Relationship between fluorescence yield and photochemical yield under water stress and intermediate light conditions

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Abstract

The dynamics between fluorescence ($F_s$) yield and photochemical ($P$) yield in a changing environment are essential for understanding the relationship between photosynthesis and fluorescence. The ratio of $F_s$ yield and $P$ yield tends to be constant under high light intensity, but the relationship between these two yields, and its response to environmental conditions, need to be explored further under intermediate and low light. In this study, we performed leaf-scale measurements of fluorescence parameters by pulse-amplitude modulation (PAM) technology in summer maize ($Zea mays$ L.) plants grown under intermediate light conditions in a climate chamber. Plants were treated as moderately water stressed and non-water stressed. Results showed that a decrease in $P$ yield was accompanied by increases in $F_s$ yield and non-photochemical quenching (NPQ) yield in response to moderate water stress under intermediate and low light conditions. $F_s$ yield was negatively correlated with $P$ yield under intermediate and low light conditions when there was sufficient soil water in the root zone. Under water stress, the correlation between $F_s$ yield and $P$ yield was negative in low light, but became positive under higher light levels. $F_s$ yield was negatively related to $P$ yield when NPQ yield was low; however, they were synergistically and positively associated when excessive light dissipation was dominated by NPQ.

Keywords: Chlorophyll fluorescence, intermediate light, leaf scale, pulse-amplitude modulation, photochemistry, summer maize, water stress.

Introduction

Chlorophyll fluorescence is red and far-red light (650–800 nm) emitted by chlorophyll a pigments a few nanoseconds after light absorption (Porcar-Castell et al., 2014; Damm et al., 2015; Verrelst et al., 2016). It is sensitive to short-term environmental stresses such as drought or nutrient deficiency, among others. (Flexas et al., 2002; Souza et al., 2004; Dobrowski et al., 2005; Zarco-Tejada et al., 2013; Cendrero-Mateo et al., 2015; Tubuxin et al., 2015; Chen et al., 2016). Chlorophyll fluorescence has been used as a non-destructive and non-intrusive probe in studies of plant photochemistry, physiology, and ecology (Flexas et al., 1999; Lee et al., 2013; Guanter et al., 2014; Cendrero-Mateo et al., 2015). Remotely sensed chlorophyll fluorescence from satellite imaging is providing new data sources to characterize the dynamics of gross photosynthesis at
regional scale, increasing our ability to monitor and assess the effects of environmental stresses on the productivity of vegetation (Lee et al., 2013; Guanter et al., 2014; Wang et al., 2016; Zhang et al., 2016a; Yang et al., 2017).

Studies have shown that solar-induced fluorescence (SIF) is closely related to gross primary production (GPP) at regional or ecosystem scale (Guanter et al., 2014; Zhang et al., 2016a), especially when there is water stress (Lee et al., 2013; Wang et al., 2016). It has been reported that SIF and GPP are consistent in terms of spatial patterns and seasonal dynamics (Guanter et al., 2014; Yang et al., 2015; Zhang et al., 2016a; Yang et al., 2017). SIF traces the variations of GPP much better than the enhanced vegetation index, normalized difference vegetation index, and land surface water index do (Lee et al., 2013; Wagle et al., 2016; Wang et al., 2016). For example, during the 2012 drought event in the Great Plains of the USA, it was found that variations of SIF and GPP were consistent, and SIF declined more significantly than the normalized difference vegetation index (Sun et al., 2015; Wang et al., 2016). As SIF is more sensitive to changes in vegetation photosynthesis and water status than greenness indices, it is a better indicator of photosynthesis (Guanter et al., 2014; Yang et al., 2015; Zhang et al., 2016a; Yang et al., 2017). So far, some empirical linear relationships between SIF and GPP have been developed to directly estimate the productivity of vegetation using remote sensing of SIF (Guanter et al., 2014; Wagle et al., 2016).

