Photosynthetic resistance and resilience under drought 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 and plant growth stage. The associations of chlorophyll concentrations with photosynthetically functional activities were stronger during post-tasselling than pre-tasselling, 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;

34 Resilience; *Zea mays* L.

35

36 **Introduction**

37 Global climate change is now leading to an enhanced frequency and intensity of
 38 drought events (Dai, 2012; Trenberth *et al.*, 2014; Donat *et al.*, 2016; Diffenbaugh *et*
 39 *al.*, 2017), that are now placing staple crop production and food security at risk
 40 (Lobell *et al.*, 2014; Myers *et al.*, 2017; Leakey *et al.*, 2019; Kimm *et al.*, 2020).
 41 These changes, coupled with the acceleration of industrialisation and the rapid
 42 development of social economy, are now placing agricultural water resources in
 43 tighter supply across the globe. Water availability has now become a bottleneck for
 44 food production and even social and economic development, and lack of water has
 45 triggered a series of environmental and ecological problems that now threaten
 46 sustainable development of crop production and exacerbate global undernutrition (e.g.,
 47 Daryanto *et al.*, 2016; Myers *et al.*, 2017; Rosa *et al.*, 2020).

48 Drought is one of the most crucial environmental factors constraining crop plant
 49 productivity due to its deleterious effects on leaf photosynthetic capacity, plant growth
 50 and crop productivity at regional and global scales (Lobell *et al.*, 2014; Daryanto *et*
 51 *al.*, 2016; Myers *et al.*, 2017). Plants that experience drought stress have their water
 52 balance destroyed and this leads to plant growth inhibition, stomatal closure, and
 53 decreases in the photosynthetic rate (e.g., Chaves *et al.*, 2003, 2009; Xu and Zhou,
 54 2009; Gupta *et al.*, 2020). However, plants can invoke a number of regulative
 55 strategies to deal with water deficit, including extending the root system, increasing
 56 leaf thickness, and activating an antioxidative defence system (e.g., Trapeznikov *et al.*,
 57 2003), increased leaf thickness (Sack and Grubb, 2002), provoked antioxidative
 58 defense system (Foyer and Noctor, 2005). The responses to water deficit depend on
 59 the duration, severity and time of occurrence of the drought. For example, plants may
 60 not be affected, even favoured under mild or moderate drought, but it can be limited
 61 and even damaged by severe drought (e.g., Fereres and Soriano, 2007; Xu *et al.*,
 62 2014). Under a mild or moderate water deficit, an increased water use efficiency
 63 (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 (Feres 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).

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 *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 rehydration. 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

94 grown crop in the world. Water deficit causes unstable and low yields in many maize
95 production areas in the world, seriously hampering plant growth and causing 25–30%
96 reductions in grain yield in some vulnerable regions (Sharp *et al.*, 2003; Ben-Ari *et al.*,
97 2016; Beyene *et al.*, 2016; Li *et al.*, 2019; Kimm *et al.*, 2020). For instance, the U.S.
98 Corn Belt, the world's biggest maize production region, is recognised as being prone
99 to drought and is therefore sensitive to climate change (Kimm *et al.*, 2020). Similarly,
100 the Corn Belt of Northeastern China (CBNC) is one of the major maize production
101 regions in China and it too shows strong sensitivity to climate variations. Drought is a
102 particularly critical factor constraining maize production in the CBNC (e.g., Liu *et al.*,
103 2012; Li and Sun, 2016).

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

112 The aim of the present study was to conduct greenhouse and field experiments to
113 determine maize plant functional responses to drought, rewatering and flooding. The
114 greenhouse experiments involved examination of these responses following different
115 water treatments, including pre-drought, drought, rewatering and flooding. The field
116 experiment was conducted in a large-sized rain shelter designed to grow maize plants
117 under 4 irrigation regimes, including pre-drought and subsequent re-irrigation. Our
118 focus was specifically on assessing the resilience of photosynthetic capacity in
119 response to drought and rewatering. Three hypotheses were tested: i) drought and
120 flooding can constrain photosynthetic capacity in maize plants, particularly under
121 severe, prolonged water stress; 2) rewatering can lead to a full recovery of
122 photosynthetic capacity with a compensatory mechanism; 3) the resilience of
123 photosynthetic capacity depends on the degree of drought stress and the plant

development stage. 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).

