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Photosynthetic resistance and resilience under drought, flooding and rewatering in maize plants

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Abstract

Abnormally altered precipitation patterns induced by climate change have profound global effects on crop production. However, the plant functional responses to various precipitation regimes remain unclear. Here, greenhouse and field experiments were conducted to determine how maize plant functional traits respond to drought, flooding and rewatering. Drought and flooding hampered photosynthetic capacity, particularly when severe and/or prolonged. Most photosynthetic traits recovered after rewatering, with few compensatory responses. Rewatering often elicited high photosynthetic resilience in plants exposed to severe drought at the end of plant development, with the response strongly depending on the drought severity/duration. The associations of chlorophyll concentrations with photosynthetically functional activities were stronger during post-tasseling than pre-tasseling, implying an involvement of leaf age/senescence in responses to episodic drought and subsequent rewatering. Coordinated changes in chlorophyll content, gas exchange, fluorescence parameters (PSII quantum efficiency and photochemical/non-photochemical radiative energy dissipation) possibly contributed to the enhanced drought resistance and resilience and suggested a possible regulative trade-off. These findings provide fundamental insights into how plants regulate their functional traits to deal with sporadic alterations in precipitation. Breeding and management of plants with high resistance and resilience traits could help crop production under future climate change.

Keywords Drought · Fluorescence · Photosynthetic capacity · Rewatering · Resistance · Resilience · *Zea mays* L.

Introduction

Global climate change is now leading to an enhanced frequency and intensity of drought events (Dai 2012; Trenberth et al. 2014; Donat et al. 2016; Diffenbaugh et al. 2017), that are now placing staple crop production and food security

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at risk (Lobell et al. 2014; Myers et al. 2017; Leakey et al. 2019; Kimm et al. 2020). These changes, coupled with the acceleration of industrialisation and the rapid development of social economy, are now placing agricultural water resources in tighter supply across the globe. Water availability has now become a bottleneck for food production and even social and economic development, and lack of water has triggered a series of environmental and ecological problems that now threaten sustainable development of crop production and exacerbate global undernutrition (e.g. Daryanto et al. 2016; Myers et al. 2017; Rosa et al. 2020).

Drought is one of the most crucial environmental factors constraining crop plant productivity due to its deleterious effects on leaf photosynthetic capacity, plant growth and crop productivity at regional and global scales (Lobell et al. 2014; Daryanto et al. 2016; Myers et al. 2017). Plants that experience drought stress have their water balance destroyed and this leads to plant growth inhibition, stomatal closure and decreases in the photosynthetic rate (e.g. Chaves et al. 2003, 2009; Xu et al. 2009; Gupta et al. 2020). However,

plants can invoke a number of regulative strategies to deal with water deficit. The responses to water deficit depend on the duration, severity and time of occurrence of the drought. For example, plants may not be affected, even favoured under mild or moderate drought, but it can be limited and even damaged by severe drought (e.g. Fereres and Soriano 2007; Xu et al. 2014b). Under a mild or moderate water deficit, an increased water use efficiency (WUE), improved nutritional content and stable grain yield often can be observed, which can improve sustainable development by allowing deficit irrigation and water-saving agricultural practices (Fereres and Soriano 2007; Geerts and Raes 2009; Du et al. 2015; Silveira et al. 2020). Further exploration of crop responses to various water conditions can therefore provide critical information for optimising crop management practices, particularly under future climate change (Lobell et al. 2014; Leakey et al. 2019; Kimm et al. 2020).

Effects of water stresses on plant growth and photosynthesis also strongly depend on leaf age/senescence and plant developmental stages (Otegui et al. 1995; Cakir 2004; Jiang et al. 2020). Most of the previous studies have indicated that severe drought could enhance senescence (e.g. David et al. 1998; Chaves et al. 2003; Xu et al. 2008; Jiang et al. 2020). Meanwhile, under water deficit, compared with mature/elder leaves, younger leaves often have higher growth rate and photosynthetic capacity, indicating that the former has high tolerance to drought stress (Hsiao 1973; Thiagarajah et al. 1981; David et al. 1998; Xu et al. 2008; Hofer et al. 2017). When maize plants were subjected to a prolonged water stress, huge grain yield losses of 66–93% were observed during tasseling and ear formation stages (Cakir 2004). The senescence rates of wheat leaf were rapider when water stress occurred at grain-filling than at greening and jointing stages (Jiang et al. 2020). This highlights the higher sensitivity to drought at the reproductive relative to vegetative growth stages, peculiarly at tasseling, flowering and early ear formation stages (e.g. Otegui et al. 1995; Farooq et al. 2014; Jiang et al. 2020). Flooding can affect the plant functional activities at different plant/leaf development stages. For instance, at early seedling stage, maize plants are highly susceptible to flooding relative to the later stages (Zaidi et al. 2004). As drought, flooding stress can also induce early leaf senescence in wheat at jointing or after anthesis (Araki et al. 2012). However, a comprehensive research on the responses of crops to drought, rewatering and flooding is still lacking.

Plants exposed to drought will frequently show a restoration of their normal physiological functions when rewatered, and to a certain degree, they can compensate for the damage caused by drought by accelerating their growth and enhancing their photosynthetic capacity (e.g. Xu and Zhou 2007; Xu et al. 2009, 2010; Hofer et al. 2017). An antecedent condition, such as soil water availability, may also drive the post-stress responses to other abiotic factors, indicating

important complexities in plant responses to environmental factors (Xu et al. 2009; Guo and Ogle 2019). This ability to regain a normal original state after being disturbed is termed resilience (Holling 1973; Müller et al. 2016; Resilience Alliance 2020), and can be represented by the interference level, recovery time or recovery speed (Müller et al. 2016; Bhaskar et al. 2018; Harrison et al. 2018; Resilience Alliance 2020).

A recent report showed that a watering treatment following a drought can lead to a greater recovery of some key functional traits in plants (Harrison et al. 2018). For example, both full and partial recoveries of leaf pigment and nitrogen contents were observed in drought-stressed maize plants following rewatering (Sun et al. 2018). Similarly, Voronin et al. (2019) documented the physiological responses of maize plants to drought and rewatering. However, information is lacking regarding the changes in photosynthetic capacity and their associations with plant growth during drought and subsequent recovery upon rewatering. The increased frequency of drought due to global climate change emphasises the importance of understanding the mechanism underlying the plant responses to drought and rewatering for both theoretical and practical applications (e.g. Hofer et al. 2017; Abid et al. 2018; Guo and Ogle 2019).

Drought has been an important factor in the growth of maize, the most widely grown crop in the world. Water deficit causes unstable and low yields in many maize production areas in the world, seriously hampering plant growth and causing 25–30% reductions in grain yield in some vulnerable regions (Sharp et al. 2004; Ben-Ari et al. 2016; Beyene et al. 2016; Li et al. 2019; Kimm et al. 2020). For instance, the U.S. Corn Belt, the world's biggest maize production region, is recognised as being prone to drought and is therefore sensitive to climate change (Kimm et al. 2020). Similarly, the Corn Belt of Northeastern China (CBNC) is one of the major maize production regions in China and it too shows strong sensitivity to climate variations. Drought is a particularly critical factor constraining maize production in the CBNC (e.g. Liu et al. 2012; Li and Sun 2016).

Future climate change scenarios envisage an increase in the occurrences of both drought and flooding during the growth period in maize-growing regions (Roudier et al. 2016; Kimm et al. 2020). Thus, elucidating the maize plant responses to drought, rewatering and flooding is crucial for the development of technology for monitoring, evaluating and minimising the damage caused by drought and flood disasters. This knowledge can also provide insight to the factors that enhance resilience in maize plants, while also serving as a feasible reference for corn yield forecasting and field water management during the growing period.