Although some studies have demonstrated close associations between chlorophyll fluorescence and GPP (Guanter et al., 2014; Zhang et al., 2016a), the quantitative relationship and inherent mechanisms of the links between them are still not clear. In photosystem II (PSII), chlorophyll fluorescence, photochemical reactions, and non-photochemical quenching (NPQ) are three pathways that consume all of the light energy absorbed by the leaf (van der Tol et al., 2014). These three pathways are closely associated, and the sum of fluorescence ($F_s$) yield, photochemical (P) yield, and NPQ yield is considered to equal 1 (Hnimina et al., 2014; van der Tol et al., 2014; Lee et al., 2015; Cendrero-Mateo et al., 2016; Zhang et al., 2016b). $F_s$ yield is the fraction of absorbed light energy re-emitted as fluorescence, and represents the light use efficiency of fluorescence (Damm et al., 2010; Lee et al., 2015; Yang et al., 2017). The P yield of PSII, which is the fraction of absorbed photons used for photochemical reactions, provides an estimation of photochemical light use efficiency (Baker, 2008; Lee et al., 2015; Yang et al., 2017). The surplus part of the absorbed light energy is dissipated as heat (i.e. NPQ), including the constitutive thermal dissipation and variable energy-dependent heat dissipation. A simple competition model has been proposed for these three processes (Butler, 1978; Baker, 2008). In situ measurements or mechanistic model simulations have revealed that the relationship between fluorescence yield and photochemical yield is not perfectly linear (van der Tol et al., 2009, 2014; Lee et al., 2015; Zhang et al., 2016b; Cui et al., 2017) and is influenced by the absorbed photosynthetically active radiation (van der Tol et al., 2009, 2014; Cui et al., 2017). At present, our understanding of the non-linear relationship between the fluorescence and photochemical yields is still insufficient. It has been observed that the ratio of the $F_s$ yield to the P yield tends to be constant under high light condition, that is, in the imaging time of satellite SIF (Damm et al., 2010; Guanter et al., 2014; Lee et al., 2015; Liu et al., 2017). However, under intermediate and low light conditions (i.e. the early morning and late afternoon), the relationship between these two yields is not clear, and needs to be further investigated.

Fluorescence and photochemical processes are sensitive to environmental stresses (Flexas et al., 2002; Cendrero-Mateo et al., 2015; Chen et al., 2016). In the context of climate change, droughts have become more frequent and severe around the world in recent decades (Spinoni et al., 2014). Drought has been reported to induce significant decreases of P yield and $F_s$, and increases of NPQ (Flexas et al., 2002; Souza et al., 2004; Baker, 2008; Faraloni et al., 2011; Liu et al., 2012; Cendrero-Mateo et al., 2015). However, few studies have explored the effects of water stress on the relationships between these parameters (Flexas et al., 2002; Cendrero-Mateo et al., 2015).

This study explored the fluorescence and photochemical physiology in response to water stress under intermediate and low light conditions. It is hypothesized that the relationship between $F_s$ yield and P yield is not perfectly linear, and depends on water status and light intensity. As summer maize ($Zea mays$ L.) is one of the most important and widely planted C₄ crops (in which photorespiration is negligible) in the world, we conducted an experiment with summer maize in a climate chamber with two soil moisture treatments (moderate water stress and no water stress). The fluorescence parameters were measured in leaves by using a pulse-amplitude modulation (PAM) fluorometer. This study aimed to explore (i) the relationship between $F_s$ yield and P yield under intermediate and low light conditions, and (ii) the effects of water stress on $F_s$ yield, P yield, and the relationship between them. The results provide new knowledge about the interaction between leaf photochemistry and fluorescence, which is crucial for improving the estimation of vegetation productivity.

**Materials and methods**

*Description of the experiment*

This experiment was conducted between 12 October 2016 and 24 February 2017 using the Water Transformation Dynamical Processes Experimental Device (WATDPED; Fig. 1) established in the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China. The WATDPED consists of a climate chamber with two $3 \times 2 \times 3$ m (length $\times$ width $\times$ height) lysimeters. The lysimeters contain alluvial soil taken from farmlands in the North China Plain, which is composed of 60.22% sand, 39.09% silt, and 0.70% clay. The field capacity is 25.12% and residual moisture is 2.66%. The climate conditions are controlled by the WATDPED (Fig. 2). The chamber has an artificial light source composed of metal halide lamps and sodium lamps with a maximum irradiance of 30000 lx. There are two centrifugal humidifiers to control the humidity and an air conditioning system to control the air temperature.

Seeds of summer maize ($Zea mays$ L., cultivar JD68) were sown in soil with an intra-row space of 40 cm and inter-row space of 30 cm; there were 36 plants in each lysimeter. According to the photosynthetic light response curve of summer maize (Stirling et al., 1994; Liu et al., 2012), when photosynthetically active radiation (PAR) is greater than $700 \, \mu$mol m$^2 \, s^{-1}$, the photosynthetic rate increases slowly with increasing PAR, while when PAR is lower than $450 \, \mu$mol m$^2 \, s^{-1}$, the
photosynthetic rate increases rapidly with PAR. Thus, PAR in the range of 450–700 μmol m−2 s−1 was taken as the intermediate light condition and PAR lower than 450 μmol m−2 s−1 was taken as the low light condition for the summer maize in this study. In order to explore the relationship between P yield and Fs yield under intermediate and low light conditions, the light intensity above the canopy was kept at 700 μmol m−2 s−1 during the whole growth period by adjusting the distance between the canopy top and the lamps. The light source was turned on at 06.00 h and off at 18.00 h automatically, so that the plants were exposed to a 12 h photoperiod. In the climate chamber, variations of 3 h averaged air temperature and daily humidity were set according to records made at the Beijing climatological station (116°28′E, 39°48′N) during the period 16 June to 29 October 2010, to represent normal climate conditions (Fig. 2). Chemical fertilizers were applied at the seedling, early jointing, and tasseling stages (Table 1).