127

128 **Materials and Methods**

129 *Greenhouse experiment design*

130 The first experimental site was located in a greenhouse (39°48'N, 116°28'E, 67 m
131 a.s.l.), Institute of Botany, Chinese Academy of Sciences, Beijing, China. The soil was
132 collected from field soil (0-30 cm soil profile) at Gucheng Ecological Environment
133 and Agro-meteorology Test Station (39°08'N, 115°40'E, 15.2m a.s.l.), Baoding city,
134 Hebei province, North China. Plastic pots (diameter 21 cm, height 25 cm) was used.
135 The maize cultivars is Zhengdan 958, which is currently planted extensively in North
136 China. The seeds were sown on June 28, 2017. We filled 5.5 kg of soil per pot; and
137 each pot was applied as 2.54 g of diammonium phosphate compound fertilizer (i.e.,
138 750 kg ha⁻¹). The three seeds were sown in each of the pot with a depth of 2.5 cm.
139 Soon afterwards, only one healthy plant was left before the third leaf of seedlings
140 emerged. The seedlings grew in the greenhouse with a day/night mean temperature of
141 *c.* 28.0/20.0 °C and maximum photosynthetic photon flux density (*PPFD*) of 1,000
142 μmol m⁻²s⁻¹).

143 The greenhouse experiment used four water treatments: 1) Control treatment: the
144 soil relative water content (SRWC) was maintained at 65–75% throughout the whole
145 experimental period. 2) Persistent drought stress: SRWC was reduced beginning at the
146 three-leaf stage and extending to jointing stages to the SRWC of the permanent
147 wilting point (PWP). 3) Flooding treatment: waterlogging stress was induced at the
148 three-leaf stage and extended until the jointing stage. 4) Drought-rehydration
149 treatment: SRWC was reduced initially at the three-leaf stage to 35% of SRWC (the
150 leaves wilted and the lowermost leaves began to turn yellow and withered); the plants
151 were then rewatered to 65–75% of SRWC.

152

153 *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', 27.4m 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, pH 6.3, with 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% (v/v), 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 (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 (details in Li *et al.*, 2019). In total, 15 plots (15 m², 5 m length, 3 m width) were under 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 tasselling to milking stages). In this design, irrigation water was supplied at 296, 246, and 221 mm across the maize plant growing period. The SRWC at 0–50 cm soil depth was monitored 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. 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, P₂O₅, and K₂O, respectively), applied at a c. 750 kg·ha⁻¹, was added before sowing (Song *et al.*, 2018; Li *et al.*, 2019).

180

181 *Leaf chlorophyll content*

182 We examined leaf chlorophyll concentrations with a SPAD 502 chlorophyll meter
183 (Minolta Co. Ltd, Japan). This is a nondestructive technique that provides feasible and

184 rapid assessment of leaf relative chlorophyll concentrations (a SPAD reading value)
185 by determining leaf transmittance of red (650 nm) and infrared (940 nm) radiation.
186 Measurements were made on 1 July (V13, 62 days after sowing [DAS]), 12 July (VT,
187 tasselling, 73 DAS), 20 July (R1, silking, 81 DAS), 5 August (R2, blistering, 97 DAS),
188 9 August (R3, milking, 101 DAS), 2 September (R4, dough, 125 DAS).

189

190 *Leaf gas exchanges and chlorophyll a fluorescence*

191 In the greenhouse experiment, the leaf gas exchange and chlorophyll *a* fluorescence
192 were measured with an open gas exchange system (LI-6400, LI-COR Inc., Lincoln,
193 NE) equipped with a LI-6400-40 fluorometer. Leaves was illuminated with a red-blue
194 LED light source. The parameters were initially obtained with acquisition software.
195 Leaves were acclimated in the chamber for at least 15 min at 28–30 °C with a CO₂
196 concentration of 400 μmol mol⁻¹ and a PPFD of 1200 μmol m⁻² s⁻¹. Chlorophyll *a*
197 fluorescence was determined with the LI-6400-40 fluorometer. The steady-state
198 fluorescence (F_s) was recorded at 1200 μmol m⁻² s⁻¹, and a second saturating pulse at
199 ~8000 μmol photons m⁻²s⁻¹ was then given to obtain the maximal light-adapted
200 fluorescence yield (F_m'). The actinic light was turned off, and the minimal
201 fluorescence at the light-adapted state (F_o') was obtained following a 3 s burst of
202 far-red illumination.