The aim of the present study was to conduct greenhouse and field experiments to determine maize plant functional responses to drought, rewatering and flooding. The

greenhouse experiments involved examination of these responses following different water treatments, including pre-drought, drought, rewatering and flooding. The field experiment was conducted in a large-sized rain shelter designed to grow maize plants under three irrigation regimes, including pre-drought and subsequent re-irrigation. Our focus was specifically on assessing the resilience of photosynthetic capacity in response to drought and rewatering. Three hypotheses were tested: (i) drought and flooding can constrain photosynthetic capacity in maize plants, particularly under severe, prolonged water stress; (2) rewatering can lead to a full recovery of photosynthetic capacity with a compensatory mechanism; (3) the resilience of photosynthetic capacity depends on the degree of drought stress. The findings may improve current knowledge and strengthen future quests to produce high-yield, drought-resistant and resilient crops (see also Gupta et al. 2020).

Materials and methods

Greenhouse experiment design

The first experimental site was located in a greenhouse (39° 48′ N, 116° 28′ E, 67 m a.s.l.), Institute of Botany, Chinese Academy of Sciences, Beijing, China. The soil was collected from field soil (0–30 cm soil profile) at Gucheng Ecological Environment and Agro-meteorology Test Station (39° 08′ N, 115° 40′ E, 15.2 m a.s.l.), Baoding city, Hebei province, North China. Plastic pots (diameter 21 cm, height 25 cm) were used. The maize cultivars is Zhengdan 958, which is currently planted extensively in North China. The seeds were sown on 28, June 2017. We filled 5.5 kg of soil per pot; and each pot was applied as 2.54 g of diammonium phosphate compound fertilizer (i.e. 750 kg ha^{-1}). The three seeds were sown in each of the pot with a depth of 2.5 cm. Soon afterwards, only one healthy plant was left before the third leaf of seedlings emerged. The seedlings were grown in a naturally illuminated glasshouse with fluorescent lamp illumination addition with the maximum photosynthetic photon flux density (*PPFD*) of 1000 µmol m^{-2} s^{-1} and a day/night photoperiod of 12-h light/12-h darkness and a day/night mean temperature of *c*. 28.0/20.0 ℃.

The greenhouse experiment used four water treatments: (1) Control treatment: the soil relative water content (SRWC) was maintained at 65–75% throughout the whole experimental period. (2) Persistent drought stress: SRWC was reduced beginning at the three-leaf stage and extending to jointing stages (i.e. seven-leaf stage) to the SRWC of the permanent wilting point (PWP). (3) Flooding treatment: waterlogging stress was induced at the three-leaf stage and extended until the jointing stage. (4) Drought-rewatering treatment: SRWC was reduced initially at the three-leaf stage to 35% of SRWC

at the jointing stage (the leaves wilted and the lowermost leaves began to turn yellow and withered); the plants were then rewatered to 65–75% of SRWC.

Field experimental design

The field experimental site was located at the Jinzhou Ecology and Agricultural Meteorology Center, Liaoning, Northeastern China (N 41° 49′, E 121° 12′, 27.4 m a.s.l.). The mean annual temperature and the mean annual precipitation over 40 years were 9.9 °C and 564 mm, respectively, with an average monthly temperature of 20.9 °C and a total precipitation of 468 mm during plant growing season. The soil is characterised as medium loam type, with pH 6.3, 1.8% organic matter and a soil bulk density of 1.61 g cm^{-3} at the 0–100 cm soil profile. The field capacity (FC) and PWP were 22.3% and 6.5% (gravimetric), respectively. The soil had an organic carbon content of 10.44 g kg^{-1}, total nitrogen content of 0.69 g kg^{-1}, phosphorus content of 0.50 g kg^{-1} and potassium content of 22.62 g kg^{-1}. The planting date and maturity date were late April and late September, respectively (Mi et al. 2018; Song et al. 2018; Li et al. 2019).

The field experimental design was as detailed previously (Li et al. 2019). In brief, an electric-powered waterproof shelter (4 m in height) set up in the maize field was used to establish the various precipitation regimes that we desired. In total, 15 plots (15 m^2, 5 m length, 3 m width) were covered to avoid rainfall falling with the rain shelter when it rained. The following three irrigation regimes were set up: a control (i.e. the normal irrigation every 7 day); moderate drought (water withholding for 20 days); and severe drought (water withholding for 27 days from the tasseling to milking stages). In this design, irrigation water was supplied at 296, 246 and 221 mm across the maize plant growing period (Table S1). The dates of measurements of chlorophyll content and photosynthetic traits were 1 July (V13, 62 days after sowing [DAS]), 12 July (VT, tasseling, 73 DAS), 20 July (R1, silking, 81 DAS), 5 August (R2, blistering, 97 DAS), 9 August (R3, milking, 101 DAS) and 2 September (R4, dough, 125 DAS). To measure SRWC, the method with soil auger was used to retrieve soil samples, and the samples were then dried at 105 °C to a constant dry weight. The SRWC at 0–50 cm soil depth was reduced progressively to reach severe drought levels at a range of 30–40% at the end of rainfall-withholding, whereas under normal irrigation, the SWRC was maintained at levels of 70–80% in the control and rewatering plots (Fig. S1). The maize cultivar was Danyu 39, with a seed sowing rate of 6.0 plants m^{-2} to ensure a planting density of 4.5 plants m^{-2}. A compound fertiliser (accounting for 28%, 11% and 12% of N, P$_2$O$_5$ and K$_2$O, respectively), applied at a *c*. 750 kg ha^{-1}, was added before sowing (Song et al. 2018; Li et al. 2019).

Leaf chlorophyll content

We examined leaf chlorophyll concentrations with a SPAD 502 chlorophyll meter (Minolta Co. Ltd, Japan). In the greenhouse experiment, SPAD was measured only on the youngest fully expanded leaf (top leaf) at 20, 22, 26, 29, 32, 34 and 37 DAS. In field experiment, measurements were made in top (16–18th leaves), middle (12–14th leaves) and bottom leaves (8–10th leaves) along the plant position from bottom to top layers. Each position was measured thrice in the middle area of the selected leaf, avoiding the leaf main vein. Both measurements on SPAD and photosynthetic parameter were on the same leaves in the same days (below).

Leaf gas exchanges and chlorophyll *a* fluorescence

In the greenhouse experiment, the leaf gas exchange and chlorophyll *a* fluorescence were measured in both the top and mature leaves (the third leaf from the top of plant) with an open gas exchange system (LI-6400, LI-COR Inc., Lincoln, NE) equipped with a LI-6400-40 fluorometer. The measurements were made at an interval of 3–5-day with the treatment time. Leaves were acclimated in the chamber for at least 15 min at 28–30 °C with a CO_2 concentration of 400 µmol mol^{-1} and a PPFD of 1200 µmol m^{-2} s^{-1}. Chlorophyll *a* fluorescence was determined with the LI-6400-40 fluorometer. The steady-state fluorescence (F_s) was recorded at 1200 µmol m^{-2} s^{-1}, and a second saturating pulse at ~8000 µmol photons m^{-2} s^{-1} was then given to obtain the maximal light-adapted fluorescence yield (F_m'). The actinic light was turned off, and the minimal fluorescence at the light-adapted state (F_o') was obtained following a 3 s burst of far-red illumination.

In the field experiment, the leaf chlorophyll *a* fluorescence was determined with a miniaturised pulse-amplitude-modulated photosynthesis yield analyser (Mini-PAM, Walz, Effeltrich, Germany). After a 30-min dark adaptation, the minimal fluorescence yield (F_o) was determined with a modulated light at a sufficiently low intensity (< 0.1 µmol photon m^{-2} s^{-1}). The maximal fluorescence yield (F_m) was made with a 0.8 s saturating pulse at a ~7000 µmol photons m^{-2} s^{-1}. Leaves were continuously illuminated at 300 µmol photons m^{-2} s^{-1} for 15 min. After the F_s was recorded, the second saturating pulse at ~7000 µmol photons m^{-2} s^{-1} was then exposed to obtain F_m'. The actinic light was turned off and F_o' was obtained following a 3 s far-red illumination. The maximal quantum efficiency of photosystem II (PSII, F_v/F_m), the efficiency of excitation captured by open PSII centres in the light-adapted leaves (F_v'/F_m') and the yield of PSII photochemistry (Φ_{PSII}) were obtained (Schreiber et al. 1994; Maxwell and Johnson 2000). Other fluorescence parameters were calculated with the following formulas by Kramer et al. (2004):

$$q_p = \left(F_m' - F_s\right)\big/\left(F_m' - F_o'\right)$$

$$q_L = q_p \times F_0'\big/F_s$$

$$q_N = \left(F_m - F_m'\right)\big/\left(F_m - F_o'\right)$$

$$\Phi_{NPQ} = F_s/F_m' - F_s/F_m$$

$$\Phi_{NO} = F_s/F_m,$$

where q_p and q_L are photochemical quenching based on puddle and lake models, respectively. NPQ or q_N is non-photochemical quenching, and both Φ_{NPQ} and Φ_{NO} are light-induced regulated non-photochemical quenching and quantum yield of non-regulated energy loss in PSII, respectively (Kramer et al. 2004).