Plants in the two lysimeters were subjected to two treatments, moderate water stress (WS) and non-water stress (NS). The soil water contents (% by volume) of the root layer (25 cm depth) were monitored automatically by 5TE soil water sensors (Decagon, Pullman, WA, USA) and were maintained at 45–50% of field capacity for the WS treatment and no less than 80% of field capacity for the NS treatment by irrigation. The weight of each lysimeter was recorded automatically at 30-min intervals with a
Measurement of growth indicators

Basic growth indicators including plant height, leaf area index (LAI), and relative leaf chlorophyll content were measured. The SPAD-502 Plus chlorophyll meter (Konica Minolta Sensing Inc., Japan) was used to measure the relative chlorophyll content. The relative amount is an indexed estimation of chlorophyll content with the value of 0–99, which is determined by measuring leaf transmittance coefficients at 650 nm and 940 nm. The length and width of each leaf were measured to estimate the leaf area (Tan et al., 2017), and LAI was calculated as the total leaf area divided by the projected land surface area of the canopy.

After harvest, the fresh weight of each corn cob in the two treatments was measured. The dry matter and the mass of 100 randomly selected seeds (the 100-seed mass) were determined after corncobs had been oven-dried for 1 hour at 105 °C and 48 hours at 85 °C. The weights of oven-dried leaves, stems, and roots of three randomly selected plants in each treatment were also measured to explore the biomass allocation strategies of plants in response to water stress.

### Table 1. Records of the growing stages of summer maize and the use of fertilizer during the experiment

| Growing stage | DAS (NS) | DAS (WS) | Fertilizer | Amount of fertilizer (g m⁻²) |
|---------------|---------|---------|------------|-----------------------------|
| Seeding       | 14–29   | 14–34   | Compound fertilizer | 40 |
| Jointing      | 30–59   | 35–64   | Urea       | 30 |
| Tasselling    | 60–74   | 65–82   | Urea       | 40 |
| Filling       | 75–105  | 83–115  | None       | –  |
| Maturity      | 106–130 | 116–135 | None       | –  |

DAS, days after sowing; NS, non-water stress; WS, water stress.

### Table 2. Fluorescence parameters measured by the OS5P+ fluorometer

| Parameter | Description |
|-----------|-------------|
| F₀/Fₘ     | Maximal fluorescence after dark adaptation |
| Fₘ/Fₚₘ    | Maximum photochemical quantum yield under dark adaptation: Fₘ/Fₚₘ=(Fₘ−F₀)/Fₘ (Yang et al., 2017), where F₀ is the minimal fluorescence after dark adaptation |
| F₀ᶜ       | Maximal fluorescence under the light condition |
| Fₛ        | Steady-state fluorescence |
| P yield   | Actual quantum yield of PSII photosynthesis, which indicates the proportion of light energy used in photosynthesis by PSII under steady-state photosynthetic light conditions. P yield=(Fₘ−Fₛ)/Fₘ (Genty et al., 1989) |
| NPQ       | Non-photochemical quenching, a process in which excess absorbed light energy is dissipated as heat. NPQ=(Fₘ−Fₛ)/Fₘ⁺ (Tietz et al., 2017) |

To explore the effects of leaf water levels on fluorescence parameters, in the early tasseling stage (65 days after sowing), after measurements of fluorescence parameters had been made on five fully expanded leaves of one randomly selected plant in each treatment, leaves were sampled and oven-dried for 1 hour at 105 °C and 48 hours at 85 °C. Leaf water content (LWC) was estimated as follows:

\[
LWC = \frac{FW - DW}{FW} \times 100\%
\]
under dark and light conditions were measured at the same position for each leaf sample.

