

1 **Photosynthetic resistance and resilience under drought and rewatering in maize**
2 **plants**

3
4 Miao Qi^{1,2}, Xiaodi Liu^{1,2}, Yibo Li^{1,2}, He Song^{1,2}, Feng Zhang¹, Zhenzhu Xu^{1,*}, Guangsheng Zhou
5 ^{1,3,*}

6 ¹State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese
7 Academy of Sciences, Beijing 100093, China; ² University of Chinese Academy of Sciences,
8 Beijing 100049, China; ³Chinese Academy of Meteorological Sciences, China Meteorological
9 Administration, Beijing 100081, China

10 *Correspondence: xuzz@ibcas.ac.cn, gszhou@ibcas.ac.cn

11
12 **Abstract**

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

33 **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,

64 which can improve sustainable development by allowing deficit irrigation and
65 water-saving agricultural practices (Fereris and Soriano, 2007; Geerts and Raes, 2009;
66 Du *et al.*, 2015; Silveira *et al.*, 2020). Further exploration of crop responses to various
67 water conditions can therefore provide critical information for optimising crop
68 management practices, particularly under future climate change (Lobell *et al.*, 2014;
69 Leakey *et al.*, 2019; Kimm *et al.*, 2020).

70 Plants exposed to drought will frequently show a restoration of their normal
71 physiological functions when rewatered, and to a certain degree, they can compensate
72 for the damage caused by drought by accelerating their growth and enhancing their
73 photosynthetic capacity (e.g., Xu *et al.*, 2009, 2010; Hofer *et al.*, 2017). An antecedent
74 condition, such as soil water availability, may also drive the post-stress responses to
75 other abiotic factors, indicating important complexities in plant responses to
76 environmental factors (Xu *et al.*, 2009; Guo and Ogle, 2019). This ability to regain a
77 normal original state after being disturbed is termed resilience (Holling, 1973; Müller
78 *et al.*, 2016. Resilience Alliance, 2020), and can be represented by the interference
79 level, recovery time or recovery speed (Müller *et al.*, 2016; Bhaskar *et al.*, 2018;
80 Harrison *et al.*, 2018; Resilience Alliance, 2020).

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

93 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

124 development stage. The findings may improve current knowledge and strengthen
125 future quests to produce high-yield, drought-resistant and resilient crops (see also
126 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 $\mu\text{mol m}^{-2}\text{s}^{-1}$).

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*

154 The field experimental site was located at the Jinzhou Ecology and Agricultural
155 Meteorology Center, Liaoning, Northeastern China (N 41°49', E 121°12', 27.4m
156 a.s.l.). The mean annual temperature and the mean annual precipitation over 40 years
157 were 9.9 °C and 564 mm, respectively, with an average monthly temperature of
158 20.9 °C and a total precipitation of 468 mm during plant growing season. The soil is
159 characterised as medium loam type, pH 6.3, with 1.8% organic matter and a soil bulk
160 density of 1.61 g·cm⁻³ at the 0–100 cm soil profile. The field capacity (FC) and PWP
161 were 22.3% and 6.5% (v/v), respectively. The soil had an organic carbon content of
162 10.44 g kg⁻¹, total nitrogen content of 0.69 g kg⁻¹, phosphorus content of 0.50 g kg⁻¹,
163 and potassium content of 22.62 g kg⁻¹. The planting date and maturity date were late
164 April and late September, respectively (Song *et al.*, 2018; Li *et al.*, 2019).

165 The field experimental design was as detailed previously (Li *et al.*, 2019). In brief,
166 an electric-powered waterproof shelter (4 m in height) set up in the maize field was
167 used to establish the various precipitation regimes that we desired (details in Li *et al.*,
168 2019). In total, 15 plots (15 m², 5 m length, 3 m width) were under the rain shelter
169 when it rained. The following three irrigation regimes were set up: a control (i.e. the
170 normal irrigation every 7 day); moderate drought (water withholding for 20 days); and
171 severe drought (water withholding for 27 days from the tasselling to milking stages).
172 In this design, irrigation water was supplied at 296, 246, and 221 mm across the maize
173 plant growing period. The SRWC at 0-50 cm soil depth was monitored to reach severe
174 drought levels at a range of 30–40% at the end of rainfall-withholding, whereas under
175 normal irrigation, the SWRC was maintained at levels of 70–80% in the control and
176 rewatering plots. The maize cultivar was Danyu 39, with a seed sowing rate of 6.0
177 plants m⁻² to ensure a planting density of 4.5 plants m⁻². A compound fertiliser
178 (accounting for 28%, 11%, and 12% of N, P₂O₅, and K₂O, respectively), applied at a c.
179 750 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

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

218

$$219 \quad F_v/F_m = (F_m - F_o)/F_m$$

$$220 \quad F_v'/F_m' = (F_m' - F_o')/F_m'$$

$$221 \quad \Phi_{\text{PSII}} = (F_m' - F_s)/F_m'$$

$$222 \quad q_p = (F_m' - F_s)/(F_m' - F_o')$$

$$223 \quad q_L = q_p \times F_o'/F_s$$

$$224 \quad q_N = (F_m - F_m')/(F_m - F_o')$$

$$225 \quad \text{NPQ} = (F_m - F_m')/F_m' = F_m/F_m' - 1$$

$$226 \quad \Phi_{\text{NPQ}} = F_s'/F_m' - F_s/F_m$$

$$227 \quad \Phi_{\text{NO}} = F_s'/F_m$$

$$228 \quad \text{NPQ} = (F_m - F_m')/F_m' = F_m/F_m' - 1$$

229 where F_v/F_m is the maximal quantum efficiency of photosystem II (PSII), and F_v'/F_m'
230 is the efficiency of excitation captured by open PSII centres in the light-adapted
231 leaves. Φ_{PSII} is the yield of PSII photochemistry, and q_p and q_L are photochemical
232 quenching based on puddle and lake models, respectively. NPQ or q_N is
233 non-photochemical quenching, and both Φ_{NPQ} and Φ_{NO} are light-induced regulated
234 non-photochemical quenching and quantum yield of non-regulated energy loss in PSII,
235 respectively (Kramer et al., 2004).

236

237 *Soil relative water content*

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

242

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).

251

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.

266

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

274 the severe drought stress level of 35%. After rewatering, the chlorophyll content
275 sharply increased, with recovery values of 14.2, 15.2 and 25.6% under consecutive
276 drought at 32, 34 and 37 DAS, respectively, indicating that a greater recovery may
277 occur at the end of the measurement period. The resilience values were -4.3, -14.0 and
278 -5.0% at 32, 34 and 37 DAS, respectively, showing that the resilience rose initially
279 following rewatering, then decreased, and then increased again. Flooding led to sharp
280 declines in SPAD after 4 days of flooding treatment, indicating that chlorophyll
281 degradation occurred under the flooded condition.

282 As shown in Fig. 2a, drought only led to a slight reduction in the net
283 light-saturated photosynthetic rate (A_{sat}) within one week after withholding water.
284 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%
285 29 DAS when RSWC dropped to 35%. After rewatering, A_{sat} sharply increased, with
286 recovery values of 5.53, 1.18 and 5.98 times the values seen under consecutive
287 drought at 32, 34 and 37 DAS, respectively. The rate approached and even exceeded
288 the control level at 32, 34 and 37 DAS. The resilience values increased gradually from
289 -12.1 to 10.2 and 25.4%, indicating a possible escalation of resilience with time after
290 rewatering. A stimulation of the A_{sat} occurred during the initial 6 days under flooding;
291 thereafter, flooding induced a decrease compared with the control treatment. However,
292 A_{sat} under flooding ultimately reached the level of the control treatment. Compared
293 with the control, stomatal conductance (g_s) was significantly decreased (-96.5%) at 29
294 DAS, just before rewatering (Fig. 2b). A greater recovery was observed, but only
295 positive resilience was detected at 34 DAS.