Soil relative water content

Soil was placed in an experimental pot with holes at the bottom and weighed 48 h after excessive watering to reach a saturated weight (SW) point. The soil was then dried at 110 °C for at least 72 h to a constant weight (DW). The FC can be expressed as FC = (SW–DW)/DW × 100. The SRWC = Current soil water content/FC × 100.

Resistance, recovery and resilience

Resistance is expressed as a ratio of functional parameters (e.g. net photosynthetic rate, A_{net}) between drought stress and ample water status as control treatment (e.g. van Ruijven and Berendse 2010; Mariotte et al. 2013; Xu et al. 2014a). Recovery can be indicated by the ratio of functional parameters between drought/pre-drought and post-rewatering treatment (van Ruijven and Berendse 2010; Mariotte et al. 2013; Xu et al. 2014a). Sometime, the recovery is also named as resilience (Ruppert et al. 2015; Bhaskar et al. 2018); however, the resilience is calculated as the ratio of functional parameters between ample watering (control) and rewatering treatments (e.g. van Ruijven and Berendse 2010; Mariotte et al. 2013; Xu et al. 2014a). These indices can be expressed in different proportional terms such as the difference (e.g. van Ruijven and Berendse 2010; ratio (Mariotte et al. 2013), log ratio (van Ruijven and Berendse 2010; Xu et al. 2014a) and percentage ratio (Xu et al. 2014a; Sakschewski et al. 2016). In the current study, we consistently used the relative percentage ratios to indicate their changes (e.g. Xu et al. 2014a; Sakschewski et al. 2016):

$$\text{Resistance} = (\text{Xck} - \text{Xd})/\text{Xck} \times 100 \qquad (1)$$

$$Recovery = (Xw - Xd)/Xd \times 100 \qquad (2)$$

$$Resilience = (Xw - Xck)/Xck \times 100 \qquad (3)$$

where Xd and Xck are functional parameter values (e.g. A_{net}) under drought stress and ample water status (control treatment); Xw is functional parameter value following rewatering.

Data statistics

The data were statistically analysed with statistical software package SPSS 20.0 (SPSS Inc., Chicago, Illinois, USA). A one-way analysis of variance (ANOVA) with post hoc tests of Duncan and LSD multiple comparisons was used to test the differences of the functional traits between leaf layer at each watering treatment and/or at each sampling time. The effects of watering treatment and leaf layer at each day of sampling or plant developmental stages, and their interaction on the functional traits of plants, were tested with two-way ANOVAs, with Duncan and LSD multiple comparisons. The correlations among the functional traits were tested with Pearson's correlation analysis, and the relationships of photosynthetically functional traits with leaf relative chlorophyll content (SPAD readings) at different plant growth stages were tested by linear regression analysis. In particular, because the VT, a transitional stage from the vegetative stage to reproductive stage, is a key stage linking the vegetative stage and reproductive stage (e.g. Abendroth et al. 2009), we separated the data for all leaves into two subsets to conduct the relationships of photosynthetically functional traits with leaf relative chlorophyll content to test whether the differences occur between the two stages. The comprehensive relationships between leaf photosynthetic functional traits, and their responses to irrigation regimes and plant/leaf developmental stages were determined by principal component analysis (PCA). The significance levels were set at $P < 0.05$ and 0.01, unless otherwise stated.

Results

Photosynthetic traits in the greenhouse

The greenhouse experiment showed that drought stress led to a slight reduction in the relative chlorophyll content (SPAD readings) in the top leaf 4 days after withholding water (i.e. 22 days after sowing, DAS), followed by a rise of 8 days after the drought-stressed treatment (Fig. 1). However, the chlorophyll content showed a sharp linear decrease from 26 to 37 DAS when the relative soil water content (RSWC) fell sharply to the severe drought stress
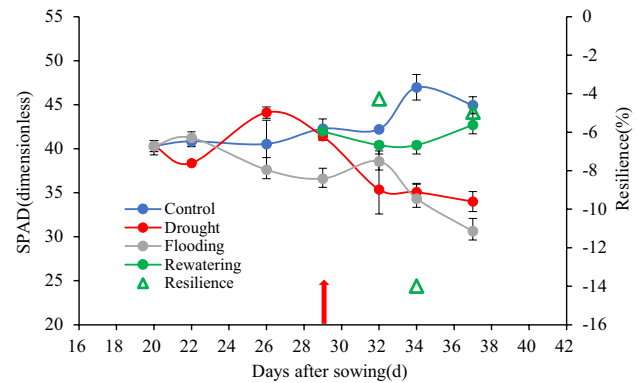

Fig. 1 The changes in leaf relative chlorophyll content (SPAD values) in the top leaves of maize plants subjected to various watering regimes (blue line, ample watering as the control; grey line, flooding; red line, drought; green line, rewatering; green open triangle, resilience). The red arrow indicates the rewatering date. The data are shown as means ± SE ($n = 3$–6)

level of 35%. After rewatering, the chlorophyll content significantly increased, with recovery values of 14.2, 15.2 and 25.6% under consecutive drought at 32, 34 and 37 DAS, respectively, indicating that a greater recovery may occur at the end of the measurement period. The resilience values were − 4.3, − 14.0 and − 5.0% at 32, 34 and 37 DAS, respectively, showing that the resilience rose initially following rewatering, then decreased and then increased again (Table S2). Compared with control, flooding led to significant declines in SPAD after 26 DAS ($P < 0.05$), indicating that chlorophyll degradation occurred under the flooded condition.

