_m'$  declined significantly as PPFD increased. The value of qP, PhiPS2,  $F_v'/F_m'$  in JD28 decreased by 17.59, 19.52 and 15.38%, while in JD261, these decreased by 34.86, 67.76 and 50.67% in the higher PPFD ( $2000 \mu\text{molm}^{-2}\text{s}^{-1}$ ) respectively (Figure 5). Simultaneously, the values of NPQ in JD28 and JD261 increased by 19.31 and by 46.77% in the higher PPFD ( $2000 \mu\text{molm}^{-2}\text{s}^{-1}$ ),



**Figure 2.** Response of  $LUE$  to PPFD of the first mature leaves between JD28 and JD261 in CK (◆JD28, ▲JD261) and DS(◇ JD28, △ JD261) treatment in elongating stage.



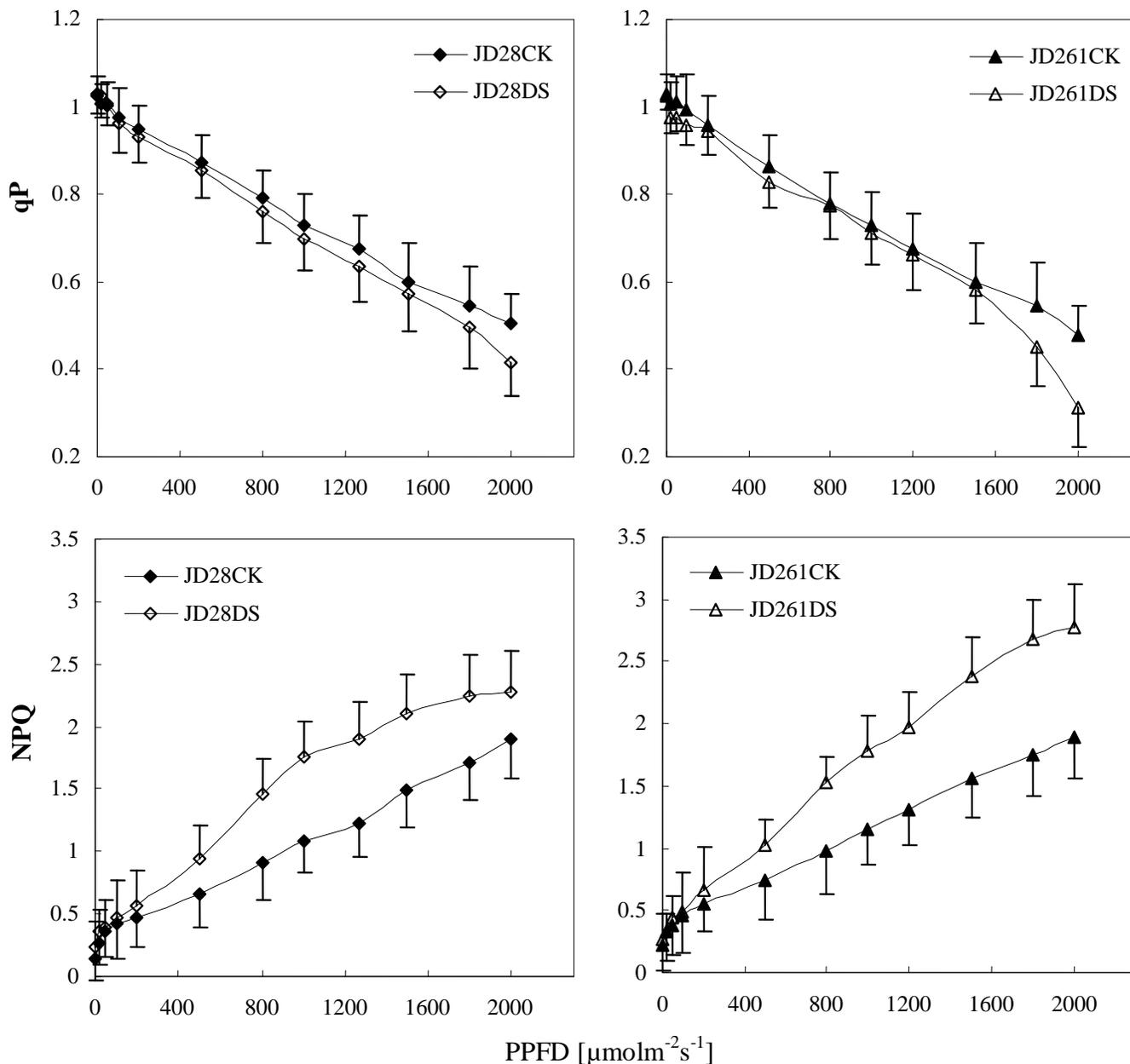
**Figure 3.** Curves of diurnal variation of  $F_v/F_m$  of the first mature leaves between JD28 and JD261 in CK (◆JD28, ▲JD261) and DS(◇ JD28, △ JD261) treatment in elongating stage.

respectively. In DS condition, JD28 still transformed a good deal of light quantum to photochemical reaction. But JD261 is a sensitive variety to DS, which harmlessly discharged excessive photon flux energy as heat, and transformed less light quantum to photochemical reaction.