**Calculation of fluorescence yield and NPQ yield**

A fluorometer was used to measure the P yield and the pulse signal intensity of $F_s$, but it cannot directly determine the $F_s$ yield. In order to explore the relationship between the two light-use efficiencies (i.e. $F_s$ yield and P yield), the method proposed in the Soil-Canopy Observation of Photosynthesis and Energy model (van der Tol et al., 2014; Lee et al., 2015; Zhang et al., 2016) was used to calculate the $F_s$ yield. As heat dissipation is one of the three pathways that consumes the absorbed photons in the photosynthetic apparatus, the NPQ yield is achieved simultaneously as an auxiliary. In this method, heat dissipation is partitioned as the constitutive dark-adapted thermal dissipation ($d$) and the energy-dependent heat dissipation ($n$) under the light condition. The yields are calculated as follows, using the method described by Lee et al. (2015), van der Tol et al. (2014), and Zhang et al. (2016):

$$
\Phi_f + \Phi_p + \Phi_d + \Phi_n = 1
$$

(3)

$$
\Phi_f = \frac{K_f}{K_f + K_d + K_p + K_n}
$$

(4)

$$
\Phi_p = \frac{K_p}{K_f + K_d + K_p + K_n}
$$

(5)

$$
\Phi_d = \frac{K_d}{K_f + K_d + K_p + K_n}
$$

(6)

$$
\Phi_n = \frac{K_n}{K_f + K_d + K_p + K_n}
$$

(7)

$$
K_d = \max (0.03 \times T + 0.0773, 0.87)
$$

(8)

$K_d$ is the rate coefficient of dark-adapted thermal dissipation, which is a function of temperature ($T$) (van der Tol et al., 2014; Lee et al., 2015). $K_n$ and $K_p$ are the rate coefficients of energy-dependent heat dissipation and photochemistry, respectively (van der Tol et al., 2014); $F_{m}$ is the maximal fluorescence after dark adaptation; $F_{m}^{l}$ is the maximal fluorescence under the light condition; and $F_s$ is the steady-state fluorescence. $\Phi_f$, $F_{m}$, $F_{m}^{l}$, and $F_s$ can all be measured directly by the OIII+ fluorometer.

**Statistical analysis**

Differences in measurements between the two water treatments, and the correlations between $F_s$ yield, P yield, and NPQ yield, were analyzed. The $t$-test was used for comparisons between the mean values of measurements under the WS and NS conditions. As the time-series samples or variables changing with light intensity were not normally distributed and were paired across the two water treatments, the pairwise Wilcoxon non-parametric method was used to test differences in these parameters between the two treatments. To evaluate the relationship between two variables, regression analysis was performed with the coefficient of determination ($R^2$) to describe its level of significance. Pearson and Spearman correlation coefficients were used for the linear and non-linear correlation analysis, respectively. Statistical significance was accepted when $P<0.05$.

**Results**

**Effects of water stress on growth of summer maize**

During the growth period, water stress indices for the NS treatment exceeded 0.77, whereas those for the WS treatment exceeded 0.87. Variations in (A) water stress index and (B) evapotranspiration (ET); (C) total amount of irrigation (Irr) and ET during the whole growth period for the water stress (WS) and non-water stress (NS) treatments. (This figure is available in colour at JXB online.)
were lower, ranging from 0.38 to 0.48 (Fig. 3A). The irrigation amounts during the whole growth period were 246 mm for the NS treatment and 39 mm for the WS treatment (Fig. 3C). ET was significantly different between the two treatments (Fig. 3B); total ET during the whole growth period was 259 mm for the NS treatment and 109 mm for the WS treatment.

As shown in Fig. 4, there were significant differences between WS and NS plants in terms of plant height, LAI, and leaf chlorophyll content during the growth period (P<0.001 for height and LAI, P=0.001 for chlorophyll content). The maximum stalk heights of NS plants were significantly higher than those in the WS treatment (P=0.047), with mean values of 186.7 cm and 171.3 cm, respectively. The maximum LAI of plants in the NS treatment was significantly higher than that for the WS treatment (P=0.031).

Significant differences between WS and NS treatments were also observed for indicators of crop yield (P=0.017 for dry matter, P=0.047 for fresh weight, and P=0.045 for 100-seed mass). Relative to the NS treatment, the mean dry matter of corn cobs and the 100-seed mass in plants subjected to WS were reduced by 28.6% and 20.4%, respectively (Fig. 5A). The water use efficiency (defined here as crop yield divided by ET) of summer maize was 3.12 kg m⁻³ in the WS treatment and 1.95 kg m⁻³ in the NS treatment. The proportions of dry mass in the roots, stems, and leaves were 23.4%, 51.0%, and 25.6%, respectively, for plants in the WS treatment, and 16.2%, 54.9% and 28.9%, respectively, for plants in the NS treatment (Fig. 5B).