296 The quantum yield of PSII electron transport (Φ_{PSII}) decreased with
297 drought-treatment time, dropping to its lowest value (by 79.3%) at 29 DAS (Fig. 2c).
298 The recovery values were 3.05, 3.38 and 4.22 times relative to continuous drought at
299 3, 5 and 8 days after rewatering, respectively. Flooding also led to an initial
300 stimulation in Φ_{PSII} ; thereafter, the value decreased below the control level. The
301 photochemical quenching (q_P) showed a substantial fluctuation even under the control
302 treatment (Fig. 2d). However, a dramatic decline of 51.9% was observed after 9 days
303 of water withholding. We also found recoveries of 1.3-, 16.6- and 14.8-fold at 3, 5 and

304 8 days following rewatering, respectively. However, the increases still did not reach
305 the level of the control, so the resilience values were negative (-5.74, -26.22 and
306 -15.22 at 3, 5 and 8 days following rewatering). A stimulation of q_p was also observed
307 initially at 2 days after flooding exposure, but this disappeared thereafter and the
308 value dropped to levels lower than the control levels.

309 The transpiration rate (E) significantly decreased due to drought stress, dropping
310 to the lowest point at 29 DAS (a decrease of 94.5% relative to control, Fig. 2e). Rapid
311 decreases occurred following the rewatering, with recovery values of 9.3-, 8.9- and
312 4.6-fold the values under continuous drought at 3, 5 and 8 days following rewatering,
313 respectively. However, the resilience values were -10.4, 6.0, and -15.7% at 3, 5 and 8
314 days following rewatering, respectively. A stimulation of E also appeared initially by
315 flooding; thereafter, however, the similar E changes were similar to those of the
316 control (Fig. 2e). Leaf water use efficiency (WUE) was initially increased by drought,
317 but subsequently decreased with drought-exposure time, indicating that the
318 enhancement of WUE may be attenuated by the water deficit intensity and its
319 persistent duration. Rewatering led to a decline in WUE at the earlier stage, but
320 thereafter WUE remained stable relative to both the control and continuous drought
321 plants. WUE was not affected significantly by flooding during the experimental
322 periods (Fig. 2f).

323 Similar responses were observed in the mature leaves (Fig. 3a-f). Drought reduced
324 A_{sat} , with great recovery and a positive resilience noted at the end of the experiment
325 (Fig. 3a). A sharp rise appeared during the initial flooding, but A_{sat} decreased thereafter.
326 A drastic g_s resilience was evident at 34 DAS (Fig. 3b). A great recovery occurred for
327 Φ_{PSII} and q_p ; however, the negative resilience was still maintained (Fig. 3c, d). A rapid
328 and drastic reduction in E was observed by imposition of drought stress, with great
329 recovery; however, the resilience remained negative (Fig. 3e). Drought always
330 elevated the WUE in the mature leaves, whereas flooding did not substantially affect
331 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

394 quadrant I, while those of Φ_{PSII} , F_m' , q_P and q_L were in quadrant II. The markers most
395 representative of non-photochemical quenching traits (e.g., NPQ, q_N and Φ_{NPQ}) in
396 relation to non-photochemical radiative energy dissipation capability were sorted into
397 quadrant III. Projection on the treatment effects showed that the three irrigation
398 regimes were sorted in the coordinate plane, with control treatment mostly in quadrant
399 II, and SD scattered in all four quadrants (Fig. 8).

400

401 **Discussion**

402 Water cycle changes could substantially impact plant growth, photosynthetic
403 processes and many crucial physiological functions and nutrient status, thereby
404 affecting plant productivity and crop yield (e.g., Izanloo *et al.*, 2008; Lobell *et al.*,
405 2014; Kimm *et al.*, 2020). Drought and rewetting may often occur at intervals and are
406 predicted to happen more frequently and severely under climatic change (Dai, 2012;
407 IPCC, 2014; Donat *et al.*, 2016; Diffenbaugh *et al.*, 2017). Indeed, sporadic
408 precipitation is a critical issue in maintaining ecosystem productivity and its structural
409 stability, particularly in arid and semi-arid areas and/or in rain-fed planting regions
410 (Reynolds, 2004; Cooper *et al.*, 2008; Song *et al.*, 2018; Guo and Ogle, 2019).

411 Maize plays a critical role in meeting the global food demands and is one of the
412 most widely planted staple crops worldwide (Haarhoff and Swanepoel, 2018; FAO,
413 2020). In this study, the greenhouse and field experiments demonstrated how maize
414 photosynthetic functional traits respond to the abnormal precipitation alterations,
415 including drought, flooding, and rewatering at different growth stages, thereby
416 providing key information for managing crop production. Our main findings were that
417 1) drought and flooding severely hampered photosynthetic capacity in maize plants,
418 particularly under severe and/or long water stress, in support of the first hypothesis; 2)
419 rewatering could result in partial recovery of some photosynthetic traits, with few
420 compensatory responses, in partial support of our second hypothesis; and 3) the
421 photosynthetic resilience to drought was dependent on the drought severity and the
422 plant developmental stage, largely supporting the third hypothesis. These findings can
423 shed light on ways to improve regulation of crop functional traits to deal with erratic

424 precipitation regimes and may lead to better breeding and management practices for
425 crops that have high drought resistance and drought-resilience traits (Kromdijk *et al.*,
426 2016; Song *et al.*, 2018; Gupta *et al.*, 2020).

427

428 *Drought and flooding*

429 In agreement with previous work (e.g., Chaves *et al.*, 2003, 2009; Xu *et al.*, 2006; Xu
430 and Zhou, 2009; Gupta *et al.*, 2020), the results of the present study indicated that
431 severe drought stress can substantially reduce photosynthetic capacity, as
432 characterised by declines in chlorophyll content, net light-saturated photosynthetic
433 rate (A_{sat}), stomatal conductance (g_s), and quantum yield of PSII electron transport
434 (Φ_{PSII}) in both the greenhouse and field experiments. However, the photosynthetic
435 capacity attenuated more substantially and steeply as the drought stress persisted in
436 our experiment, indicating a strong dependence on the duration, severity and timing of
437 droughts. Thus, only mild or moderate or short drought stresses were conducive to the
438 development of a regulative response of plants for resistance to water deficit in terms
439 of the changes in the root system (e.g., Trapeznikov *et al.*, 2003), leaf thickness (Sack
440 and Grubb, 2002) and antioxidative defence system (Foyer and Noctor, 2005). This
441 observation may aid in implementations of deficit irrigation, water saving agriculture,
442 and sustainable development (Feres and Soriano, 2007; Geerts and Raes, 2009; Du
443 *et al.*, 2015; Silveira *et al.*, 2020; Kimm *et al.*, 2020).

444 The present findings also demonstrated that flooding led to a decline in SPAD and
445 A_{sat} , but not g_s . Indeed, under an anaerobic environment, plants may have adaptive
446 responses to flooding stress that include aerenchyma formation in the roots and the
447 development of adventitious roots (Mano *et al.*, 2006), alteration of the profile of
448 protein synthesis related to anoxic tolerance (Subbaiah and Sachs, 2003), and
449 enhanced starch accumulation (Mutava *et al.*, 2015). An involvement of ethylene
450 regulation is also associated with an enhancement of photochemical and
451 non-photochemical radiative energy dissipation capability (De Pedro *et al.*, 2020).
452 Our results also indicated a higher tolerance of maize to flooding stress in terms of
453 Φ_{PSII} and photochemical quenching (q_P), relative to drought stress, highlighting the

454 distinct effects of these two stresses (Mutava *et al.*, 2015; Zhu *et al.*, 2020). An
455 antagonistic effect on g_s has been reported (see also Zhu *et al.*, 2020). Maintaining
456 stomatal opening may promote water release to alleviate the stress due to excessive
457 water, again highlighting the positive regulation in response to anoxic conditions (Zhu
458 *et al.*, 2020).