203 In the field experiment, the leaf chlorophyll *a* fluorescence was determined with a
204 miniaturised pulse-amplitude-modulated photosynthesis yield analyser (Mini-PAM,
205 Walz, Effeltrich, Germany) equipped with a leaf clip holder (2030-Br). Light
206 intensities (380–710 nm) were measured with the Mini-PAM microquantum sensor.
207 After a 30 min dark adaptation, the minimal fluorescence yield (F_o) was determined
208 with a modulated light at a sufficiently low intensity (< 0.1 μmol photon m⁻² s⁻¹) to
209 induce the minimal fluorescence. The maximal fluorescence yield (F_m) was made
210 with a 0.8 s saturating pulse at a ~7000 μmol photons m⁻² s⁻¹. The difference between
211 the measured values (F_m , F_o) is the variable fluorescence (F_v). Leaves were
212 continuously illuminated at 300 μmol photons m⁻² s⁻¹ with an actinic light for 15 min.
213 The F_s was recorded, and the second saturating pulse at ~7000 μmol photons m⁻²s⁻¹
214 was then exposed to obtain F_m' . The actinic light was turned off and F_o' was obtained
215 following a 3 s far-red illumination. The fluorescence parameters were calculated with

the following formulas (Schreiber et al., 1994; Maxwell and Johnson, 2000; Kramer et al., 2004):

$$F_v/F_m = (F_m - F_o)/F_m$$

$$F_v'/F_m' = (F_m' - F_o')/F_m'$$

$$\Phi_{PSII} = (F_m' - F_s)/F_m'$$

$$q_p = (F_m' - F_s)/(F_m' - F_o')$$

$$q_L = q_p \times F_o'/F_s$$

$$q_N = (F_m - F_m')/(F_m - F_o')$$

$$NPQ = (F_m - F_m')/F_m' = F_m/F_m' - 1$$

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

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

$$NPQ = (F_m - F_m')/F_m' = F_m/F_m' - 1$$

where F_v/F_m is the maximal quantum efficiency of photosystem II (PSII), and F_v'/F_m' is the efficiency of excitation captured by open PSII centres in the light-adapted leaves. Φ_{PSII} is the yield of PSII photochemistry, and 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 $FC = (SW - DW) / DW \times 100$. The SRWC = Current soil water content / FC $\times 100$.

243 *Resistance, recovery and resilience*

244 Resistance was expressed as the difference/ratio in functional parameters between
245 drought stress and ample watering as control treatments. Recovery was indicated by
246 the difference/ratio in functional parameters between drought/pre-drought and
247 rewatering. Resilience was calculated as the difference/ratio in functional parameters
248 between ample watering (control treatment) and rewatering (Van Ruijven and
249 Berendse, 2010; Ruppert *et al.*, 2015; Bhaskar *et al.*, 2018). Here, we prefer to use the
250 percentage ratios to express these changes (Ruppert *et al.*, 2015).

252 *Data statistics*

253 The data were statistically analysed with statistical software package SPSS 20.0
254 (SPSS Inc., Chicago, Illinois, USA). A one-way analysis of variance (ANOVA) with
255 Duncan's multiple comparison was used to test the differences of the functional traits
256 between the watering treatments. The effects of watering treatment and plant/leaf
257 developmental stages, and their interaction on the functional traits of plants, were
258 tested with a two-way ANOVA. The correlations among the functional traits were
259 tested with Pearson's correlation analysis, and the relationships of photosynthetically
260 functional traits with leaf relative chlorophyll content (SPAD readings) at different
261 plant growth stages were tested by linear regression analysis. The comprehensive
262 relationships between leaf photosynthetic functional traits, plant growth and their
263 responses to irrigation regimes and plant/leaf developmental stages were determined
264 by principal component analysis (PCA). The significance levels were set at $P < 0.05$
265 and 0.01, unless otherwise stated.