## DISCUSSION

### Photoinhibition and LUE

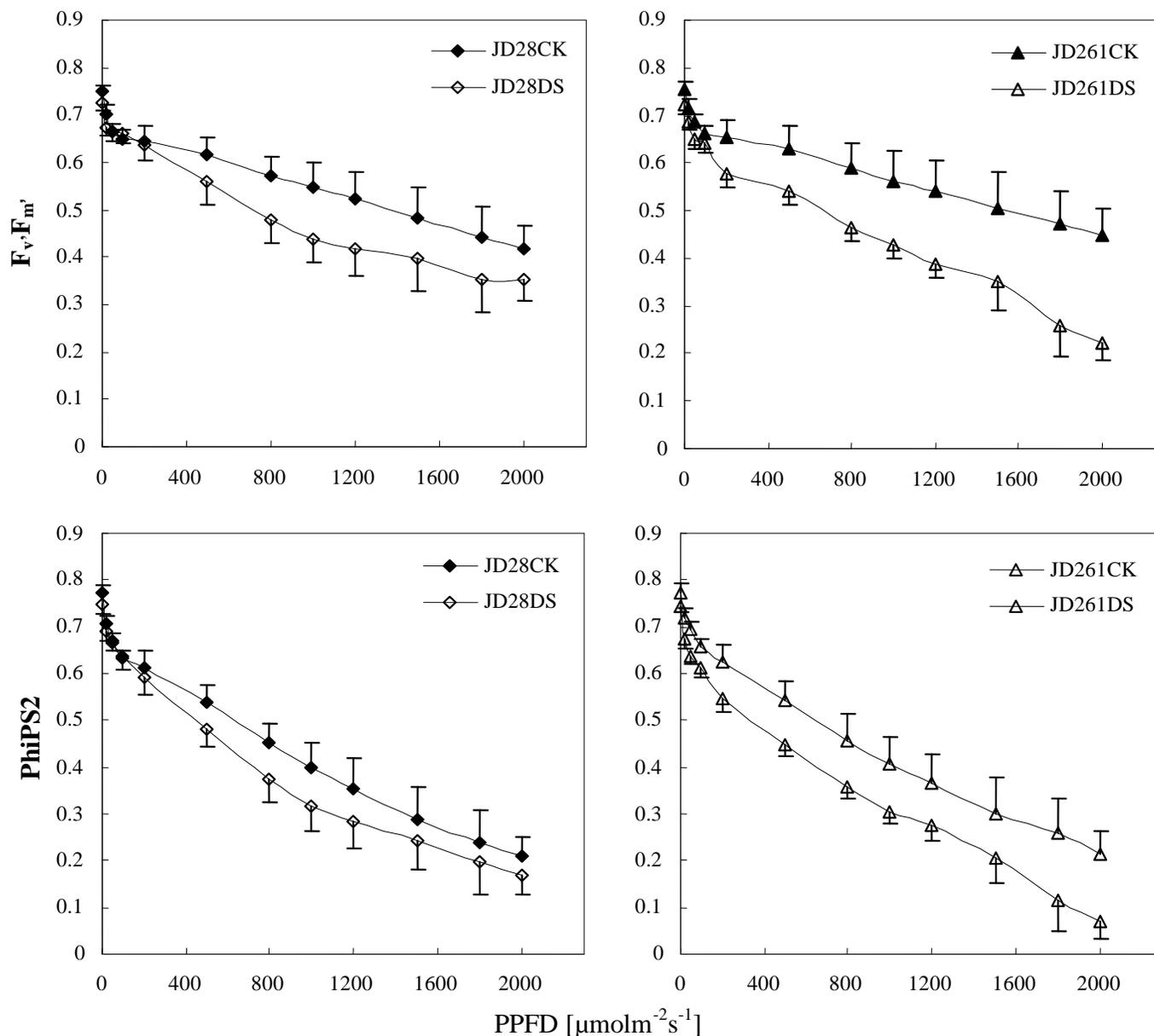
Drought stress suppresses leaf expansion and midday photosynthesis (Kramer and Boyer, 1995), resulting in