As shown in Fig. 2a, drought only led to a slight reduction in the net light-saturated photosynthetic rate (A_{sat}) in top leaf within one week after withholding water. However, this rate sharply decreased from 28.8 to 4.8 μmol m^{-2} s^{-1} by 85.2% at 29 DAS when RSWC dropped to 35%. After rewatering, A_{sat} sharply and significantly increased ($P < 0.05$), with recovery values of 5.53, 1.18 and 5.98 times the values seen under consecutive drought at 32, 34 and 37 DAS, respectively. The rate approached and even exceeded the control level at 32, 34 and 37 DAS. The resilience values increased gradually from − 12.1 to 10.2 and 25.4%, indicating a possible escalation of resilience with time after rewatering. Compared to control, a significant stimulation of the A_{sat} occurred during the initial 6 days under flooding ($P < 0.05$); thereafter, flooding induced a decrease compared with the control treatment after 32 DAS ($P < 0.05$). However, A_{sat} under flooding ultimately reached the level of the control treatment. The responses were also observed in the mature leaves. Drought also reduced A_{sat} in mature leaf with great recovery and a positive resilience noted at the end of the experiment (Fig. 2d; Table S2). A sharp rise appeared during the initial flooding, but A_{sat} decreased thereafter.
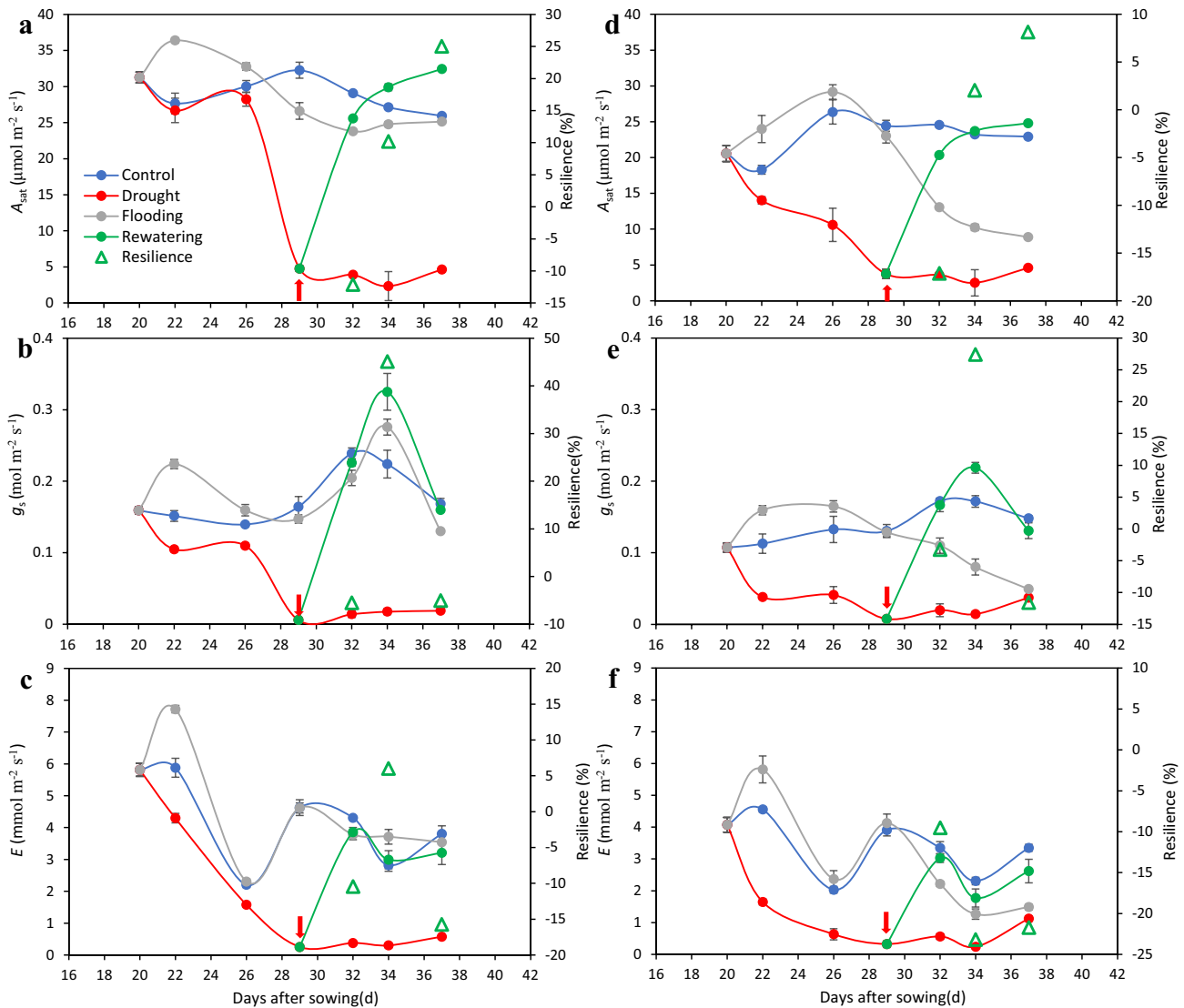
Fig. 2 The changes in net light-saturated photosynthetic rate (A_{sat}, **a**, **d**), stomatal conductance (g_s, **b**, **e**) and transpiration rate (E, **c**, **f**) in both the top leaves (**a–c**) and mature leaves (**d–f**) of maize plants subjected to various watering regimes (blue line, ample watering as the control; grey line, flooding; red line, drought; green line, rewatering; green open triangle, resilience). Red arrows indicate the rewatering date; the data are shown as means ± SE ($n = 3$–6). Note different scales in the second y-axis

Compared with the control, stomatal conductance (g_s) was significantly decreased (− 96.5%) at 29 DAS, just before rewatering (Fig. 2b). A greater recovery was observed, but only positive resilience was detected at 34 DAS. In mature leaves, a drastic g_s resilience was also evident at 34 DAS (Fig. 2e). However, the low recovery was observed in mature leaves (Fig. 2b, e).

The transpiration rate (E) significantly decreased due to drought stress ($P < 0.05$), dropping to the lowest point at 29 DAS (a decrease of 94.5% relative to control, Fig. 2c). Rapid increases occurred following the rewatering, with recovery values of 9.3-fold, 8.9-fold and 4.6-fold the values under continuous drought at 3, 5 and 8 days following rewatering,

respectively. However, the resilience values were − 10.4, 6.0 and − 15.7% at 3, 5 and 8 days following rewatering, respectively. A stimulation of E also appeared initially by flooding; thereafter, however, the similar E changes were similar to those of the control (Fig. 2c). In mature leaves, a rapid and drastic reduction in E was also observed by imposition of drought stress, with great recovery; however, the resilience remained negative (Fig. 2f).

The quantum yield of PSII electron transport (Φ_{PSII}) decreased with drought-treatment time, dropping to its lowest value (by 79.3%) at 29 DAS (Fig. 3a). The recovery values were 3.05, 3.38 and 4.22 times relative to continuous drought at 3, 5 and 8 days after rewatering, respectively.
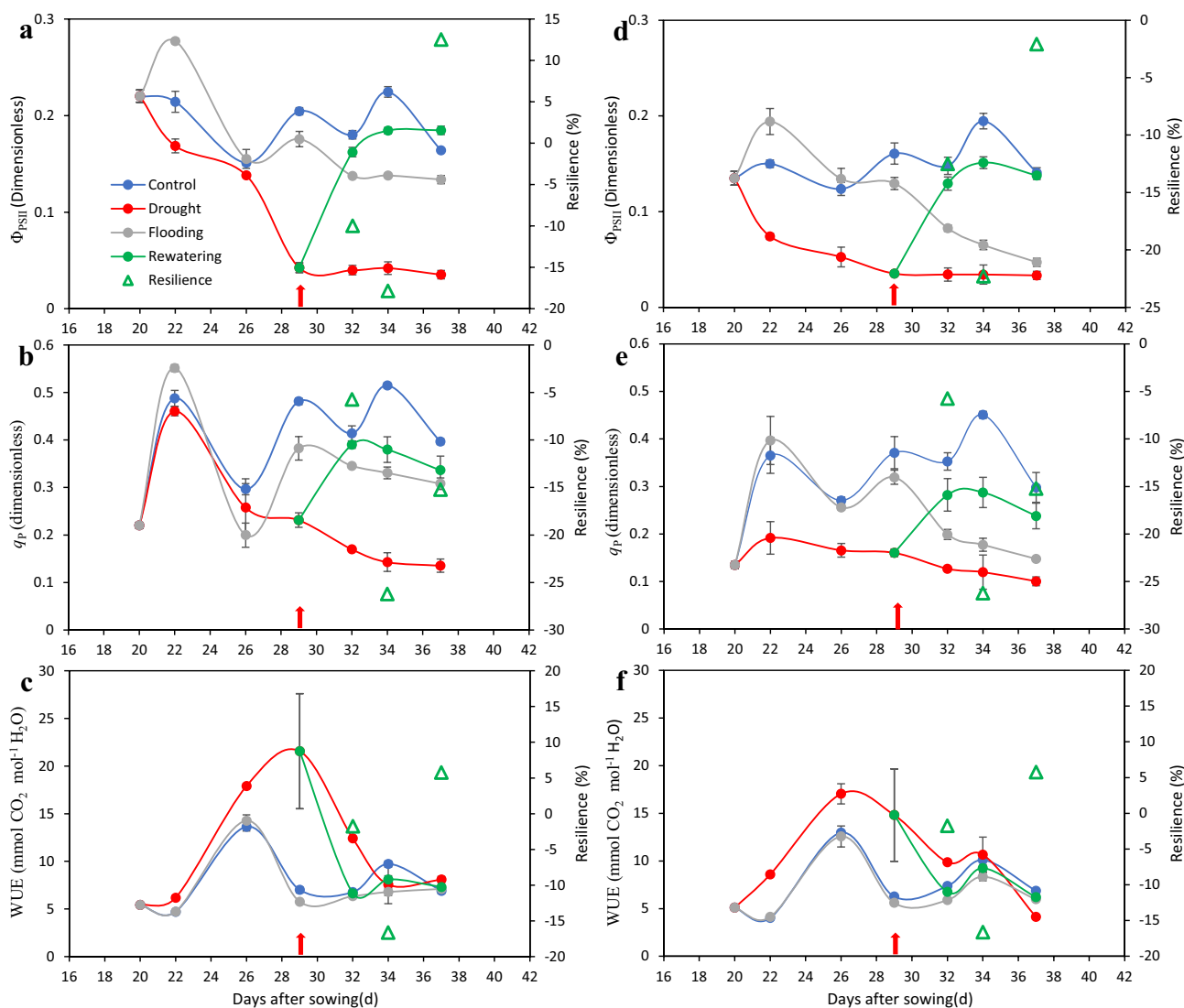
Fig. 3 The changes in quantum yield of PSII electron transport (Φ_{PSII}, **a**, **d**), photochemical quenching (q_P, **b**, **e**) and water use efficiency (WUE, **c**, **f**) in both the top leaves (**a**–**c**) and mature leaves (**d**–**f**) of maize plants subjected to various watering regimes (blue line, ample watering as the control; grey line, flooding; red line, drought; green line, rewatering; green open triangle, resilience). Red arrows indicate the rewatering dates; the data are shown as means ± SE ($n = 3$–6). Note different scales in the second y-axis

