



Tracking chlorophyll fluorescence as an indicator of drought and rewatering across the entire leaf lifespan in a maize field



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ABSTRACT

Plant growth and photosynthesis in response to water status have been extensively investigated. However, elucidating the photosynthetic process and its indicators under a drought episode and rewatering across the entire leaf lifespan is often neglected. In this experiment, three water treatments were set during two growth seasons: a control treatment, moderate persistent drought (T_1), and severe persistent drought (T_2). Maize leaf chlorophyll fluorescence emission was analyzed to determine the regulative responses of the photosynthetic potentials and photosystem II (PSII) photochemistry process to drought and rewatering *in situ*. A severe drought episode during the peak vegetative growth stage resulted in decreases in chlorophyll content, the maximal efficiency of PSII photochemistry (F_v/F_m), and photochemical quenching, but increases in non-photochemical quenching and the yield for dissipation by downregulation. Rewatering only restored partial PSII functions in plants that had undergone historical drought episodes. An analysis of non-photochemical pathways of thermal dissipation indicates that regulative photoprotection of the photosystem apparatus may occur through heat dissipation when an effect of severe drought episode appeared on a young leaf; however, rewatering did not enhance photoprotection with leaf aging. Compared to the control treatment, the yield of T_1 and T_2 decreased by 25.1% and 27.1% in 2015, and 26.4% and 54.3% in 2016, respectively. The chlorophyll content was significantly and closely correlated with F_v/F_m ($R = 0.65$, $P < 0.001$) and the maximum versus minimum fluorescence yield in the dark-adapted state (F_m/F_o) ($R = 0.72$, $P < 0.001$). Additionally, the two parameters can be suggested to feasibly track chlorophyll content changes and the degree of leaf senescence in responses to a drought episode and its interaction with leaf aging: F_m/F_o and the relative limitation to photosynthesis (RLP). The current results may provide a profound insight into better understanding the underlying mechanism of photosynthetic potentials and photochemistry efficiency and photoprotection in response to drought episodes and rewatering over the entire leaf lifespan.

1. Introduction

Climate change is expected to result in abnormal changes in precipitation patterns, including the enhanced severity and accelerated frequency of droughts (IPCC, 2014). Water shortage, a worldwide

concern, is a crucial constraint to crop growth, productivity, and yield grain yield in many regions across the world (Lobell et al., 2014; Myers et al., 2017; Hussain et al., 2018). The limitations on biological process related to photosynthesis due to drought include reductions in chlorophyll content, the net assimilation rate (A_{net}), stomatal conductance,

Abbreviations: F_s , chlorophyll fluorescence in steady state conditions; F_o , F_o' , minimal fluorescence from dark- and light-adapted leaves, respectively; F_m , F_m' , maximal fluorescence from dark- and light-adapted leaves, respectively; F_v , F_v' , variable fluorescence from dark- and light-adapted leaves, respectively; F_v/F_m , maximal efficiency of PSII photochemistry from dark-adapted leaves; F_v'/F_m' , efficiency of excitation capture by open PSII centers; q_p , q_L , photochemical quenching based on puddle and lake models, respectively; Φ_{PSII} , the quantum efficiency of PSII from light-adapted leaves; Φ_{NPQ} , the yield for dissipation by downregulation; Φ_{NO} , the yield of other non-photochemical losses; F_m/F_o , a parameter related to changes in heat dissipation; PSII, photosystem II; NPQ, non-photochemical quenching; SPAD, relative chlorophyll contents; LRI, leaf rolling index; RLP, relative limitation to photosynthesis

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and photosystem photochemical efficiency parameters, as well as other related biochemical processes (e.g., Li et al., 2006; Guanter et al., 2014). This limitation leads to plant growth inhibition, and finally, decreased crop production and grain yields (Berger et al., 2016; Jin et al., 2017).

Zea mays L. is one of the three major staple crops (maize, *Triticum aestivum* L., and *Oryza sativa* L.) and also produces the main resources of the animal feed and industrial raw materials (Ribaut et al., 2009; FAO, 2017). In China, it is also a crucial crop in ensuring food security and husbandry industry development (Meng et al., 2013; PING, 2018). As reported, water shortage is a major constraint in maize production, particularly under climatic changes (Jiao et al., 2014; Avramova et al., 2015), leading to a grain yield reduction of 25–30%, even without any harvests during extremely severe drought events (Ben-Ari et al., 2016). In the United States (US), a major maize production zone, drought has had a greater effect on maize production in the past two decades, despite cultivar and agronomic management improvements (Lobell et al., 2014). Climatic warming is expected to further enhance the adverse impact of droughts, potentially leading to a considerable decrease in maize yields (Ribaut et al., 2009; Jiao et al., 2014). Thus, research on maize drought-tolerance and its underlying mechanisms, as well as the implications, remain hot topics under the pressure of escalating environmental conditions (Lobell et al., 2014; Jin et al., 2017; Myers et al., 2017).