Effects of water stress on fluorescence, photochemistry, and NPQ

In PSII, the absorbed light has three fates: the photochemical reaction, heat dissipation, and fluorescence emissions by chlorophyll (Porcar-Castell et al., 2014; van der Tol et al., 2014). There are trade-offs between these three yields when plants acclimate to a changing environment (Baker, 2008). Fluorescence parameters measured in plants subjected to different water treatments and light conditions in two critical growth stages (the jointing and filling stages) are shown in Fig. 6. Significant differences in \( F_v/F_m \) measurements between the two treatments were observed in the filling stage (P=0.013) but not in the jointing stage (Fig. 6G). This difference may be related to the smaller water deficit in the jointing stage than in the filling stage (Fig. 3A). Nevertheless, in both stages, the \( F_v/F_m \) of WS leaves was lower than that of NS leaves, revealing the negative effects of water stress on the potential photon quantum yield. The actual P yields were also lower in the WS condition (Fig. 6C, D), whereas Fₛ yields increased under WS (Fig. 6A, B), indicating that more absorbed light was emitted as fluorescence. The NPQ yields in the two water treatments were consistent with those of Fₛ yields (Fig. 6E, F), because under the WS condition a higher proportion of energy was dissipated as heat to avoid damage resulting from excess light. The differences in P yields and NPQ yields between the two water treatments were significant in both the jointing and filling stages under the low light condition (PAR=100 μmol m⁻² s⁻¹; P<0.001 and P=0.023 for P yield in the jointing and filling stages, P<0.001 and P=0.023 for NPQ yield in the jointing and filling stages, respectively), but were significant only in the filling stage under the intermediate light condition (PAR=500 μmol m⁻² s⁻¹; P=0.008 and P=0.009 for P yield and NPQ yield, respectively). The Fₛ yields of the two water treatments showed significant differences in the jointing stage under the low light condition (P=0.033), and in both stages under the intermediate light condition (P=0.026 in the jointing stage and P=0.015 in the filling stage). Light intensity also affected the three yields. Fₛ yields and NPQ yields were significantly higher, while P yields were significantly lower, under the intermediate light condition (Fig. 6B, D, F) compared with the low light condition (Fig. 6A, C, E) (all P values <0.001).

In the early tasseling stage, five fully expanded leaves from plants subjected to each treatment were oven-dried to estimate LWC after measuring the fluorescence parameters. As shown in Fig. 7A, the differences in leaf water statuses between the two treatments were significant (P<0.001), with LWC being 75.7% for WS leaves and 79.3% for NS leaves. The rapid light response curves of Fₛ yield, P yield,
and NPQ yield also showed significant differences between the WS and NS conditions ($P=0.003$ for all three yields). Under the WS condition, $P$ yield was lower and NPQ yield and $F_s$ yield were higher than the respective yields in the NS treatment (Fig. 7B–D). The $P$ yield decreased with increasing PAR, indicating higher light use efficiency under low light levels. The increase of NPQ yield with increasing PAR indicated that more absorbed light was dissipated under higher light levels. The response of $F_s$ yield to light intensity was not linear: $F_s$ yield increased with PAR when PAR was $<400 \, \mu\text{mol m}^{-2} \text{s}^{-1}$, and then decreased as PAR increased from 450 to 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Fig. 5. (A) Dry matter, fresh weight, and 100-seed mass per corn cob ($n=33$; error bars represent ±1 SD); (B) mean proportions of biomass in the roots, stems, and leaves for the water stress (WS) and non-water stress (NS) treatments ($n=3$). (This figure is available in colour at JXB online.)

Fig. 6. Comparisons of $F_v/F_m$, $F_s$ yield, $P$ yield, and NPQ yield in leaves of summer maize between the water stress (WS) and non-water stress (NS) treatments at the jointing stage (45 days after sowing) and filling stage (90 days after sowing) under (A, C, E) low light ($\text{PAR}=100 \, \mu\text{mol m}^{-2} \text{s}^{-1}$) and (B, D, F) intermediate light ($\text{PAR}=500 \, \mu\text{mol m}^{-2} \text{s}^{-1}$) conditions. Data are based on measurements made on five plants in each treatment. The top and bottom of the box represent the quartiles; the horizontal line in the box represents the median value; the whiskers represent ±1 SD. Mean values in the two treatments were compared by the $t$-test; different letters indicate significant differences: *$p<0.05$, **$p<0.01$. (This figure is available in colour at JXB online.)
Effects of water stress on the relationship between photochemical and fluorescence yields

As shown in Fig. 7B, there is a tipping point for the light response curve of Fs yield at light intensity ~450 μmol m⁻² s⁻¹. In view of this finding, we explored the relationships between Fs yield and P yield at light intensities lower and higher than 450 μmol m⁻² s⁻¹ (Fig. 8). We found that the correlation of Fs yield and P yield was negative under the low light condition (PAR <450 μmol m⁻² s⁻¹) for both the WS ($R^2=0.400$, $P<0.01$) and NS ($R^2=0.490$, $P<0.01$) treatments (Fig. 8). When PAR exceeded 450 μmol m⁻² s⁻¹, the relationships were