459

460 *Recovery and resilience*

461 As previously reported, a depression in photosynthesis potentials by a previous
462 drought can be markedly stimulated by rewetting; however, whether or how much
463 these potentials recover depends on drought intensity and/or the persistence period
464 (e.g., Xu *et al.*, 2009, 2010; Creek *et al.*, 2018). In the current experiment, partial, full
465 and over recovery of photosynthetic traits were all observed in terms of both recovery
466 and resilience indices, specifically depending on the duration and persistence of the
467 drought, the plant developmental stages and the different functional traits, as well as
468 the crop species and cultivar (Figs 1-6; Xu *et al.*, 2009; Creek *et al.*, 2018). For
469 instance, an over-compensatory recovery (i.e., a positive percentage of the resilience)
470 in g_s was observed in maize (Figs. 2b, 3b); however, g_s only achieved a partial
471 recovery in a grass species (Xu *et al.*, 2009). Creek *et al.* (2008) recently reported that,
472 after rewatering, the A_{net} of a semiarid species can return to the pre-drought stress
473 level within 2-4 weeks, whereas g_s performs a slower recovery. A recent report by
474 Johnson *et al.* (2018) indicated that photosynthesis was not fully recovered in wheat
475 plants because of the photosynthetic damage due to hydraulic decline in the leaves
476 subjected to drought. Increased embolism is tightly related to a complete lack of
477 photosynthetic recovery. However, Creek *et al.* (2018) found that photosynthetic
478 recovery can be decoupled from the recovery of plant hydraulics, indicating that the
479 impaired hydraulic function throughout the recovery period perhaps does not
480 influence the complete recovery of A_{net} from drought. Thus, the underlying
481 mechanism needs to be investigated further.

482 The enhancement of plant growth due to rewatering has been addressed by many
483 researchers (Reynolds *et al.*, 2004; Siopongco *et al.*, 2006; Xu *et al.*, 2009; Song *et al.*,

484 2018). As recently reported by Abid *et al.* (2018), tolerant wheat plants showing high
485 photosynthetic capacity during drought and rapid recovery after re-irrigating did not
486 show marked yield declines relative to the sensitive cultivars, indicating that the
487 plant's ability to maintain/restore growth and physiological functions during
488 pre/post-drought in the vegetative period might play a crucial role in determining crop
489 productivity. Upon rewatering, the rapid growth of new tissues, such as a new leaf,
490 might accelerate plant growth, potentially enhancing CO₂ assimilation (Pinheiro *et*
491 *al.*, 2004). This may be a result of positive source–sink interactions, as a strong sink
492 requirement (e.g. new tissue) can enhance the carbon assimilation rate (Minchin and
493 Lacoite, 2005; White *et al.*, 2015; Parvin *et al.*, 2020). Higher resilience of A_{sat} and
494 g_s occurred in the younger leaves relative to mature ones, implying a greater ability to
495 recover in the new leaves that serve as both active source–sink organs (Figs 2, 3;
496 Roitsch, 1999). The maize plants were exposed to drought stress for only several days,
497 so leaf length after rewatering was restored to a similar level to that of the control
498 plants, indicating no occurrence of overcompensation (Acevedo *et al.*, 1971; Xu *et al.*,
499 2009; Hofer *et al.*, 2017). Thus, the extent of compensation for drought by the
500 triggering of new tissues following rewatering might determine the final plant/crop
501 production and would depend strongly on the severity, duration, and timing of the
502 drought stress (Hsiao, 1973; Xu *et al.*, 2009; Hofer *et al.*, 2017).

503

504 *Associations between functional traits*

505 The distinct responses of the functional traits such as A_{sat} and g_s to drought, flooding
506 and rewetting suggested that coordinated associations between the functional traits
507 could reveal the underlying mechanism (see also Creek *et al.*, 2018). For instance, the
508 SPAD reading (e.g., Ciganda *et al.*, 2009), as an indicator of relative chlorophyll
509 concentration, has different associations with photosynthetic function activities at
510 different plant development stages: stronger associations were observed post-VT
511 (tasselling stage) than pre-VT (Fig. 7). This might indicate that a greater coupling
512 relationship appears at later plant developmental stages and that leaf age/senescence
513 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

544 and resilience of plants. The associations of chlorophyll concentrations with
545 photosynthetic functional activities were also stronger post-VT than pre-VT, implying
546 that leaf age/senescence may be involved in the responses to drought and rewatering.
547 These findings may further improve our understanding of how plants respond to water
548 status changes at different plant developmental stages. This knowledge can be helpful
549 for breeding crops with high drought-resistant and drought-resilience traits and for
550 establishing management practices when facing climate change (e.g., Kromdijk *et al.*,
551 2016; Leakey *et al.*, 2019; Kimm *et al.*, 2020; Gupta *et al.*, 2020).

552

553 **Acknowledgements**

554 This study was jointly funded by the National Key Research and Development
555 Program of China (2016YFD0300106), National Natural Science Foundation of
556 China (31661143028), and China Special Fund for Meteorological Research in the
557 Public Interest (GYHY201506001-3). The authors are grateful to Yuhui Wang,
558 Bingrui Jia, Yanling Jiang, and Jian Song for their help during the study. The authors
559 are also grateful to Hongying Yu, Quanhui Ma, and Liang Li for their loyal
560 assistances during the two experiments.

561

562 **Author contributions**

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

567

568 **Availability of data and materials**

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

571

572 **References**

573 Abid M, Ali S, Qi LK, Zahoor R, Tian Z, Jiang D, Snider JL, Dai T. 2018. Physiological and
574 biochemical changes during drought and recovery periods at tillering and jointing stages in
575 wheat (*Triticum aestivum* L.). *Scientific Reports* **8**, 4615.

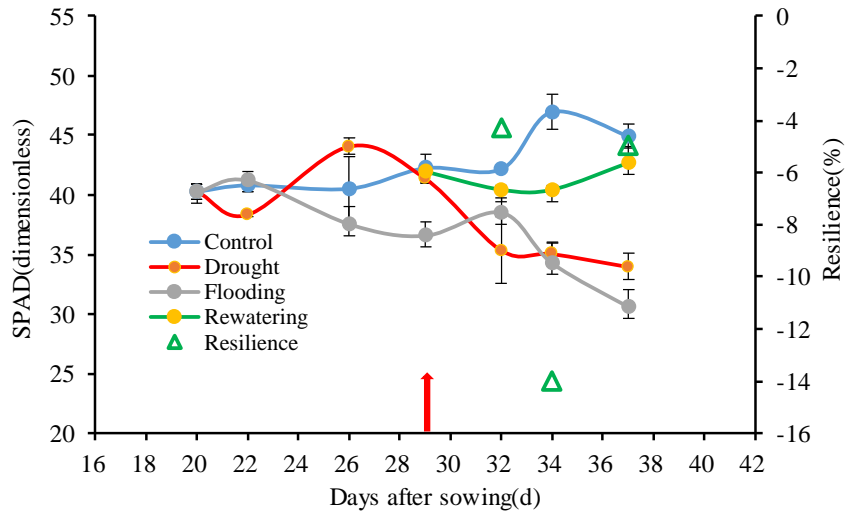
- 576 Acevedo E, Hsiao TC, Henderson DW. 1971. Immediate and subsequent growth responses of
577 maize leaves to changes in water statuses. *Plant Physiology* **48**, 631-636.
- 578 Ben-Ari T, Adrian J, Klein T, Calanca P, Van der Velde M, Makowski D. 2016. Identifying
579 indicators for extreme wheat and maize yield losses. *Agricultural and Forest Meteorology* **220**,
580 130-140.
- 581 Bhaskar R, Arreola F, Mora F, Martinez-Yrizar A, Martinez-Ramos M, Balvanera P. 2018.
582 Response diversity and resilience to extreme events in tropical dry secondary forests. *Forest*
583 *Ecology and Management* **426**, 61-71.
- 584 Chaves MM, Flexas J, Pinheiro C. 2009. Photosynthesis under drought and salt stress: regulation
585 mechanisms from whole plant to cell. *Annals of Botany* **103**, 551-560.
- 586 Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought—from genes
587 to the whole plant. *Functional Plant Biology* **30**, 239-264.
- 588 Ciganda V, Gitelson A, Schepers J. 2009. Non-destructive determination of maize leaf and canopy
589 chlorophyll content. *Journal of Plant Physiology* **166**, 157-167.
- 590 Cooper PJM, Dimes J, Rao KPC, Shapiro B, Shiferaw B, Twomlow S. 2008. Coping better with
591 current climatic variability in the rain-fed farming systems of sub-Saharan Africa: An essential
592 first step in adapting to future climate change? *Agriculture, Ecosystems & Environment* **126**,
593 24-35.
- 594 Creek D, Blackman C, Brodribb TJ, Choat B, Tissue DT. 2018. Coordination between leaf, stem
595 and root hydraulics and gas exchange in three arid-zone angiosperms during severe drought and
596 recovery. *Plant, Cell and Environment* **41**, 2869-2881.
- 597 Dai A. 2012. Increasing drought under global warming in observations and models. *Nature*
598 *Climate Change* **3**, 52-58.
- 599 Daryanto S, Wang L, Jacinthe PA. 2016. Global synthesis of drought effects on maize and wheat
600 production. *PloS one* **11**, 5.
- 601 David MM, Coelho D, Barrote I, Correia MJ. 1998. Leaf age effects on photosynthetic activity
602 and sugar accumulation in droughted and rewatered *Lupinus albus* plants. *Australian Journal of*
603 *Plant Physiology* **25**, 299-306.
- 604 De Pedro LF, Mignolli F, Scartazza A, Melana Colavita JP, Bouzo CA, Vidoz ML. 2020.
605 Maintenance of photosynthetic capacity in flooded tomato plants with reduced ethylene
606 sensitivity. *Physiologia Plantarum* doi:10.1111/ppl.13141.
- 607 Diffenbaugh NS, Singh D, Mankin JS, Horton DE, Swain DL, Touma D, Charland A, Liu Y,
608 Haugen M, Tsiang M, Rajaratnam B. 2017. Quantifying the influence of global warming on
609 unprecedented extreme climate events. *Proceedings of the National Academy of Sciences* **114**,
610 4881-4886.
- 611 Du T, Kang S, Zhang J, Davies WJ. 2015. Deficit irrigation and sustainable water-resource
612 strategies in agriculture for China's food security. *Journal of Experimental Botany* **66**,
613 2253-2269.
- 614 FAO. 2020. FAOSTAT database. FAO, Rome. <http://www.fao.org/faostat/en/#data/QC> (accessed
615 on 19 June 2020).
- 616 Fereres E, Soriano MA. 2007. Deficit irrigation for reducing agricultural water use. *Journal of*
617 *Experimental Botany* **58**, 147-259.
- 618 Foyer CH, Noctor G. 2005. Oxidant and antioxidant signaling in plants: a reevaluation the concept
619 of oxidative stress in a physiological context. *Plant, Cell and Environment* **28**, 1056-1071.
- 620 Geerts S, Raes D. 2009. Deficit irrigation as an on-farm strategy to maximize crop water
621 productivity in dry areas. *Agricultural water management* **96**, 1275-1284.
- 622 Guo JS, Ogle K. 2019. Antecedent soil water content and vapor pressure deficit interactively
623 control water potential in *Larrea tridentata*. *New Phytologist* **221**, 218-232.
- 624 Gupta, A., Rico-Medina, A., & Caño-Delgado, A. I. (2020). The physiology of plant responses to
625 drought. *Science*, 368(6488), 266-269.