**Figure 4.** Comparison of qP and NPQ versus PPFD of the first mature leaves in CK (◆JD28, ▲JD261) and DS(◇ JD28, △ JD261) treatment in elongating stage.

less assimilate production and may also cause premature black layer formation in the kernels and terminating starch deposition. All of these factors are responsible for early senescence and a reduction in grain yield under drought condition. It is well known that inhibition of photosynthesis (photoinhibition) is one of the primary physiological consequences of drought stress (Cornic, 1994; Lawlor, 1995). Baker and Bowyer (1994) indicated that alterations of PSII activity under water stress are related to photoinhibition rather than to a direct damage to PSII. Photoinhibition is characterized by a decrease of

the initial slope of photosynthetic response curve to light (Osmond, 1994). According to the data obtained from this study, the light response curves of net photosynthesis demonstrated that the photoinhibition phenomenon surely existed. DS has added to photoinhibition levels (Figure 1).  $\alpha$  presented the slope of light response curve in weak light. The value of  $\alpha$  in JD261 decreased significantly than that of JD28 under DS. The light compensation point (LCP) in DS plants were also significantly lower ( $0.01 < P < 0.05$ ) than the ones in CK. This conclusion was, however, different from previous researches (Colom,



**Figure 5.** Comparison of  $\Phi_{PS2}$  and  $F_v/F_m'$  versus PPFD of the first mature leaves between CK (◆JD28, ▲JD261) and DS (◇ JD28, △ JD261) treatment in elongating stage.

2003). Although JD261 exhibited a lower LCP, the light use efficiency of weak light declined. In addition, the use efficiency of high irradiation correspondingly declined in DS (Table 1), and JD28 had a higher light saturation point (*LSP*) than JD261 in DS. In natural conditions, the illumination intensity was lower than the *LSP* of  $C_4$  plant. Therefore, the variety maintained higher photosynthetic rate relatively, which could keep a higher *LSP* in DS.

Additionally, substantial differences were noticed in the shape of  $P_n$  and LUE light-response curves between JD28 and JD261 grown respectively in CK and DS (Figure 2). The LUE of JD28 and JD261 reached the

maximum value of 4.15 and 4.06% at the irradiation of  $200 \mu\text{molm}^{-2}\text{s}^{-1}$  in CK, while the LUE of JD28 and JD261 reached the maximum value 3.34 and 2.15% at the irradiation of  $200 \mu\text{molm}^{-2}\text{s}^{-1}$  in DS. This indicated that the LUE of JD261 was significantly ( $P < 0.005$ ) lower than that of JD28 under DS. The photoinhibition level of JD261 was also increased by DS. Under high irradiance, however, the PSII reaction centers absorbed excessive light energy which resulted in the impairment or inactivation of the chlorophyll-containing reaction centers of the chloroplasts (Bertamina et al., 2006). Consequently, photoinhibition depressed photosynthetic

activity. It is well known that water deficits strictly influence the sensitivity of the photosynthetic apparatus to photoinhibition (Ludlow and Powles, 1988; Osmond, 1994). This research shows that DS aggravated the degree of photoinhibition and could protect the maize leaf from light-induced damage through heat dissipation, and there were differences between different cultivars. Diagnosis and early detection of various stresses using this non-invasive method is highly useful (Lichtenthaler and Miehe, 1997).

### Photochemical efficiency

According to Chechin (1998), analysis of chlorophyll 'a' fluorescence showed that photosystem 2 (PS2) was rather tolerant to the water stress imposed. Water stress caused a slight decrease in the efficiency of excitation capture by open PS2 reaction centre ( $F_v/F_m$ ). Declining values of  $F_v/F_m$  are an indicator of stress. Dark adapted values of  $F_v/F_m$  reflect the potential quantum efficiency of PSII and are used as sensitive indicators of plant photosynthetic performance, with optimal values for healthy plants generally being 0.83 (Björkman and Demming, 1987; Burke, 2007). Values are lower when the plants are exposed to stress, indicating in particular, the phenomenon of photoinhibition or the degree of damage to PSII complex (Kate, 2000; Ronáček et al., 1999).  $F_v/F_m$  was used to screen maize (Jovanovic et al., 1991) and was found to be correlated with decreased  $CO_2$  assimilation and electron transport (Sayed, 2003).