Flooding also led to an initial stimulation in Φ_{PSII}; thereafter, the value decreased below the control level. The photochemical quenching (q_P) showed a substantial fluctuation even under the control treatment (Fig. 3b). However, a dramatic decline of 51.9% was observed after 9 days of water withholding. We also found recoveries of 1.3-fold, 16.6-fold and 14.8-fold at 3, 5 and 8 days following rewatering, respectively. However, the increases still did not reach the control level, so the resilience values were negative (− 5.74, − 26.22 and − 15.22 at 3, 5 and 8 days following rewatering). A stimulation of q_P was also observed initially at 2 days after flooding exposure, but this disappeared thereafter and the value dropped to levels lower than the control levels. For mature

leaves, a great recovery occurred for Φ_{PSII} and q_P; however, the negative resilience was still maintained (Fig. 3d, e).

Leaf water use efficiency (WUE) was significantly increased by drought during 26–32 DAS ($P < 0.001$), but subsequently decreased with drought-exposure time, indicating that the enhancement of WUE may be attenuated by the water deficit intensity and its persistent duration. Rewatering led to a decline in WUE at the earlier stage, but thereafter WUE remained stable relative to both the control and continuous drought plants. WUE was not affected significantly by flooding during the experimental periods (Fig. 3c). Drought always also elevated the WUE in the mature leaves, whereas flooding did not substantially affect it. Only a small

positive resilience was observed at the end of the experiment (Fig. 3f).

Based on one-way ANOVA, there were significant effects on photosynthetic traits except for WUE before watering treatment at 20 DAS (Table S3). The two-way ANOVAs indicated that the effects on photosynthetic parameters including the leaf gas exchange and chlorophyll fluorescence traits were significant from watering treatment, and leaf layer as a single factor alone (except leaf layer for WUE at 26, 29, 32 DAS). However, significant interactions between water and leaf layer occurred only for some photosynthetic traits (Table S4).

Photosynthetic traits in the field

In the field experiment, the top leaves in the control treatment showed gradual increases in the relative chlorophyll content (SPAD values) from 1 July (62 DAS, V13), 12 July (73 DAS, VT, tasseling), July 20 (81 DAS, R1, silking), to August 5 (97 DAS, R2, blistering), until reaching a maximum on 97 DAS; the relative chlorophyll content

then decreased as plant development progressed (Fig. 4a). Episodic severe drought led to significant dramatic declines ($P < 0.05$), whereas rewatering led to more increases (i.e. a positive recovery) under moderate drought (MD) than under severe drought (SD). Negative resilience values were observed under both drought treatments at 101 and 125 DAS. Similar responses were also observed in both middle and bottom leaves: SPAD values significantly decreased under SD ($P < 0.05$), particularly on 97 DAS; and no positive resilience was observed (Fig. 4d, g; Table S5).

The maximum quantum efficiency of PSII (F_v/F_m) in top leaves showed a similar pattern to that seen for the relationship of SPAD with DAS; i.e. a unimodal curve (Fig. 4b). A decline seemed to appear under SD; however, recovery was greater following rewatering. In the middle leaves, positive resilience was noted for F_v/F_m at 125 DAS (Fig. 4e). In the bottom leaves, a severe drought episode resulted in a marked reduction in F_v/F_m at 97 DAS, but a rapid recovery occurred at 4 d after rewatering. Rewatering resulted in high F_v/F_m resilience in the plants exposed to previous MD and SD at the end of plant development (Fig. 4h).
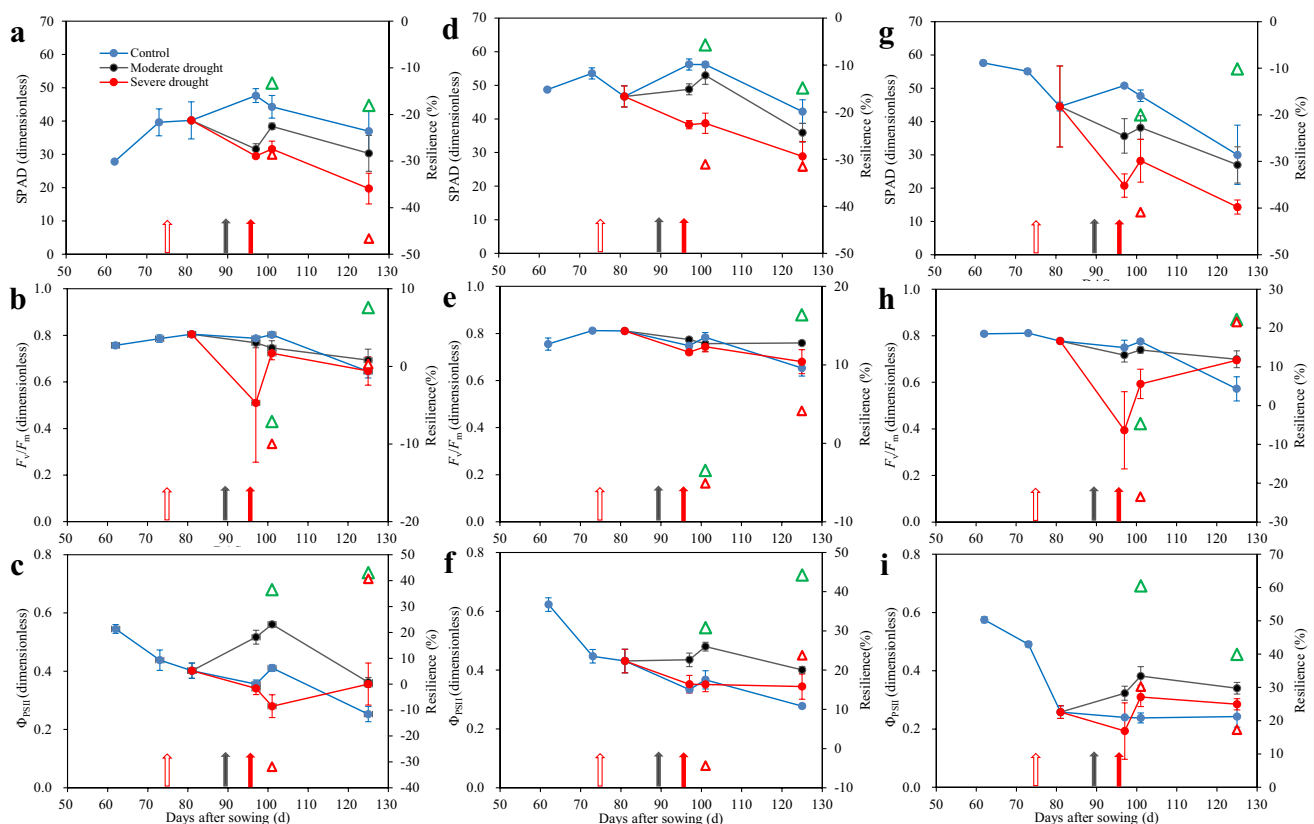