- 626 Haarhoff SJ, Swanepoel PA. 2018. Plant population and maize grain yield: a global systematic
627 review of rainfed trials. *Crop Science* **58**, 1-11.
- 628 Harrison SP, LaForgia ML, Latimer AM. 2018. Climate-driven diversity change in annual
629 grasslands: Drought plus deluge does not equal normal. *Global Change Biology* **24**, 1782-1792.
- 630 Hofer D, Suter M, Buchmann N, Lüscher A. 2017. Nitrogen status of functionally different forage
631 species explains resistance to severe drought and post-drought overcompensation. *Agriculture,
632 Ecosystems and Environment* **236**, 312-322.
- 633 Holling CS. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and
634 Systematics* **4**, 1-23.
- 635 Hsiao TC. 1973. Plant responses to water stress. *Annual Review of Plant Physiology* **24**, 519-570.
- 636 IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and
637 III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Core
638 Writing Team, Pachauri RK, Meyer LA, eds.)*. IPCC, Geneva, Switzerland, 151 pp.
- 639 Izanloo A, Condon AG, Langridge P, Tester M, Schnurbusch T. 2008. Different mechanisms of
640 adaptation to cyclic water stress in two South Australian bread wheat cultivars. *Journal of
641 Experimental Botany* **59**, 3327-46.
- 642 Jiang T, Dou Z, Liu J, Gao Y, Malone RW, Chen S, Feng H, Yu Q, Xue G, He J. 2020. Simulating
643 the influences of soil water stress on leaf expansion and senescence of winter wheat.
644 *Agricultural and Forest Meteorology* **291**, 108061.
- 645 Johnson KM, Jordan GJ, Brodribb TJ. 2018. Wheat leaves embolised by water stress do not
646 recover function upon rewatering. *Plant, Cell and Environment* **41**, 2704-2714.
- 647 Kimm H, Guan K, Gentine P, Wu J, Bernacchi CJ, Sulman BN, Griffis TJ, Lin C. 2020.
648 Redefining droughts for the US Corn Belt: The dominant role of atmospheric vapor pressure
649 deficit over soil moisture in regulating stomatal behavior of Maize and Soybean. *Agricultural
650 and Forest Meteorology* **287**, 107930.
- 651 Kramer DM, Johnson G, Kiirats O, Edwards GE. 2004. New fluorescence parameters for the
652 determination of QA redox state and excitation energy fluxes. *Photosynthesis Research* **79**,
653 209-218.
- 654 Kromdijk J, Głowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP. 2016. Improving
655 photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science*
656 **354**, 857-861.
- 657 Leakey AD, Ferguson JN, Pignou CP, Wu A, Jin Z, Hammer GL, Lobell DB. 2019. Water use
658 efficiency as a constraint and target for improving the resilience and productivity of C₃ and C₄
659 crops. *Annual Review of Plant Biology* **70**, 781-808.
- 660 Li Y, Song H, Zhou L, Xu Z, Zhou G. 2019. Vertical distributions of chlorophyll and nitrogen and
661 their associations with photosynthesis under drought and rewatering regimes in a maize field.
662 *Agricultural and Forest Meteorology* **272**, 40-54.
- 663 Li Z, Sun Z. 2016. Optimized single irrigation can achieve high corn yield and water use
664 efficiency in the Corn Belt of Northeast China. *European Journal of Agronomy*, **75**, 12-24.
- 665 Liu Z, Yang X, Hubbard KG, Lin X. 2012. Maize potential yields and yield gaps in the changing
666 climate of northeast China. *Global Change Biology* **18**, 3441-3454.
- 667 Lobell DB, Roberts MJ, Schlenker W, Braun N, Little BB, Rejesus RM, Hammer GL. 2014.
668 Greater sensitivity to drought accompanies maize yield increase in the US Midwest. *Science*
669 **344**, 516-519.
- 670 Mano Y, Omori F, Takamizo T, Kindiger B, Bird RM, Loaisiga CH. 2006. Variation for root
671 aerenchyma formation in flooded and non-flooded maize and teosinte seedlings. *Plant and Soil*
672 **281**, 269-279.
- 673 Maxwell K, Johnson GN. 2000. Chlorophyll fluorescence—a practical guide. *Journal of
674 Experimental Botany* **51**, 659-668.
- 675 Müller F, Bergmann M, Dannowski R, Dippner JW, Gnauck A, Haase P, Jochimsen M, Kasprzak