The diurnal patterns of  $F_v/F_m$  obtained herein had indicated that the value of  $F_v/F_m$  in CK was two hours early to reach the lowest point than that of DS, which might be caused by the increasing irradiation that had led to declined PSII photochemical activity. This decline does not imply the damage of photosynthetic apparatus, but harmlessly discharging excessive photon flux energy in order to protect photosynthetic apparatus from damage. The value of  $F_v/F_m$  tended to recover from 16:00 and reached 99.08% of the value at 06:00, which demonstrated the repairing function in lower irradiance (Figure 3). The value of  $F_v/F_m$  in DS declined significantly and it was two hours late to reach the lowest value than that of CK and have not recovered to the value that measured at 06:00, as was shown by the diurnal patterns curves of  $F_v/F_m$ . At the same time, DS induced a decline in  $F_v/F_m$ , which suggested that photoinhibition is accompanied by an over-reduction of PSII (Colom, 2003).

### Fluorescence quenching and efficiency of PSII

The study showed that with increasing irradiance, there was a steady decline in qP, PhiPS2, open PSII energy capture efficiency ( $F_v'/F_m'$ ) and a clear increase in NPQ, and DS significantly increased the change extent. The qP

is an indication of the proportion of open PSII reaction centers, and translates light quantum energy into chemical energy process, which reflects the photosynthetic efficiency and the light use situation of plant. NPQ can represent the energy which cannot be utilized to transport photosynthetic electrons but be dissipated harmlessly as heat energy from PSII antennae (Kate and Giles, 2000). In the two cultivars, a decrease of the qP was observed in response to the drought stress treatment, indicating that a larger percentage of the PSII reaction centers would close at any time, which also indicated that the balance between excitation rate and electron transfer rate have changed (Efeoğlu, 2009). Through allocating excitation energy after DS, the value of PhiPS2 and  $F_v'/F_m'$  declined by 43.64 and 33.03% on average in the irradiation of  $2000 \mu\text{molm}^{-2}\text{s}^{-1}$  after DS (Figure 5).

$F_v'/F_m'$  is of great value in assessing the relative contributions of PSII photochemical capacity and thermal decay processes to the overall efficiency of photochemistry at PSII (Oxborough et al., 1997). PhiPS2 is the effective quantum yield of photochemical energy conversion in PSII (Ronáček et al., 1999). PhiPS2 is related to significant reductions of  $F_v'/F_m'$  (Colom, 2003). Such reductions would be expected to occur with increases in thermal energy dissipation. A pronounced increase in non-photochemical fluorescence quenching (NPQ), as one means of estimating the level of energy dissipation, was indeed observed in these leaves with increasing incident photon flux densities (Demming-Adams, 1996). The decrease of qP and PhiPS2 is accompanied by increase in DS (Shangguan et al., 2000). The decrease of qP was indicated that open level of reaction-center of PSII was decreased, which led the primary quinone acceptor  $Q_A$  to be in the oxidized or reduced form during steady-state illumination (Melis, 1999). This charge recombination reaction has a high probability of generating P680 triplet. The P680 triplet is quenched efficiently by  $^3O_2$ , thus generating the highly reactive singlet oxygen ( $^1O_2$ ) (Telfer et al., 1994).

Xanthophyll cycle relying on photo-protection is believed to be the main mechanism for plants to deal with excessive light energy (Lin et al., 2002), and it plays an indirect role in thermal dissipation by mediating a critical conformational change within the PSII antenna (Ort, 2001). With the increase of NPQ of xanthophyll cycle, excessive energy was dissipated as thermal energy to protect the maize leaf from light-induced damage in DS. The variation trend of NPQ increased along with the increasing irradiation, and it increased significantly in DS. Ort (2001) indicated that the NPQ got involved in the competition between the thermal dissipation of chlorophyll and fluorescence emission as well as photosynthesis. The value of NPQ was increased by 33.04% at  $2000 \mu\text{molm}^{-2}\text{s}^{-1}$  in DS than that of in CK. This illustrates that excessive excitation energy was generated in DS (Demming-Adams and Adams, 1994). Moreover, JD261 was sensitive to DS and its photochemistry

decreased significantly than JD28.

## Conclusion

This study confirmed that the capability of assimilation, transfer and use of light energy is decreased under drought stress in maize. Furthermore, dissipation and photo-protection mechanisms were different in the two maize cultivars studied. JD28 maintained high light use efficiency and exchanged excessive energy as thermal energy to protect the maize leaf from light-induced damage under DS. It should be highlighted that this study only examined maize in elongating stage. However, drought can occur in the whole growing process of maize; therefore the similarities and differences of photosynthesis mechanism in other growth stages under drought needs further investigation.

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