267 **Results**

268 *Photosynthetic traits in the greenhouse*

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

the severe drought stress level of 35%. After rewatering, the chlorophyll content sharply 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. Flooding led to sharp declines in SPAD after 4 days of flooding treatment, 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}) within one week after withholding water. However, this rate sharply decreased from $28.8 \mu\text{mol m}^{-2}\text{s}^{-1}$ to $4.8 \mu\text{mol m}^{-2}\text{s}^{-1}$ by 85.2% 29 DAS when RSWC dropped to 35%. After rewatering, A_{sat} sharply increased, 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. A stimulation of the A_{sat} occurred during the initial 6 days under flooding; thereafter, flooding induced a decrease compared with the control treatment. However, A_{sat} under flooding ultimately reached the level of the control treatment. 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.

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. 2c). 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. 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. 2d). However, a dramatic decline of 51.9% was observed after 9 days of water withholding. We also found recoveries of 1.3-, 16.6- and 14.8-fold at 3, 5 and

8 days following rewatering, respectively. However, the increases still did not reach the level of the control, 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.

The transpiration rate (E) significantly decreased due to drought stress, dropping to the lowest point at 29 DAS (a decrease of 94.5% relative to control, Fig. 2e). Rapid decreases occurred following the rewatering, with recovery values of 9.3-, 8.9- 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. 2e). Leaf water use efficiency (WUE) was initially increased by drought, 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. 2f).

Similar responses were observed in the mature leaves (Fig. 3a-f). Drought reduced A_{sat} , with great recovery and a positive resilience noted at the end of the experiment (Fig. 3a). A sharp rise appeared during the initial flooding, but A_{sat} decreased thereafter. A drastic g_s resilience was evident at 34 DAS (Fig. 3b). A great recovery occurred for Φ_{PSII} and q_p ; however, the negative resilience was still maintained (Fig. 3c, d). A rapid and drastic reduction in E was observed by imposition of drought stress, with great recovery; however, the resilience remained negative (Fig. 3e). Drought always 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).

332

333 *Photosynthetic traits in the field*

334 In the field experiment, the upper canopy leaves in the control treatment showed
335 gradual increases in the relative chlorophyll content (SPAD values) from 1 July (62
336 DAS, V13), 12 July (73 DAS, VT, tasselling), July 20 (81 DAS, R1, silking), to
337 August 5 (97 DAS, R2, blistering), until reaching a maximum on 97 DAS; the relative
338 chlorophyll content then decreased as plant development progressed (Fig. 4a).
339 Episodic droughts led to dramatic declines, whereas rewatering led to more increases
340 (i.e., a positive recovery) under moderate drought (MD) than under severe drought
341 (SD). Negative resilience values were observed under both drought treatments at 101
342 and 125 DAS. The maximum quantum efficiency of PSII (F_v/F_m) showed a similar
343 pattern to that seen for the relationship with DAS; i.e., a unimodal curve (Fig. 4b). A
344 drastic decline occurred under SD; however, recovery was greater following
345 rewatering.

346 A high resilience was found with MD at 125 DAS. The Φ_{PSII} values decreased
347 with plant growth (Fig. 4b). An increase occurred under MD, but SD led to a marked
348 decline with greater resilience at both 101 and 125 DAS. The changes in q_p and its
349 resilience were similar to those of Φ_{PSII} (Fig. 4d). The changes in non-photochemical
350 quenching (q_N) and the yield of light-induced regulated non-photochemical quenching
351 (Φ_{NPQ}) and their resilience showed the same changing trends (Fig. 4d): they increased
352 with DAS, and MD led to a drastic decline with a high resilience at 101 DAS.

353 In the middle canopy leaves, SPAD values decreased under SD, and no positive
354 resilience was observed (Fig. 5a). Positive resilience was noted for F_v/F_m at 125 DAS
355 (Fig. 5b). The Φ_{PII} and q_p values decreased with plant development under the control
356 treatment, but greater resilience appeared under MD at 101 and 125 DAS and under
357 SD at 125 DAS (Fig. 5c, d). Both q_N and Φ_{NPQ} increased with DAS, with greater
358 resilience under MD at both 101 and 125 DAS (Fig. 5e, f).