Fig. 4 SPAD and chlorophyll *a* fluorescence in top (**a–c**), middle (**d–f**) and bottom (**g–i**) leaves under drought and rewatering. Green and red open triangles represent the resilience of moderate and severe drought, respectively, at 101 and 125 days after sowing (DAS). Red open arrows indicate the DAS of water withholding; while grey and red close arrows indicate the rewatering DASs of moderate and severe drought treatments, respectively. SPAD, leaf relative chlorophyll content; F_v/F_m maximal quantum efficiency of photosystem II (PSII); Φ_{PSII} the yield of PSII photochemistry. The data are shown as means ± SE ($n = 3–6$)

In top leaves, Φ_{PSII} values under control decreased with plant growth (Fig. 4c). An increase occurred under MD, but SD led to a marked decline with greater resilience at both 101 and 125 DAS. In middle leaves, greater resilience appeared under MD at 101 and 125 DAS and under SD only at 125 DAS (Fig. 4f). In bottom leaves, a decline in Φ_{PSII} was observed from 62 to 81 DAS, but a stable Φ_{PSII} change remained thereafter during the later plant developmental periods. Marked resilience appeared for both pre-drought treatments at the two final developmental stages (Fig. 4i).

The changes in q_p and its resilience in top leaves were similar to those of Φ_{PSII} (Fig. 5a). In middle leaves, the q_p values decreased with plant development under the control treatment, but greater resilience appeared under MD at 101 DAS (Fig. 5d). In bottom leaves, the changes in q_p showed a similar pattern to that in top leaves. However, a great recovery and marked resilience appeared at 101 DAS (Fig. 5g).

In top leaves, the changes in non-photochemical quenching (q_N) and the yield of light-induced regulated non-photochemical quenching (Φ_{NPQ}) and their resilience showed the same changing trends (Fig. 5b, c): they increased with

DAS, and MD led to a drastic decline with a high resilience under SD at 101 DAS. In middle leaves, both q_N and Φ_{NPQ} also increased with DAS, with negative resilience under MD at both 101 and 125 DAS (Fig. 5e, f). In bottom leaves, under ample irrigation, both q_N and Φ_{NPQ} increased until 81 DAS and then remained stable. Drought led to declines in q_N and Φ_{NPQ} with considerable recovery at 125 DAS in the plants exposed to the SD episode; however, the resilience still remained negative (Fig. 5h, i).

Across all leaf types, SPAD decreased under both MS and SD, and no positive resilience was observed (Fig. S2a). A decline F_v/F_m occurred at 97 DAS, and a positive resilience appeared at 125 DAS (Fig. S2b). Both Φ_{PII} and q_p values decreased with plant development under control treatment, but greater resilience was observed under MD at 101 and 125 DAS (Fig. S2c, d). Both q_N and Φ_{NPQ} increased under control treatment, but decreased under MD and SD with DAS, with the negative resilience values (Fig. S2e, f).

One-way ANOVAs indicated the effects on photosynthetic parameters of leaf layer before watering treatment (Table S6): There were significant effects of leaf layer on
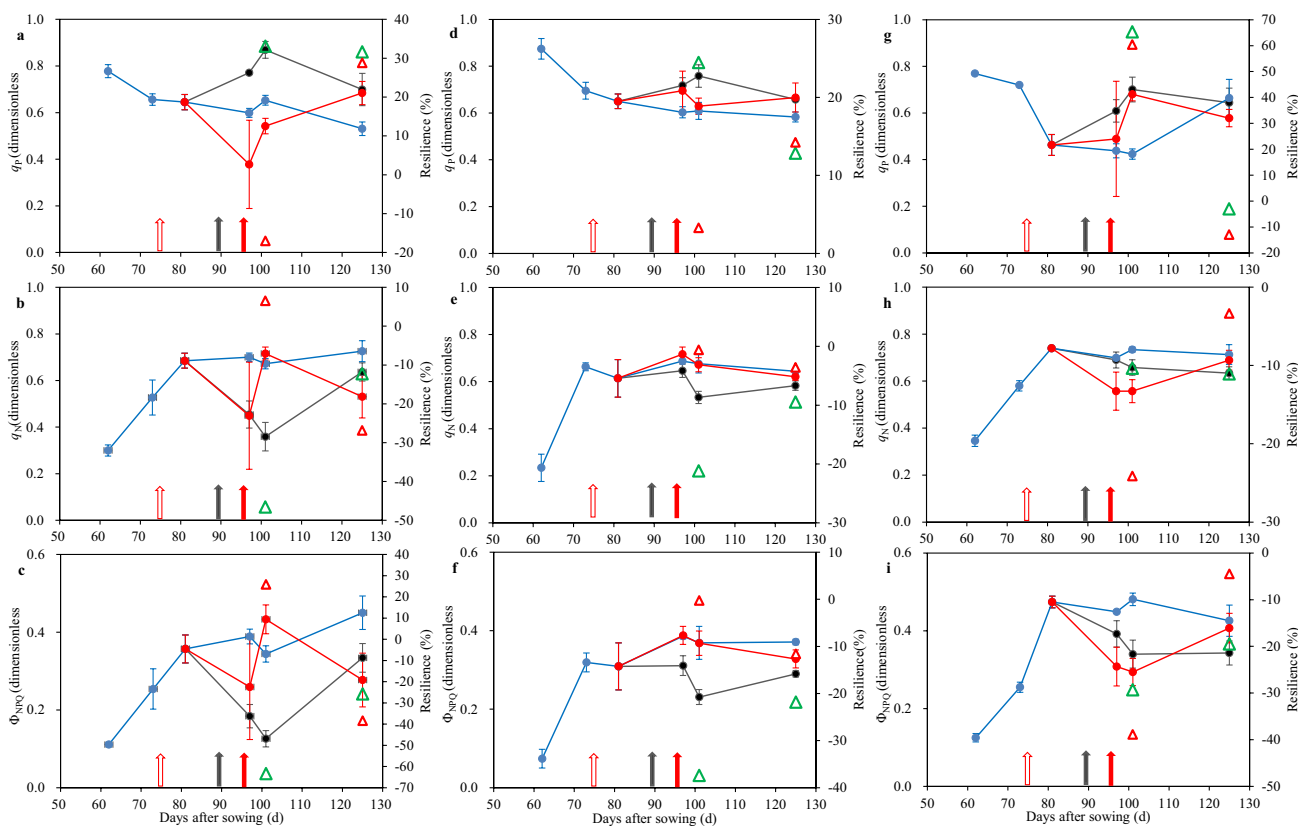

Fig. 5 Chlorophyll *a* fluorescence in in top (**a–c**), middle (**d–f**) and bottom (**g–i**) leaves under drought and rewatering. Green and red open triangles represent the resilience of moderate and severe drought, respectively, at 101 and 125 days after sowing (DAS). Red open arrows indicate the DAS of water withholding; while grey and red close arrows indicate the rewatering DASs of moderate and severe drought treatments, respectively. q_p photochemical quenching based on puddle model; q_N non-photochemical quenching; Φ_{NPQ} light-induced regulated non-photochemical quenching. The data are shown as means ± SE (*n* = 3–6)

SPAD, F_v/F_m and Φ_{PSII} at 62 DAS; only on SPAD at 73 DAS; on F_v/F_m, Φ_{PSII} and q_p at 81 DAS. According to the two-way ANOVAs (Table S7), the effects on SPAD, F_v/F_m, Φ_{PSII} and Φ_{NPQ} were all significant from watering treatment alone at each DAS following rewatering ($P < 0.05$). Significant effects of water on q_p and q_N appeared only at 101 DAS. All photosynthetic traits measured were affected significantly from leaf layer alone at 101 DAS, but significant effects on SPAD and Φ_{PSII} appeared only at 97 DAS. The interactive effects of two factors occurred on SPAD only at 97 DAS; Φ_{PSII} at 62 DAS; Φ_{PSII}, q_p, q_N and Φ_{NPQ} at 101 DAS.