- 676 P., Kröncke I, Kümmerlin R, Küster M. 2016. Assessing resilience in long-term ecological data
677 sets. *Ecological Indicators* **65**, 10-43.
- 678 Mutava RN, Prince SJK, Syed NH, Song L, Valliyodan B, Chen W, Nguyen HT. 2015.
679 Understanding abiotic stress tolerance mechanisms in soybean: a comparative evaluation of
680 soybean response to drought and flooding stress. *Plant Physiology and Biochemistry* **86**,
681 109-120.
- 682 Myers, SS, Smith, MR, Guth, S., Golden, CD, Vaitla, B., Mueller, ND, Dangour AD, Huybers P.
683 2017. Climate change and global food systems: potential impacts on food security and
684 undernutrition. *Annual Review of Public Health*, **38**, 259-277.
- 685 Parvin S, Uddin S, Tausz-Posch S, Armstrong R, Tausz M. 2020. Carbon sink strength of nodules
686 but not other organs modulates photosynthesis of faba bean (*Vicia faba*) grown under elevated
687 [CO₂] and different water supply. *New Phytologist* **227**, 132-145.
- 688 Pinheiro C, Passarinho JA, Ricardo CP. 2004. Effect of drought and rewatering on the
689 metabolism of *Lupinus albus* organs. *Journal of Plant Physiology* **161**, 1203-1210.
- 690 Resilience Alliance. 2020. <http://www.resalliance.org/about>.
- 691 Reynolds JF, Kemp PR, Ogle K, Fernández RJ. 2004. Modifying the 'pulse-reserve' paradigm for
692 deserts of North America: precipitation pulses, soil water and plant responses. *Oecologia* **141**,
693 194-210.
- 694 Roitsch T. 1999. Source-sink regulation by sugar and stress. *Current Opinion in Plant Biology* **2**,
695 198-206.
- 696 Rosa L, Chiarelli DD, Rulli MC, Dell'Angelo J, D'Odorico P. 2020. Global agricultural economic
697 water scarcity. *Science Advances* **6**, eaaz6031.
- 698 Roudier P, Andersson JC, Donnelly C, Feyen L, Greuell W, Ludwig F. 2016. Projections of future
699 floods and hydrological droughts in Europe under a +2°C global warming. *Climatic Change*
700 **135**, 341-355.
- 701 Ruppert JC, Harmoney K, Henkin Z, Snyman HA, Sternberg M, Willms W, Linstädter A. 2015.
702 Quantifying drylands' drought resistance and recovery: the importance of drought intensity,
703 dominant life history and grazing regime. *Global Change Biology* **21**, 1258-1270.
- 704 Sacharz J, Giovagnetti V, Ungerer P, Mastroianni G, Ruban A. 2017. The xanthophyll cycle affects
705 reversible interactions between PsbS and light-harvesting complex II to control
706 non-photochemical quenching. *Nature Plants* **3**, 16225.
- 707 Sack L, Grubb PJ. 2002 The combined impacts of deep shade and drought on the growth and
708 biomass allocation of shade-tolerant woody seedlings. *Oecologia* **131**, 175-185.
- 709 Schreiber UBWN, Bilger W, Neubauer C. 1994. Chlorophyll fluorescence as a noninvasive
710 indicator for rapid assessment of in vivo photosynthesis. *Ecophysiology of Photosynthesis* **100**,
711 49-70.
- 712 Shah NH, Paulsen GM. 2003. Interaction of drought and high temperature on photosynthesis and
713 grain-filling of wheat. *Plant and Soil* **257**, 219-226.
- 714 Sharp RE, Poroyko V, Hejlek LG, Spollen WG, Springer GK, Bohnert HJ, Nguyen HT. 2004.
715 Root growth maintenance during water deficits: physiology to functional genomics. *Journal of*
716 *Experimental Botany* **55**, 2343-2351.
- 717 Silveira LK, Pavão GC, dos Santos Dias CT, Quaggio JA, de Matos Pires RC. 2020. Deficit
718 irrigation effect on fruit yield, quality and water use efficiency: A long-term study on Pêra-IAC
719 sweet orange. *Agricultural Water Management* **231**, 106019.
- 720 Siopongco JDLC, Yamauchi A, Salekdeh H, Bennett J, Wade LJ. 2006. Growth and water use
721 response of doubled-haploid rice lines to drought and rewatering during the vegetative stage.
722 *Plant Production Science* **9**, 141-151.
- 723 Song H, Li Y, Zhou L, Xu Z, Zhou G. 2018. Maize leaf functional responses to drought episode
724 and rewatering. *Agricultural and Forest Meteorology* **249**, 57-70.
- 725 Subbaiah CC, Sachs MM. 2003. Molecular and cellular adaptations of maize to flooding stress.

- 726 Annals of Botany **91**, 119-127.
- 727 Sun CX, Li CC, Zhang CY, Hao LY, Song M, Liu W, Zhang YL. 2018. Reflectance and
728 biochemical responses of maize plants to drought and re-watering cycles. *Annals of Applied*
729 *Biology* **172**, 332-345.
- 730 Trapeznikov VK, Ivanov II, Kudoyarova GR. 2003. Effect of heterogeneous distribution of
731 nutrients on root growth, ABA content and drought resistance of wheat plants. *Plant and Soil*,
732 **252**, 207-214.
- 733 Trenberth KE, Dai A, Van Der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J. 2014.
734 Global warming and changes in drought. *Nature Climate Change* **4**, 17-22.
- 735 Van Ruijven J, Berendse, F. 2010. Diversity enhances community recovery, but not resistance,
736 after drought. *Journal of Ecology* **98**, 81-86.
- 737 Voronin PY, Maevskaia SN, Nikolaeva MK. 2019. Physiological and molecular responses of
738 maize (*Zea mays* L.) plants to drought and rehydration. *Photosynthetica* **57**, 850-856.
- 739 White AC, Rogers A, Rees M, Osborne CP. 2015. How can we make plants grow faster? A
740 source-sink perspective on growth rate. *J Exp Bot* **67**, 31-45.
741 <https://doi.org/10.1093/jxb/erv447>.
- 742 Xu Z, Shimizu H, Ito S, Yagasaki Y, Zou C, Zhou G, Zheng Y. 2014. Effects of elevated CO₂,
743 warming and precipitation change on plant growth, photosynthesis and peroxidation in
744 dominant species from North China grassland. *Planta* **239**, 421-435.
- 745 Xu Z, Zhou G, Shimizu H. 2009. Are plant growth and photosynthesis limited by pre-drought
746 following rewatering in grass? *Journal of Experimental Botany* **60**, 3737-3749.
- 747 Xu Z, Zhou G. 2011. Responses of photosynthetic capacity to soil moisture gradient in perennial
748 rhizome grass and perennial bunchgrass. *BMC Plant Biology* **11**, 21.
- 749 Xu ZZ, Zhou GS, Shimizu H. 2009. Are plant growth and photosynthesis limited by pre-drought
750 following rewatering in grass? *Journal of Experimental Botany* **60**:3737-3749.
- 751 Xu ZZ, Zhou GS, Shimizu H. 2010. Plant responses to drought and rewatering. *Plant Signaling &*
752 *Behavior* **5**: 649-654.
- 753 Xu ZZ, Zhou GS, Wang YL, Han GX, Li YJ. 2008. Changes in chlorophyll fluorescence in maize
754 plants with imposed rapid dehydration at different leaf ages. *Journal of Plant Growth*
755 *Regulation* **27**, 83-92.
- 756 Xu ZZ, Zhou GS. 2007. Photosynthetic recovery of a perennial grass *Leymus chinensis* after
757 different periods of soil drought. *Plant Production Science* **10**, 277-285.
- 758 Zhu R, Wu F, Zhou S, Hu T, Huang J, Gao Y. 2020. Cumulative effects of drought-flood abrupt
759 alternation on the photosynthetic characteristics of rice. *Environmental and Experimental*
760 *Botany* **169**, 103901.
- 761