The effects of drought on the change patterns of chlorophyll *a* fluorescence (ChlF) emissions are well established and have been extensively reported (e.g., Kramer et al., 2004; Li et al., 2006; Kalaji et al., 2017). A large amount of research has shown that water deficit stress has negative effects on the potential and actual photochemical efficiency of PSII as indicated by ChlF parameters, such as F_v'/F_m' , Φ_{PSII} , and q_p , and hence, plant growth (Gallé et al., 2007; Sekhar et al., 2017). However, a body of evidence also indicates that the responses of some ChlF parameters to drought may not be more sensitive relative to these gas exchanges (Marques da Silva and Arrabaca, 2004; Xu et al., 2008; Kalaji et al., 2017). Lu and Zhang (1999) reported there were no changes in ChlF parameters, such as F_v/F_m , in maize leaves under moderate drought conditions. Nevertheless, ChlF's response to drought may depend on the species or cultivars (Li et al., 2006), leaf age, and plant development stages (Xu et al., 2008), as well as drought severity, drought-treated duration, and persistence (Marques da Silva and Arrabaca, 2004; Kalaji et al., 2017). For instance, maize's young leaves often maintain a relatively stable level, but a significant decrease may occur in the elder leaves (Xu et al., 2008), indicating the younger and healthier photosynthetic tissues may have a high drought-tolerance, at least in terms of ChlF emission behaviors. The results reported by Marques da Silva and Arrabaca (2004) showed that NPQ tended to increase under moderate water deficit stress but decrease under severe water deficit stress. Furthermore, different fluorescence parameters may also have different sensitivities (Kromdijk et al., 2016). For example, the overall photosynthetic performance index (PIABS) may become a more sensitive indicator than F_v/F_m with leaf aging for distinguishing grain yield potentials between hybrid rice cultivars (Zhang et al., 2015). However, the analysis of chlorophyll fluorescence and responses to drought episodes and rewatering across the entire leaf lifespan have received less attention, particularly *in situ* in the field.

In our previous study, episodic drought limitations on leaf physiological traits and partial recovery after rewatering were reported (Song et al., 2018). However, in the current study, we focused on monitoring successive changes in chlorophyll fluorescence indicators across the entire maize leaf lifespan under different watering regimes. Thus, the present aims were to (1) explore the photosynthetically physiological effects of a drought episode during a leaf's entire developmental process and (2) evaluate interactive effects between the watering regimes and leaf ages (i.e., plant developmental stages). We hypothesized the following: (1) drought-tolerance indicated by changes in chlorophyll fluorescence emissions may be found in the youngest and fully

expanded leaves; (2) an inhibition of PSII photochemistry may occur at either the juvenile or elder leaf stage; and (3) this inhibition may be exacerbated by a drought episode or ameliorated by rewatering. Furthermore, especially in view of the response process, we expect to obtain some new essential and critical expression parameters from chlorophyll *a* fluorescence emissions to highly and efficiently indicate sensitivity to a drought episode and rewatering, as well as their association with stages of leaf development.

2. Methods and materials

2.1. Site statement

The present field experiment was carried out from April to September in 2015 to 2016 directly *in situ* at an agricultural ecosystem research station (41°49'N, 121°12'E, 27.4 m a.s.l.) operated by the Jinzhou Ecology and Agricultural Meteorology Center in Liaoning, a northeastern Chinese province in the renowned northeastern maize production belt (PING, 2018). This region is located in northeastern Eurasia, characterized by a warm temperate semi-humid monsoon climate and atmospheric circulation patterns mainly composed of westerlies and subtropical systems with four distinct seasons. Over a recent 30-year period (1981–2010), the mean annual temperature was 9.9 °C with extreme maximum and minimum temperatures of 41.8 °C and –31.3 °C, respectively; the mean annual precipitation was 568 mm with 60%–70% of rainfall concentrated during the major growing season. The frost-free period was 144–180 days annually. The soil is the typical brown type with a pH value of 6.3, bulk density of 1.62 g cm⁻³, field capacity of 22.3% (gravimetric), and wilting coefficient of 6.5%. The soil's organic carbon, total nitrogen, soil phosphorus, and soil potassium content are 10.44 g kg⁻¹, 0.69 g kg⁻¹, 0.50 g kg⁻¹, and 22.62 g kg⁻¹, respectively. The staple crop in the region is maize (Song et al., 2018).

2.2. Experimental design

This study was conducted over two entire growing seasons from late April to late September in 2015 and 2016 in a large electric-powered water-proof shelter 4 m in height, which is used to keep out natural rainfall and simulate artificial precipitation via sprayers installed on the ceiling. When it rains, this shelter covers the plots to keep out natural rainfall, but at other times, it is moved from the experimental areas, so the plots can be consistent with the field environment. The area of each plot is 15 m² (5 m long, 3 m wide) and surrounded by a cement wall to avoid water penetration across the plots. The maize cultivar used in this experiment was Danyu 39 in 2015 and Danyu 405 in 2016, which are commonly planted across northeast China. It was sown in late April, and the distance between the two adjacent rows and plants were 0.70 and 0.32 m respectively. Seeds were sown directly in drills with a 5 cm soil depth. The seed rate was 6.0 m⁻² to ensure the final planting density was 4.5 plants m⁻² in both 2015 and 2016, and the crops were harvested in late September. A compound fertilizer containing 28%, 11%, and 12% of N, P₂O₅, and K₂O, respectively, of c. 750 kg ha⁻¹ was applied conventionally before sowing.

This experimental design is illustrated in Fig. 1. Three water treatments were set each year: control, T₁, and T₂, which denote the control treatment (i.e., normal irrigation every 7 days), withholding 20-day and 27-day water treatments in 2015, and withholding 27-day and 41-day water treatments in 2016 from the jointing stage. Before and after the drought treatment period, the irrigation management practice was the same as the control treatment. As measured, the soil's relative water content (SRWC, 0–50 cm depth) was decreased to water deficit stress levels of 30–40% at the end of each drought episode; meanwhile, a normal level of 70–80% was maintained in the control and drought plots after rewatering. It indicated that the both T₁ and T₂ withholding water treatments led to severe water deficit stress at end of each

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