Relationships between the functional traits

The relationships between fluorescence parameters and chlorophyll contents (SPAD values) in the maize field are shown in Fig. S3. Before/at previous tasseling stages (i.e. VT, a transitional stage from the vegetative stage to reproductive stage), only strong relationship was observed between F_v/F_m and chlorophyll content ($R^2 = 0.39$, $P < 0.001$; Fig. S3a). Using the data after VT revealed significant and positive relationships of SPAD values with fluorescence parameters, especially for F_v/F_m ($R^2 = 0.61$, $P < 0.001$, Fig. S3a). However, others with low R^2 may imply that SPAD does not explain much of the existing variation in fluorescence parameters, possibly due to excessive random variation, due to other parameters or (to a lower extend) to a substantial non-linearity.

We also performed a PCA to test the relationships between functional traits and the different patterns in both greenhouse (Fig. S4) and field experiments (Fig. 6). In the greenhouse experiment (Fig. S4), the first two principal components (PCs) explained 60.3% of the total photosynthetic variations. The loadings of F_m', F_O', q_P and q_N were sorted in quadrant I, while that of F_v'/F_m' was in quadrant IV. The loadings of the gas exchange traits and Φ_{PSII} were placed between quadrant I and quadrant IV, with positive loadings of A_{sat}, g_s, E, Φ_{PSII} and a negative loading of WUE. PC scores of control and rewatering were distributed in the right parts, whereas those of drought were placed in the left area (Fig. S4). In the field experiment, the first two principal components (PCs) accounted for 70.1% of the total variations. The loadings of SPAD, F_v/F_m, F_m, F_O and F_O' were in quadrant I, while those of Φ_{PSII}, F_m', q_P and q_L were in quadrant II. The markers most representative of non-photochemical quenching traits (e.g. NPQ, q_N and Φ_{NPQ}) in relation to non-photochemical radiative energy dissipation capability were sorted into quadrant III. Projection on the treatment effects showed that the three irrigation regimes were sorted in the coordinate plane, with control treatment mostly in quadrant II and severe drought scattered in all four quadrants (Fig. 6).
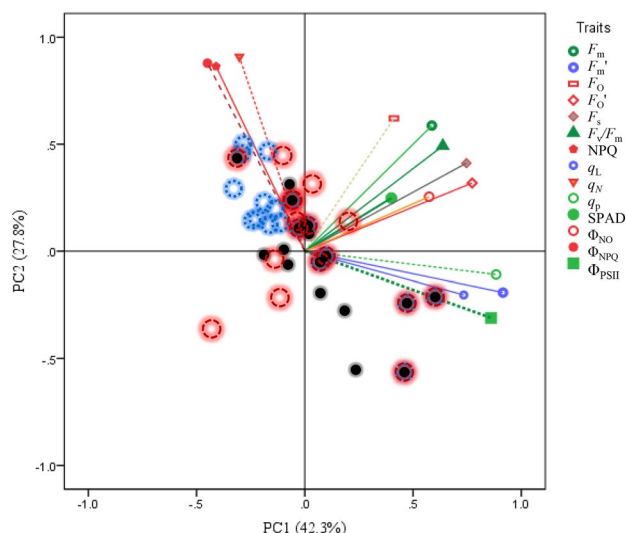

Fig. 6 Principal component analysis on plant functional traits under the three irrigation regimes [i.e. control, moderate drought (MD) and severe drought (SD)]. The traits' loadings on the first two principal components (PCs) are shown, and their projections are sorted by the three irrigation regimes. Dotted blue, closed black and dotted red circles with glowing represent the PC scores of control, moderate and severe drought treatments, respectively. F_m maximal fluorescence yield; F_m' maximal light-adapted fluorescence yield; F_o minimal fluorescence yield; F_o' minimal fluorescence at light-adapted state; F_s steady-state fluorescence; F_v/F_m maximal quantum efficiency of photosystem II (PSII); Φ_{PSII} yield of PSII photochemistry; q_p photochemical quenching based on puddle model; q_L photochemical quenching based on lake models, q_N non-photochemical quenching; Φ_{NPQ} light-induced regulated non-photochemical quenching; Φ_{NO} quantum yield of non-regulated energy loss

Discussion

Water cycle changes could substantially impact plant growth, photosynthetic processes and many crucial physiological functions and nutrient status, thereby affecting plant productivity and crop yield (e.g. Izanloo et al. 2008; Lobell et al. 2014; Kimm et al. 2020). Drought and rewetting may often occur at intervals and are predicted to happen more frequently and severely under climatic change (Dai 2012; IPCC 2014; Donat et al. 2016; Diffenbaugh et al. 2017). Indeed, sporadic precipitation is a critical issue in maintaining ecosystem productivity and its structural stability, particularly in arid and semi-arid areas and/or in rain-fed planting regions (Reynolds et al. 2004; Cooper et al. 2008; Song et al. 2018; Guo and Ogle 2019).

Maize plays a critical role in meeting the global food demands and is one of the most widely planted staple crops worldwide (Haarhoff and Swanepoel 2018; FAO 2020). In this study, the greenhouse and field experiments demonstrated how maize photosynthetic functional traits respond to drought, flooding and rewatering, particularly at different growth stages, thereby providing key information for

managing crop production. Our main findings were that (1) drought hampered photosynthetic capacity in both young and mature leaves, whereas flooding only limited them for mature leaves, in major support of the first hypothesis; (2) rewatering could result in partial recovery of some photosynthetic traits, with few compensatory responses, in partial support of our second hypothesis; and (3) the photosynthetic resilience to drought was dependent on the drought severity, largely supporting the third hypothesis. In particular, the associations of chlorophyll concentrations with photosynthetically functional activities were stronger during post-tasseling than pre-tasseling (Fig. S3), implying an involvement of leaf age/senescence in responses to episodic drought and subsequent rewatering. A PCA clearly illuminated the associations and trade-off among chlorophyll content, gas exchange and photosynthetic potentials, and the effect patterns of the watering treatments (Figs. S4, 6). These findings can shed light on ways to improve regulation of crop functional traits to deal with erratic precipitation regimes and may lead to better breeding and management practices for crops that have high drought resistance and drought-resilience traits at different growth stages (Kromdijk et al. 2016; Song et al. 2018; Gupta et al. 2020).

Drought and flooding

In agreement with the previous work (e.g. Chaves et al. 2003, 2009; Xu and Zhou 2006; Xu et al. 2009; Gupta et al. 2020), the results of the present study indicated that severe drought stress can substantially reduce photosynthetic capacity, as characterised by declines in chlorophyll content, net light-saturated photosynthetic rate (A_{sat}), stomatal conductance (g_s) and quantum yield of PSII electron transport (Φ_{PSII}) in both the greenhouse and field experiments. However, the photosynthetic capacity attenuated more substantially and steeply as the drought stress persisted in our experiment, indicating a strong dependence on the duration, severity and timing of droughts. Thus, only mild or moderate or short drought stresses were conducive to the development of a regulative response of plants for resistance to water deficit. For instance, maintaining A_{sat} at a stable level with a low g_s can elevate WUE during moderate drought stress (e.g. Chaves et al. 2009; Xu and Zhou 2011). This observation may aid in implementations of deficit irrigation, water-saving agriculture and sustainable development (Fereres and Soriano 2007; Geerts and Raes 2009; Du et al. 2015; Silveira et al. 2020; Kimm et al. 2020).

The present findings demonstrated that flooding led to a decline in SPAD and A_{sat}, but not g_s. Our results also indicated a higher tolerance of maize to flooding stress in terms of Φ_{PSII} and photochemical quenching (q_P), relative to drought stress, highlighting the distinct effects of these two stresses (Mutava et al. 2015; Zhu et al. 2020). An antagonistic effect on g_s has been reported (see also Zhu et al. 2020). Maintaining stomatal opening may promote water release to alleviate the stress due to excessive water, again highlighting the positive regulation in response to anoxic conditions (Zhu et al. 2020).