762



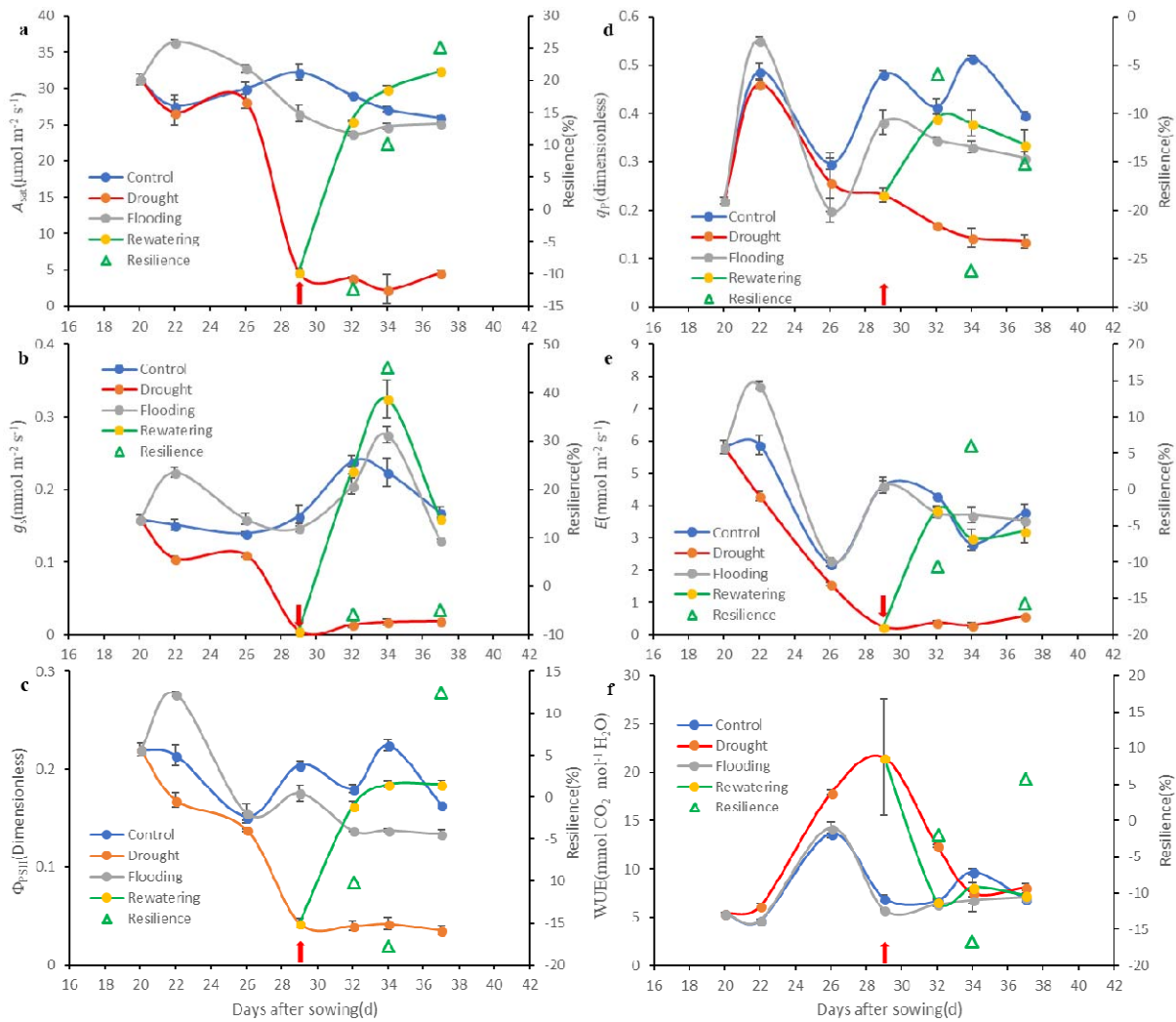
763

764 Fig. 1. The changes in leaf relative chlorophyll content (SPAD values) in the youngest and fully
765 expanded leaves of maize plants subjected to various watering regimes (blue line, ample watering
766 as the control; grey line, flooding; red line, drought; green line, rewatering; green open triangle,
767 resilience). The red arrow indicates the rewatering date; the data are shown as means \pm SE (n =
768 3-6).