![Graphs showing the relationships between Fs yield and P yield at different light intensities for WS and NS treatments.](image-url)
different. P yield and F<sub>s</sub> yield were still negatively related in the NS condition (R<sup>2</sup>=0.109, P<0.01), although the correlation was weaker. By contrast, for the WS treatment, the relationship was now positive (R<sup>2</sup>=0.071, P<0.01). Generally, under intermediate and low light conditions, higher light intensity causes the closure of photosynthetic reaction centers by reducing the primary quinone acceptor of PSII (Q<sub>A</sub>); consequently, photochemical quenching is reduced while fluorescence intensifies (Baker, 2008; Porcar–Castell et al., 2014). Thus, F<sub>s</sub> yield is negatively related to P yield. However, for the WS treatment, due to the dominant role of NPQ in dissipating excessive light (Flexas et al., 2002; Liu et al., 2012), F<sub>s</sub> yield and P yield both decreased with increases of PAR above 450 μmol m<sup>-2</sup> s<sup>-1</sup> (Fig. 7), leading to a positive relationship between the two yields. Therefore, light intensity and water status are critical factors that comprehensively regulate the relationship between F<sub>s</sub> yield and P yield.

The relationships between the yields of the three energy consumption pathways under low light conditions (PAR at 100 μmol m<sup>-2</sup> s<sup>-1</sup>) were further explored. For the WS treatment, the NPQ yield was negatively and linearly related to the P yield (R<sup>2</sup>=0.9997, P<0.001) and non-linearly related to the F<sub>s</sub> yield (R<sup>2</sup>=0.317, P<0.01) (Fig. 9A), resulting in a non-linear relationship between F<sub>s</sub> yield and P yield (R<sup>2</sup>=0.304, P<0.01) (Fig. 9C). As shown in Fig. 9C, the F<sub>s</sub> yield increased and then decreased as the P yield increased, along with the declining NPQ yield. When the P yield was below 0.40, NPQ played a dominant role in consuming light energy (NPQ yield >0.58), and the relationship between the F<sub>s</sub> yield and P yield was positive. As the NPQ yield decreased (<0.58) and P yield increased (> 0.40), however, the F<sub>s</sub> yield decreased and was negatively correlated with the P yield (Fig. 9C). Under the NS condition (Fig. 9B, D), the F<sub>s</sub> yield and NPQ yield changed synergistically, and the P yield was negatively related to both the NPQ yield (R<sup>2</sup>=0.9995, P<0.001) and the F<sub>s</sub> yield (R<sup>2</sup>=0.269, P<0.01).

**Discussion**

**Effects of water stress on plant growth and photosynthetic physiology**

Our study revealed that water stress reduced the proportion of dry matter contributed by stems and leaves, and increased that of roots (Fig. 5). Plants under water stress transferred more biomass to roots in order to take up water from deeper soil to relieve the stress (Yin et al., 2005; Ge et al., 2012). The lower proportion of the biomass attributable to leaves (or decreased LAI, as shown in Fig. 4) may also help the stressed plants adapt to the water-limited environment by reducing transpiration (Craufurd et al., 1999). We also found that water use efficiency increased under the WS condition, as has also been reported in previous studies (Craufurd et al., 1999; Yin et al., 2005).