Recovery and resilience

As previously reported, a depression in photosynthesis potentials by a previous drought can be markedly stimulated by rewetting; however, whether or how much these potentials recover depends on drought intensity and/or the persistence period (e.g. Xu et al. 2009, 2010; Creek et al. 2018). In the current experiment, partial, full and over recovery of photosynthetic traits were all observed in terms of both recovery and resilience indices, specifically depending on the duration and persistence of the drought, the plant developmental stages and the different functional traits, as well as the crop species and cultivar (Figs. 1, 2, 3, 4 and 5; Xu et al. 2009; Creek et al. 2018). For instance, an over-compensatory recovery (i.e. a positive percentage of the resilience) in g_s was observed in maize (Fig. 2b, e); however, g_s only achieved a partial recovery in a grass species (Xu et al. 2009). Creek et al. (2018) reported that, after rewatering, the A_{net} of a semi-arid species can return to the pre-drought stress level within 2–4 weeks, whereas g_s performs a slower recovery. A recent report by Johnson et al. (2018) indicated that photosynthesis was not fully recovered in wheat plants because of the photosynthetic damage due to hydraulic decline in the leaves subjected to drought. Increased embolism is tightly related to a complete lack of photosynthetic recovery. However, Creek et al. (2018) found that photosynthetic recovery can be decoupled from the recovery of plant hydraulics, indicating that the impaired hydraulic function throughout the recovery period perhaps does not influence the complete recovery of A_{net} from drought. Thus, the underlying mechanism needs to be investigated further.

The enhancement of plant functional activities (e.g. plant growth rate, grain yield and A_{sat}) following rewatering has been found by many researchers (Reynolds et al. 2004; Siopongco et al. 2006; Xu et al. 2009; Song et al. 2018). As recently reported by Abid et al. (2018), tolerant wheat plants showing high photosynthetic capacity during drought and rapid recovery after re-irrigating did not show marked yield declines relative to the sensitive cultivars, indicating that the plant's ability to maintain/restore growth and physiological functions during pre/post-drought in the vegetative period might play a crucial role in determining crop productivity. Upon rewatering, the rapid growth of new tissues, such as a new leaf, might accelerate plant growth, potentially enhancing CO_2 assimilation (Pinheriro et al. 2004). This may be a result of positive source–sink interactions, as a strong sink requirement (e.g. new tissue) can enhance

the carbon assimilation rate (Minchin and Lacointe 2005; White et al. 2015; Parvin et al. 2020). Higher resilience of A_{sat} and g_s occurred in the younger leaves relative to mature ones, implying a greater ability to recover in the new leaves that serve as both active source–sink organs (Fig. 2; Roitsch 1999). The maize plants were exposed to drought stress for only several days, so leaf length after rewatering was restored to a similar level to that of the control plants, indicating no occurrence of overcompensation (Acevedo et al. 1971; Xu et al. 2009; Hofer et al. 2017). Thus, the extent of compensation for drought by the triggering of new tissues following rewatering might determine the final plant/crop production and would depend strongly on the severity, duration and timing of the drought stress (Hsiao 1973; Xu et al. 2009; Hofer et al. 2017).

Associations between functional traits

The distinct responses of the functional traits such as A_{sat} and g_s to drought, flooding and rewetting suggested that coordinated associations between the functional traits could reveal the underlying mechanism (see also Creek et al. 2018). For instance, the SPAD reading (e.g. Ciganda et al. 2009), as an indicator of relative chlorophyll concentration, has different associations with photosynthetic function activities at different plant development stages: stronger associations were observed post-VT (tasseling stage) than pre-VT (Fig. S3). This might indicate that a greater coupling relationship appears at later plant developmental stages and that leaf age/senescence could be involved in the responses to drought and rewatering (also see Valentinuz and Tollenaar 2004; Song et al. 2018; Jiang et al. 2020). This finding may further improve our understanding of how plants respond to water status changes at different developmental stages. For instance, many previous studies have indicated that drought damage increases, while tolerance decreases, with increasing senescence (e.g. David et al. 1998; Shah and Paulsen 2003; Chaves et al. 2003; Xu et al. 2008; Jiang et al. 2020). However, rewatering may lessen the senescence processes (Xu et al. 2010; Jiang et al. 2020), thereby leading to changes in associations between functional traits such as coupling and trade-off occurrences. As revealed by the PCA in greenhouse experiment (Fig. S4), the distinctive distribution of loadings of gas exchange (i.e. A_{sat}, g_s, E, WUE), PSII functional activities (i.e. F_v'/F_m', Φ_{PSII}) and photochemical quenching processes (i.e. q_p and q_N) (Schreiber et al. 1994; Maxwell and Johnson 2000), reflect their coordination and/or trade-off in response to watering regimes (Xu et al. 2014b). Moreover, from the PCA in field experiment (Fig. 6), a distinct pattern of loadings between Φ_{PSII}, Φ_{NPQ} and Φ_{NO} highlights a feasible trade-off strategy by balancing the yields among photochemical processes for the energy absorbed by PSII, dissipation of non-photochemical responses and

other non-photochemical losses, which would involve the xanthophyll cycle and PsbS protein expression (Murchie and Lawson 2013; Kromdijk et al. 2016; Sacharz et al. 2017). In addition, the contribution of the photosynthetic parameters for the discrimination between watering treatments could be demonstrated by the PCA plots. For instance, those representing photochemical quenching processes (q_N, NPQ and Φ_{NPQ}) may contribute to more variation of control treatment in the field experiment (Fig. 6). Together, the association between functional traits and their effects of environmental factors can be well illustrated with PCA (e.g. Vile et al. 2012; Xu et al. 2014b).

As noted, leaf ranks of maize plants could be each considered as an entity to indicate the time course of senescence (e.g. Escobar-Gutiérrez and Combe 2012). In the greenhouse, because the maize seedings were only used during this experiment, we measured the two types of leaf: the young and mature leaves. The changes in photosynthetic traits measured in the two types of leaf with DAS time would roughly reflect the effects of leaf age. In the field experiment, the maize plants were used at later stages of plant development; thus, we conveniently selected the three-leaf layers of plant canopy to measure the photosynthetic traits. The top, middle and bottom leaves along plant height may represent the leaf development ages/stages: relatively young leaf, mature leaf and elderly leaf, respectively (Xu et al. 2008; Song et al. 2018; Li et al. 2019; Feng et al. 2020). However, the more information on relations among the leaf age, leaf senescence and its position along plant height, and the response to climatic change may deserve further study with its specific design.

Conclusion

Quantifying and defining plant functional traits to assess and predict drought effects and post-drought recovery are relevant issues due to the pressing needs imposed by climate change (e.g. Creek et al. 2018; Gupta et al. 2020). In this study, we conducted greenhouse and field experiments to explore how maize photosynthetic functional traits respond to drought, flooding and rewatering at different growth stages. The main findings were the following: (1) drought and flooding constrains photosynthetic capacity, particularly under severe and/or long water stress; (2) rewatering results in a partial recovery of most of the photosynthetic traits, with few compensatory responses; (3) photosynthetic resilience to drought following rewetting strongly depends on the drought severity and its persistence and duration. The distinct responses of various functional traits to drought, flooding and rewetting can translate to a regulative strategy of trade-off. The coordinated changes in chlorophyll content, gas exchange, fluorescence parameters (quantum efficiency

of PSII, and photochemical and non-photochemical radiative energy dissipation) may largely contribute to the enhancements of drought resistance and resilience of plants. The associations of chlorophyll concentrations with photosynthetic functional activities were also stronger post-VT than pre-VT, implying that leaf age/senescence may be involved in the responses to drought and rewatering. These findings may further improve our understanding of how plants respond to water status changes at different plant developmental stages. This knowledge can be helpful for breeding crops with high drought-resistant and drought-resilience traits and for establishing management practices when facing climate change (e.g. Kromdijk et al. 2016; Leakey et al. 2019; Kimm et al. 2020; Gupta et al. 2020).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11120-021-00825-3.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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