359 In the bottom canopy leaves, the relative chlorophyll content steeply decreased
360 with DAS under all irrigation regimes, with a marked decline under SD. Rapid
361 recoveries occurred with rewatering; however, only negative resilience was observed
362 (Fig. 6a). A severe drought episode resulted in a reduction in F_v/F_m at 97 DAS, but a
363 rapid recovery occurred at 4 d after rewatering (Fig. 6b). Rewatering resulted in high

364 F_v/F_m resilience in the plants exposed to previous MD and SD at the end of plant
365 development. A decline in Φ_{PSII} was observed from 62 to 81 DAS, but a stable Φ_{PSII}
366 change remained thereafter during the later plant developmental periods. Marked
367 resilience appeared for both pre-drought treatments at the two final developmental
368 stages (Fig. 6c). The changes in q_p showed a similar pattern to that of Φ_{PSII} . However,
369 the marked resilience appeared only at 101 DAS (Fig. 6d). Under ample irrigation,
370 both q_N and Φ_{NPQ} increased until 81 DAS and then remained stable. Drought led to
371 declines in q_N and Φ_{NPQ} with considerable recovery at 125 DAS in the plants exposed
372 to the SD episode; however, the resilience still remained negative (Fig. 6e, f).

373

374 *Relationships between the functional traits*

375 The relationships between fluorescence parameters and chlorophyll contents (SPAD
376 values) in the maize field are shown in Fig. 7. We separated the data into
377 sub-categories to explore how their relationships are altered at the two developmental
378 stages. We only considered the data before/at previous tasselling stages (i.e., VT, a
379 transitional stage from the vegetative stage to reproductive stage); therefore, the only
380 significant and strong relationship was observed between F_v/F_m and chlorophyll
381 content (SPAD readings, $R^2 = 0.318$, $P < 0.001$; Fig. 4a). The other parameters (i.e.,
382 Φ_{PSII} , q_p , q_N and Φ_{NPQ}) showed no significant relationships ($P > 0.05$, Fig. 4c-f),
383 except for a significant and negative relationship between F_s and the SPAD values
384 (Fig. 4b). Using the data after VT revealed significant and positive relationships of
385 SPAD values with fluorescence parameters, including F_v/F_m ($R^2 = 0.607$, $P < 0.001$,
386 Fig. 4a), F_s ($R^2 = 0.193$, $P = 0.022$, Fig. 4b), Φ_{PSII} ($R^2 = 0.210$, $P = 0.016$, Fig. 4c), q_p
387 ($R^2 = 1.48$, $P = 0.047$, Fig. 4d), q_N ($R^2 = 0.378$, $P = 0.001$, Fig. 4e) and Φ_{NPQ} ($R^2 =$
388 0.248 , $P = 0.008$, Fig. 4f). This indicates that stronger and closer associations emerged
389 between chlorophyll content and the key fluorescence parameters, but only at later
390 developmental stages.

391 We also performed a PCA to test the relationships between functional traits and
392 the different patterns (Fig. 8). The first two principal components (PCs) accounted for
393 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 SD scattered in all four quadrants (Fig. 8).

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, 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 the abnormal precipitation alterations, including drought, flooding, and rewetting at different growth stages, thereby providing key information for managing crop production. Our main findings were that 1) drought and flooding severely hampered photosynthetic capacity in maize plants, particularly under severe and/or long water stress, in support of the first hypothesis; 2) rewetting 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 and the plant developmental stage, largely supporting the third hypothesis. 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 (Kromdijk *et al.*, 2016; Song *et al.*, 2018; Gupta *et al.*, 2020).

Drought and flooding

In agreement with previous work (e.g., Chaves *et al.*, 2003, 2009; Xu *et al.*, 2006; Xu and Zhou, 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 in terms of the changes in the root system (e.g., Trapeznikov *et al.*, 2003), leaf thickness (Sack and Grubb, 2002) and antioxidative defence system (Foyer and Noctor, 2005). This observation may aid in implementations of deficit irrigation, water saving agriculture, and sustainable development (Feres and Soriano, 2007; Geerts and Raes, 2009; Du *et al.*, 2015; Silveira *et al.*, 2020; Kimm *et al.*, 2020).