Water stress has a significant influence on plant photochemical and fluorescence characteristics (Flexas et al., 2002; Faraloni et al., 2011; Liu et al., 2012; Cendrero–Mateo et al., 2015). The three fluorescence parameters (F<sub>s</sub>, P yield, and NPQ) can effectively identify water stress, as suggested by previous studies.
In this experiment, summer maize grown under intermediate light conditions and subjected to moderate water stress and non-water stress treatments showed significant differences in their photosynthetic physiology: the P yield decreased and the F\textsubscript{i} yield and NPQ yield increased in response to water stress. P yield is directly related to photosynthesis since it quantifies the light-use efficiency of PSII. It is sensitive to stress and decreases under drought conditions (Lu and Zhang, 1999; Liu et al., 2012; Mishra et al., 2012). The reduction of P yield associated with water stress has been reported in tomato (Mishra et al., 2012), maize (Liu et al., 2012), cowpea (Souza et al., 2004), wheat (Lu and Zhang, 1999), grapevine (Flexas et al., 2000), and aloe (Hazzati et al., 2016). In these studies, the decrease of P yield was accompanied by an increase in NPQ. We found similar results in the present study. The physiological mechanism for the decreased P yield and the increased NPQ yield of C\textsubscript{3} plants under water stress can be explained as follows. Water stress induces stomatal closure (Flexas et al., 2002; Rosales et al., 2012; Mathobo et al., 2017; Ouyang et al., 2017); as a consequence, the intercellular CO\textsubscript{2} concentration decreases, inducing a decline in the rate of carbohydrate (Baker and Rosenqvist, 2004; Souza et al., 2004). This results in feedback on the photorespiration to reduce electron use efficiency and retard electron transport (Baker, 2008; van der Tol et al., 2014). Then, more photosynthetic reaction centers are closed because reduced Q\textsubscript{A} cannot be reoxidized in time, resulting in the inhibition of photochemical quenching and an increase in fluorescence (Baker, 2008). In addition, when the electron transport chain is saturated, protons accumulate and the thylakoid lumen pH decreases, which may amplify NPQ (Porcar-Castell et al., 2014). In this case, electron and light energy are excessive (Flexas et al., 2002), and fluorescence and NPQ are utilized to consume the excessive light. This explains the observed increase of F\textsubscript{i} yield in summer maize (a C\textsubscript{4} crop) under moderate water stress in this study.

The response of F\textsubscript{i} to water stress in C\textsubscript{3} plants can also help us understand the results observed in this study. Decreased fluorescence in C\textsubscript{3} plants in response to water stress has been reported (Flexas et al., 2000, 2002; Cendrero-Mateo et al., 2015). For example, Flexas et al. (1999, 2000, 2002) reported that F\textsubscript{i} or F\textsubscript{i}/F\textsubscript{o} of grapevines decreased under water stress, which may result from photorespiration (Flexas et al., 2000; Flexas and Medrano, 2002; Porcar-Castell et al., 2014). Photorespiration increases as the CO\textsubscript{2} concentration reduces due to stomatal closure under water stress (Flexas et al., 2000). Photorespiration consumes NADPH (triphosphopyridine nucleotide) (Flexas et al., 2000), which promotes electron transfer from reduced Q\textsubscript{A} to the secondary electron acceptor and thus quenches fluorescence (Baker, 2008). Therefore, the fluorescence of C\textsubscript{3} plants decreases under water stress. However, when the photorespiration of C\textsubscript{3} plants was inhibited by exposing leaves to high CO\textsubscript{2} concentrations in the absence of O\textsubscript{2}, the decrease of F\textsubscript{i}/F\textsubscript{o} under water stress was suppressed and an increase of F\textsubscript{i}/F\textsubscript{o} in response to water stress was observed with PAR <600 μmol m\textsuperscript{-2} s\textsuperscript{-1} (Flexas et al., 2002). This observation indicates that fluorescence may increase under water stress in intermediate and low light conditions when there is no photorespiration. This is consistent with observations made in this study. In addition, Cendrero-Mateo et al. (2015) showed that the F\textsubscript{i} yield of C\textsubscript{3} plants under water stress decreased significantly at PAR of 300 or 500 μmol m\textsuperscript{-2} s\textsuperscript{-1}, but it increased (albeit not significantly) when PAR was <300 μmol m\textsuperscript{-2} s\textsuperscript{-1}. In the present study, the increase of F\textsubscript{i} yield in response to moderate water stress was also observed for summer maize grown under intermediate and low light conditions (0–700 μmol m\textsuperscript{-2} s\textsuperscript{-1}).

Relationships between photochemistry, fluorescence, and heat dissipation

Chlorophyll fluorescence is an effective indicator for accurately estimating gross photosynthesis (Flexas et al., 2002; Baker and Rosenqvist, 2004; Damm et al., 2010; Lee et al., 2013; van der Tol et al., 2014; Lee et al., 2015). Some studies have found that fluorescence and photosynthesis are positively related (Grunder et al., 2014; Cendrero-Mateo et al., 2015). For example, the CO\textsubscript{2} assimilation rate is positively related to F\textsubscript{i} measured by PAM in leaves of Camelina sativa (Cendrero-Mateo et al., 2015). Guanter et al. (2014) used a positive linear relationship to directly estimate global GPP by solar-induced fluorescence. However, a negative relationship between fluorescence and photosynthetic light use efficiency or P yield has also been reported (Damm et al., 2010; Liu and Cheng, 2010). Liu and Cheng (2010) stated that photosynthetic light use efficiency is negatively related to chlorophyll fluorescence due to their competition for light energy. In PSII, light energy is partitioned between photochemistry, heat dissipation, and chlorophyll fluorescence (Baker, 2008; Cendrero-Mateo et al., 2015; Guo et al., 2015). Under non-stress conditions, most light energy is channeled into photochemistry, with smaller amounts of energy destined for heat dissipation and fluorescence emission (Porcar-Castell et al., 2014). In the presence of stress, more energy is dissipated to relieve the stress, but the trade-off between, and changes in, the three pathways are still unclear.