769

770

771



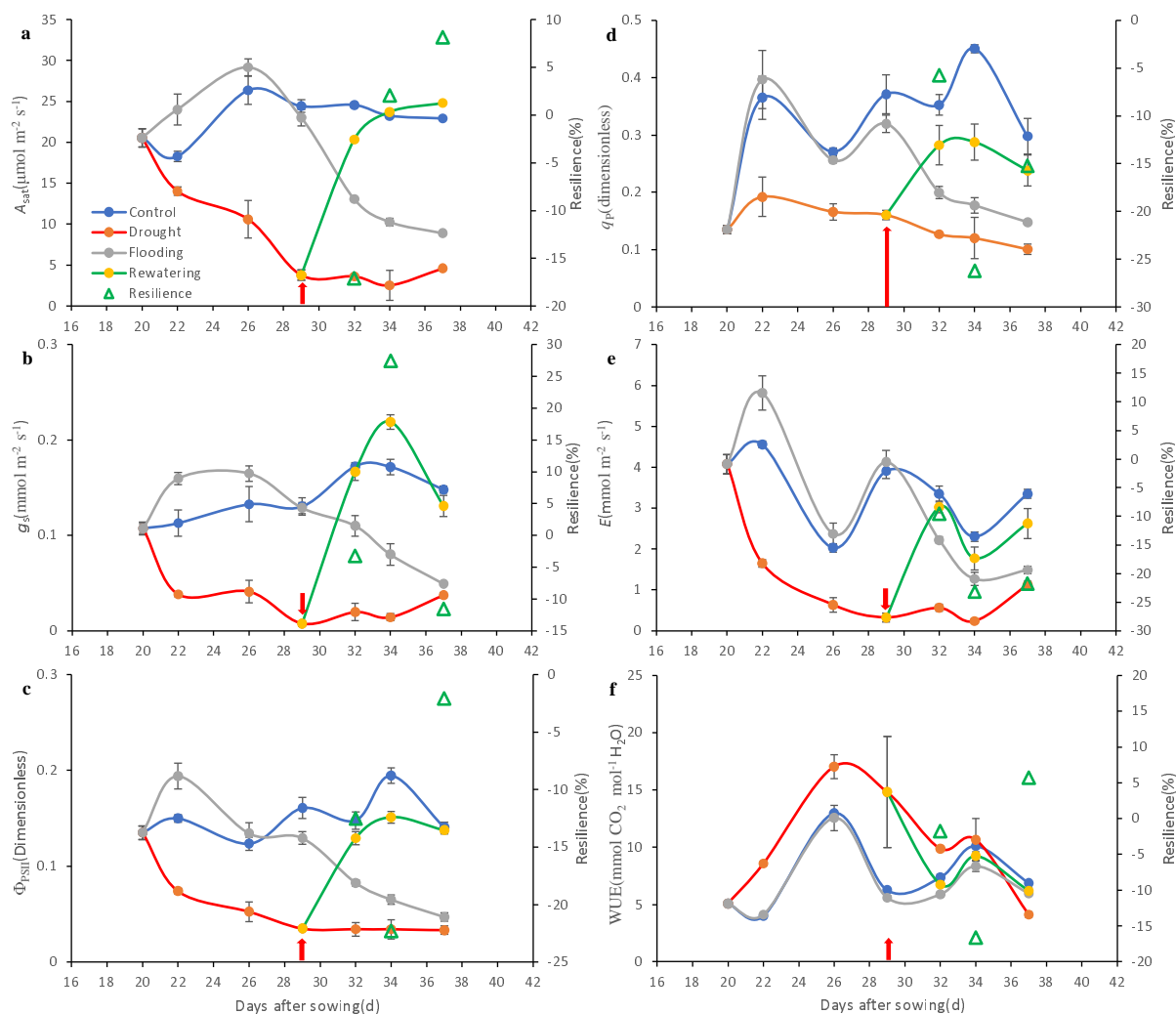
772

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

779

780

781



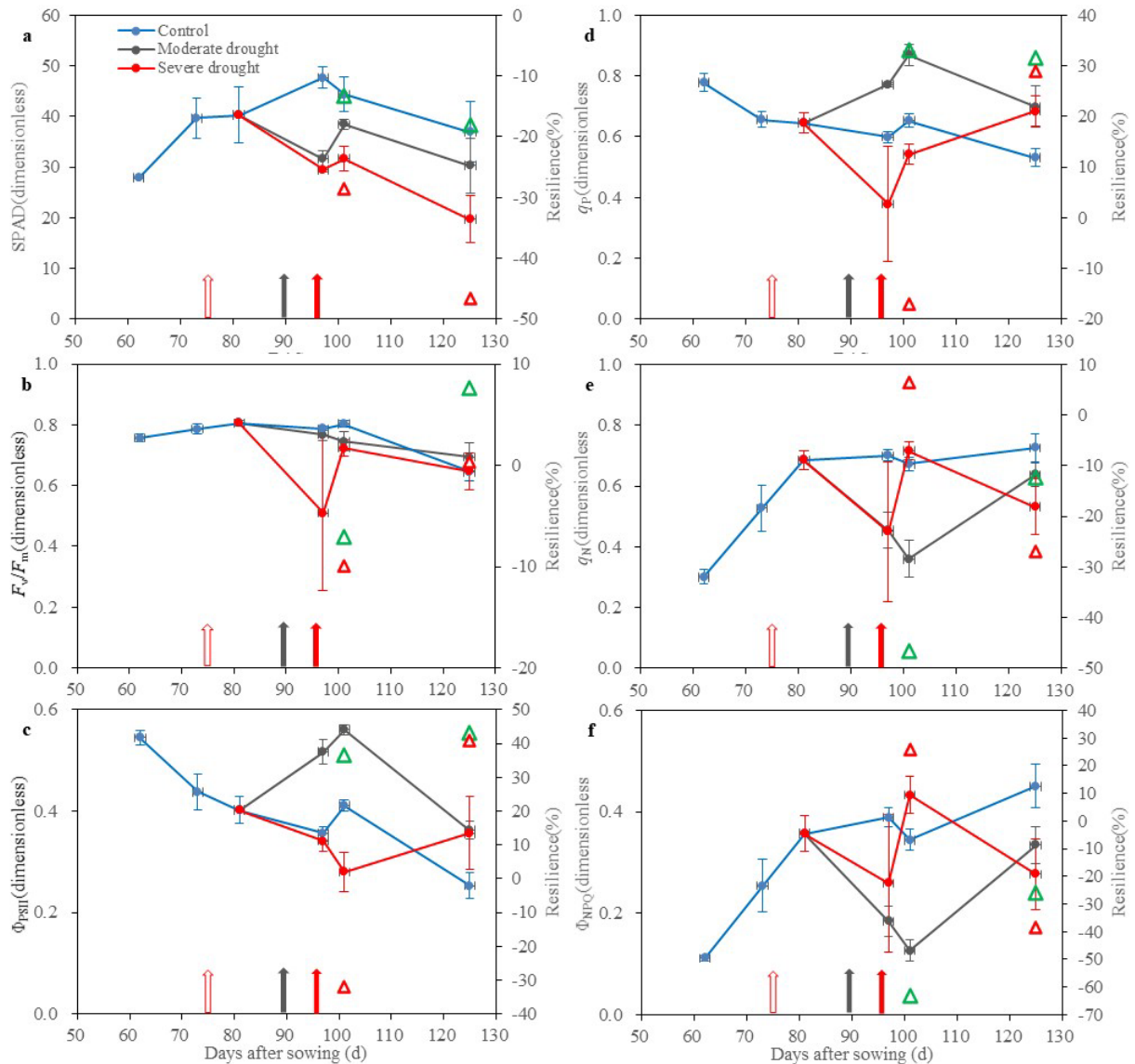
782

783 Fig. 3. The changes in net light-saturated photosynthetic rate (A_{sat} , a),
 784 stomatal conductance (g_s , b),
 785 quantum yield of PSII electron transport (Φ_{PSII} , c), photochemical quenching (q_P , d), transpiration
 786 rate (E , e), and water use efficiency (WUE, f) in the mature leaves of maize plants subjected to
 787 various watering regimes (blue line, ample watering as the control; grey line, flooding; red line,
 788 drought; green line, rewatering; green open triangle, resilience). Red arrows indicate the
 789 rewatering dates; the data are shown as means \pm SE (n = 3-6).

789

790

791



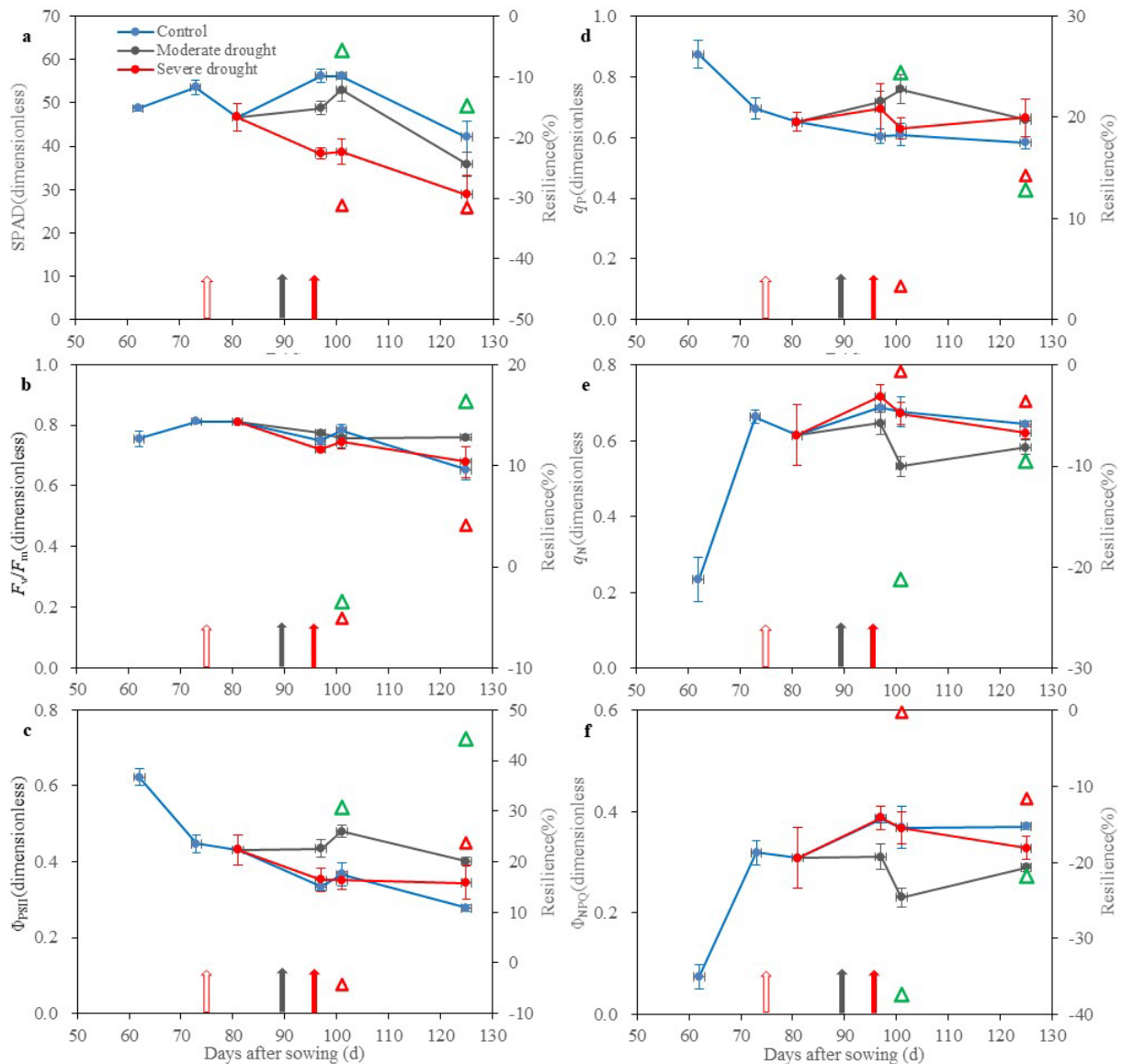
792

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.