The present findings also demonstrated that flooding led to a decline in SPAD and A_{sat} , but not g_s . Indeed, under an anaerobic environment, plants may have adaptive responses to flooding stress that include aerenchyma formation in the roots and the development of adventitious roots (Mano *et al.*, 2006), alteration of the profile of protein synthesis related to anoxic tolerance (Subbaiah and Sachs, 2003), and enhanced starch accumulation (Mutava *et al.*, 2015). An involvement of ethylene regulation is also associated with an enhancement of photochemical and non-photochemical radiative energy dissipation capability (De Pedro *et al.*, 2020). 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 1-6; 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 (Figs. 2b, 3b); however, g_s only achieved a partial recovery in a grass species (Xu *et al.*, 2009). Creek *et al.* (2008) recently reported that, after rewatering, the A_{net} of a semiarid 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 growth due to rewatering has been addressed 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 CO₂ assimilation (Pinheiro *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 Lacombe, 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 (Figs 2, 3; 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).

503

504 *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 (tasselling stage) than pre-VT (Fig. 7). 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. This finding may

514 further improve our understanding of how plants respond to water status changes at
 515 different developmental stages. For instance, many previous studies have indicated
 516 that drought damage increases, while tolerance decreases, with increasing senescence
 517 (e.g., David *et al.*, 1998; Shah and Paulsen, 2003; Chaves *et al.*, 2003; Xu *et al.*, 2008;
 518 Jiang *et al.*, 2020). However, rewatering may lessen the senescence processes (Xu *et*
 519 *al.*, 2010; Jiang *et al.*, 2020), thereby leading to changes in associations between
 520 functional traits such as coupling and trade-off occurrences. Moreover, as revealed by
 521 the PCA (Fig.8), a distinct pattern of loadings between Φ_{PSII} , Φ_{NPQ} and Φ_{NO} highlights
 522 a feasible trade-off strategy by balancing the yields among photochemical processes
 523 for the energy absorbed by PSII, dissipation of non-photochemical responses and
 524 other non-photochemical losses, which would involve the xanthophyll cycle and PsbS
 525 protein expression (Murchie and Lawson, 2013; Kromdijk *et al.*, 2016; Sacharz *et al.*,
 526 2017).

527

528 **Conclusions**

529 Quantifying and defining plant functional traits to assess and predict drought effects
 530 and post-drought recovery are relevant issues due to the pressing needs imposed by
 531 climate change (e.g., Creek *et al.*, 2018; Gupta *et al.*, 2020). In this study, we
 532 conducted greenhouse and field experiments to explore how maize photosynthetic
 533 functional traits respond to drought, flooding, and rewatering at different growth
 534 stages. The main findings were the following: 1) drought and flooding constrains
 535 photosynthetic capacity, particularly under severe and/or long water stress; 2)
 536 rewatering results in a partial recovery of most of the photosynthetic traits, with few
 537 compensatory responses; 3) photosynthetic resilience to drought following rewetting
 538 strongly depends on the drought severity and its persistence and duration, as well as
 539 the plant growth stage. The distinct responses of various functional traits to drought,
 540 flooding, and rewetting can translate to a regulative strategy of trade-off. The
 541 coordinated changes in chlorophyll content, gas exchange, fluorescence parameters
 542 (quantum efficiency of PSII, and photochemical and non-photochemical radiative
 543 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; Leahey *et al.*, 2019; Kimm *et al.*, 2020; Gupta *et al.*, 2020).

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Author contributions

Zhenzhu Xu and Guagnsheng Zhou conceived and designed the study; Miao Qi, Xiaodi Liu, Yibo Li, He Song, and Feng Zhang conducted the experiment works. Miao Qi, Xiaodi Liu, Yibo Li, and Zhenzhu Xu performed the data analyses. All authors wrote and proofread the manuscript.

Availability of data and materials

The data sets supporting the results of this article are included within the article and its supporting information file.

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Fig. 1. The changes in leaf relative chlorophyll content (SPAD values) in the youngest and fully expanded 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 $\pm$ SE (n = 3-6).

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773 Fig. 2. The changes in net light-saturated photosynthetic rate (A_{sat} , a), stomatal conductance (g_s , b),
774 quantum yield of PSII electron transport (Φ_{PSII} , c), photochemical quenching (q_P , d), transpiration
775 rate (E , e), and water use efficiency (WUE, f) in the youngest and fully expanded leaves of maize
776 plants subjected to various watering regimes (blue line, ample watering as the control; grey line,
777 flooding; red line, drought; green line, rewatering; green open triangle, resilience). Red arrows
778 indicate the rewatering date; the data are shown as means $\pm$ SE (n = 3-6).