Recently, studies have reported that the relationship between GPP and fluorescence is affected by physiological and ecological factors, such as vegetation type (Damm et al., 2015; Guan et al., 2016), land surface temperature (Cui et al., 2017), irradiation (Zhang et al., 2016; Cui et al., 2017), LAI, and chlorophyll content (Zhang et al., 2016; Cui et al., 2017). This study revealed the relationship between fluorescence and photochemistry and the changes in this relationship depending on water status and light intensity. Light intensity is a crucial factor regulating the photosynthetic physiological processes (Flexas et al., 2002; van der Tol et al., 2009; Cendrero-Mateo et al., 2015; Zhang et al., 2016; Cui et al., 2017). Under low light conditions (PAR<450 μmol m\textsuperscript{-2} s\textsuperscript{-1}), NPQ was inhibited by the proton gradient (Losdal et al., 2011; Porcar-Castell et al., 2014) and F\textsubscript{i} yield increased, while P yield decreased with increasing light intensity (Fig. 7). In this case, F\textsubscript{i} was negatively related to photochemistry. However, under water stress and intermediate light conditions of 450–700 μmol m\textsuperscript{-2} s\textsuperscript{-1}, as the light intensity increased, the electron transport chain became saturated (as mentioned above). NPQ increased as protons accumulated and the thylakoid lumen pH decreased.
of the processes that dissipate the excess light. In this case, fluorescence was negatively related to that emitted as fluorescence in the NS condition (Fig. 9). For leaves under the WS condition, we inferred that when NPQ took up a large proportion of the absorbed light energy, fluorescence and photochemistry were concurrently inhibited, resulting in a positive relationship between F_s yield and P yield. By contrast, when NPQ was not the primary light consumption pathway, the output between fluorescence and photochemistry changed. Together, these factors mean that the relationship between F_s yield and P yield for water-stressed plants was non-linear. Similar phenomena have been observed in previous research (Damm et al., 2010; Liu and Cheng, 2010; Porcar-Castell et al., 2014). For example, Porcar-Castell et al. (2014) reported that F_s yield is negatively related to P yield when NPQ is low, but the relationship becomes positive with increasing NPQ. Damm et al. (2010) illustrated that F_s yield may be positively or negatively related to photosynthetic light use efficiency, and that the slope of their relation function changes across different growing stages. Liu and Cheng (2010) also illustrated that fluorescence and photosynthesis have a competitive relationship only when NPQ is not operating. Baker (2008) and Damm et al. (2010) suggested that the principal inverse relationship between the energy used for fluorescence and that used for primary photosynthesis is usually lost due to the dominant role of NPQ in dissipating the excess light. Thus, it can be concluded that when NPQ is low, fluorescence emission is one of the processes that dissipate the excess light. In this case, F_s yield and P yield are inversely correlated. However, when NPQ plays a dominant role in dissipating the excess energy, F_s yield and P yield are both suppressed by NPQ yield; as a consequence, they are synergistic and positively related. Owing to complex relationships between fluorescence and photochemistry under changing environmental conditions, an increase in fluorescence may be associated with either an increase or a decrease in photochemistry. Thus, knowledge of the ambient environment is a prerequisite for assessing photochemistry by fluorescence (van der Tol et al., 2009).

Water stress has a significant influence on plant photosynthetic physiology. For plants grown in intermediate light conditions, the F_s yield and NPQ yield increase and the P yield decreases in response to water stress. Light intensity and water status affect the apportioning of light energy between heat dissipation, fluorescence, and photochemistry. Specifically, in the absence of water stress, F_s yield is negatively related to P yield in intermediate and low light conditions, regardless of the changes in NPQ yield. However, under water stress, the relationship between F_s yield and P yield is negative in low light conditions (PAR <450 μmol m^{-2} s^{-1}) but positive in intermediate light conditions (PAR ≥450 μmol m^{-2} s^{-1} and ≤700 μmol m^{-2} s^{-1}); F_s yield is negatively related to P yield when NPQ is <0.58, but when NPQ is >0.58, F_s yield and P yield are synergistically and positively associated.

These results reveal that in intermediate and low light conditions there are no single positive or negative relationships between P yield and F_s yield; the relationship between these yields may depend on light intensity and water status, and these factors should be considered when using measurements of chlorophyll fluorescence to estimate plant production.

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