801

802

803

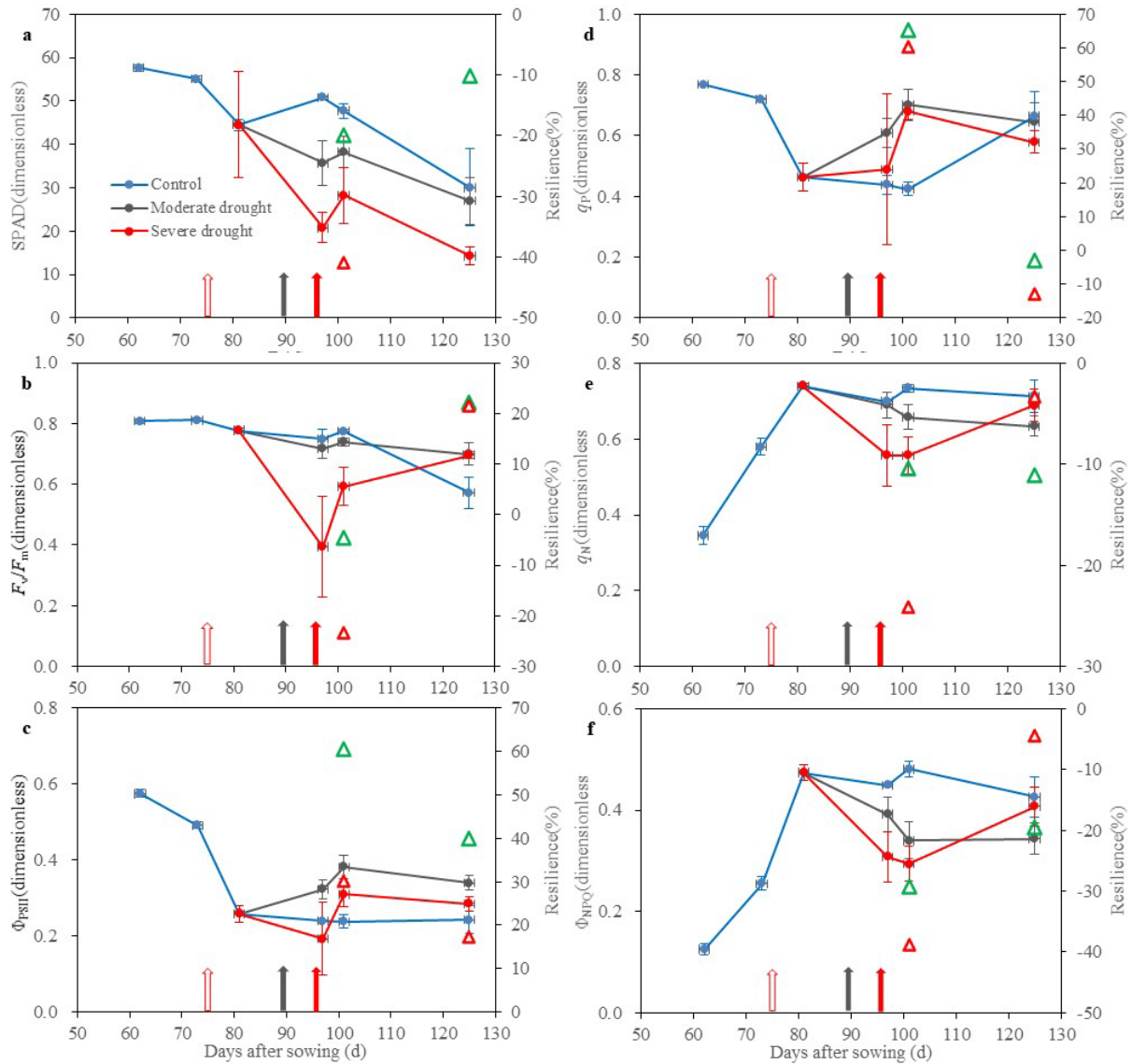


804

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.

813

814

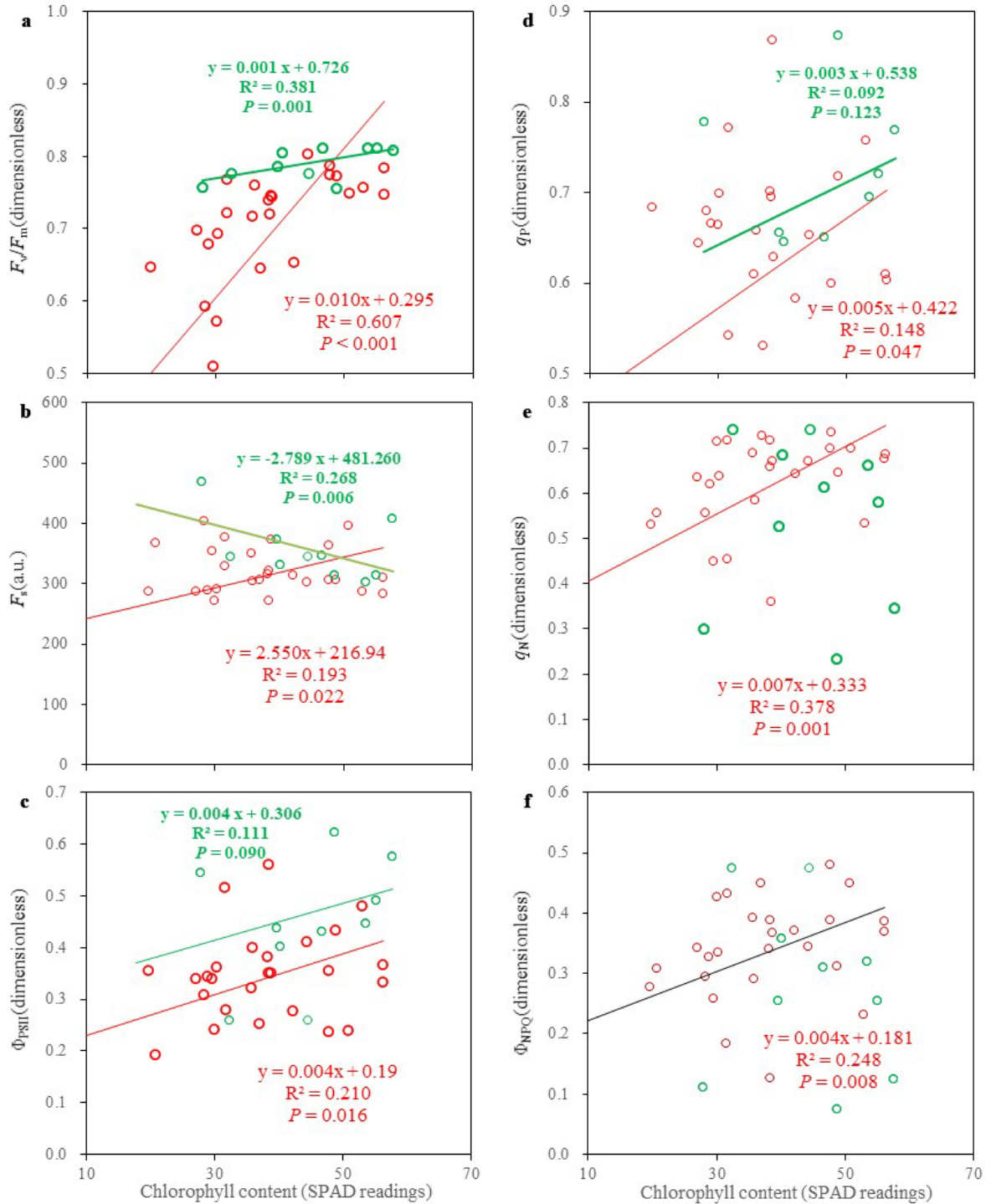


815

816

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

825

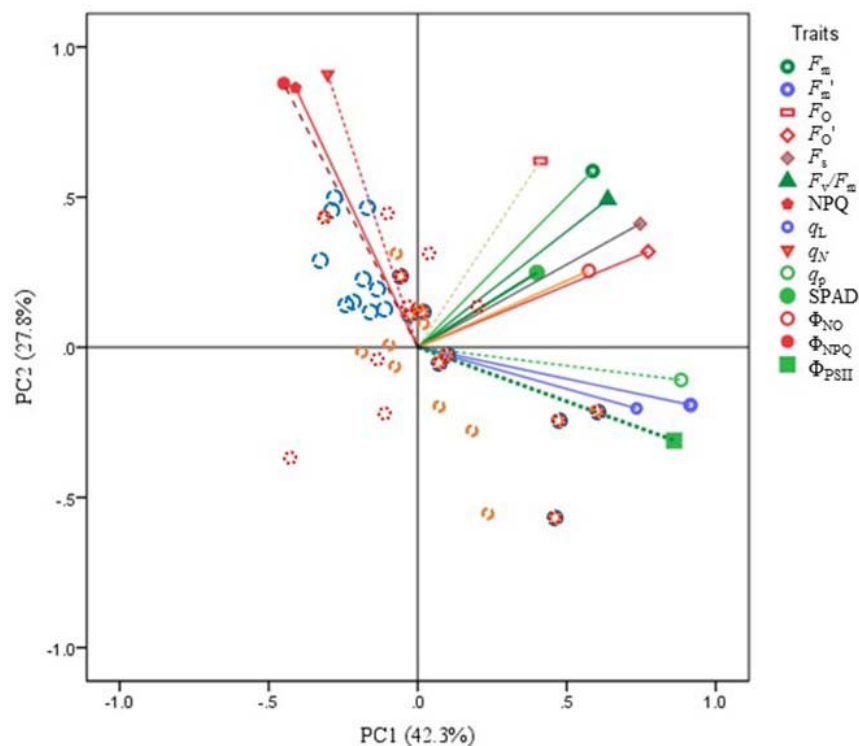


826

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.

832

833



834

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.

845

846