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Fig. 3. The changes in net light-saturated photosynthetic rate (A_{sat} , a), stomatal conductance (g_s , b), quantum yield of PSII electron transport (Φ_{PSII} , c), photochemical quenching (q_P , d), transpiration rate (E , e), and water use efficiency (WUE, f) in the mature 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). Red arrows indicate the rewatering dates; the data are shown as means $\pm$ SE ($n = 3-6$).

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793 Fig. 4. Chlorophyll *a* fluorescence in **upper** leaves under drought and rewatering. Green and red
794 open triangles represent the resilience of moderate and severe drought at 101 and 125 days after
795 sowing (DAS), respectively. Red open arrows indicate the DAS of water withholding; while grey
796 and red close arrows indicate the rewatering DASs of moderate and severe drought treatments,
797 respectively. The data are shown as means $\pm$ SE (n = 3-6). F_v/F_m , maximal quantum efficiency of
798 photosystem II (PSII); Φ_{PSII} , the yield of PSII photochemistry; q_p , photochemical quenching based
799 on puddle model; q_N , non-photochemical quenching; Φ_{NPQ} , light-induced regulated
800 non-photochemical quenching.

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805 Fig. 5. Chlorophyll *a* fluorescence in *middle* leaves under drought and rewatering. Green and red
806 open triangles represent the resilience of moderate and severe drought at 101 and 125 days after
807 sowing (DAS), respectively. Red open arrows indicate the DAS of water withholding; while grey
808 and red close arrows indicate the rewatering DASs of moderate and severe drought treatments,
809 respectively. The data are shown as means $\pm$ SE (n = 3-6). F_v/F_m , maximal quantum efficiency of
810 photosystem II (PSII); Φ_{PSII} , the yield of PSII photochemistry; q_p , photochemical quenching based
811 on puddle model; q_N , non-photochemical quenching; Φ_{NPQ} , light-induced regulated
812 non-photochemical quenching.

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Fig.6. Chlorophyll *a* fluorescence in **bottom** leaves under drought and rewatering. Green and red open triangles represent the resilience of moderate and severe drought at 101 and 125 days after sowing (DAS), respectively. 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. The data are shown as means $\pm$ SE (n = 3-6). F_v/F_m , maximal quantum efficiency of photosystem II (PSII); Φ_{PSII} , the yield of PSII photochemistry; q_p , photochemical quenching based on puddle model; q_N , non-photochemical quenching; Φ_{NPQ} , light-induced regulated non-photochemical quenching.

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 827 Fig. 7. Relationships between fluorescence parameters and chlorophyll content at pre-tasseling
 828 (VT, green parts) and post-VT (red parts) stages in maize field (2015). F_v/F_m , maximal quantum
 829 efficiency of photosystem II (PSII); F_s , steady-state fluorescence; Φ_{PSII} , the yield of PSII
 830 photochemistry; q_p , photochemical quenching based on puddle model; q_N , non-photochemical
 831 quenching; Φ_{NPQ} , light-induced regulated non-photochemical quenching.

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835 Fig. 8. Principal component analysis on plant functional traits under the three irrigation regimes
836 [i.e., control, moderate drought (MD), and severe drought (SD)]. The traits' loadings on the first
837 two principal components (PCs) are shown, and their projections are sorted by the three irrigation
838 regimes. Dotted green, orange, and red circles represent the PC scores of control, MD, and SD
839 treatments, respectively. F_m , maximal fluorescence yield; F_m' , maximal light-adapted fluorescence
840 yield; F_o , minimal fluorescence yield; F_o' , minimal fluorescence at light-adapted state; F_s ,
841 steady-state fluorescence; F_v/F_m , maximal quantum efficiency of photosystem II (PSII); Φ_{PSII} , yield
842 of PSII photochemistry; q_p , photochemical quenching based on puddle model; q_L , photochemical
843 quenching based on lake models, q_N , non-photochemical quenching; Φ_{NPQ} , light-induced regulated
844 non-photochemical quenching; Φ_{NO} , quantum yield of non-regulated energy loss.

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