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Maize leaf functional responses to drought episode and rewatering

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ABSTRACT

Effects of crop growth and physiological activities to drought and irrigation regimes have been extensively studied; however, the combined responses of plant growth, morphological and photosynthetic behaviors to drought episodes and thereafter rewatering receive a less attention. This field experiment was carried out directly *in situ* at an agricultural ecosystem research station across two entire growing seasons during 2015–2016, in northeastern China, on the renowned northeastern maize production belt, where is being threatened by severe drought. A field automatic rain-shelter was used, and five irrigation regimes including control, four drought episodes, and rewatering treatments were established. The chlorophyll contents (SPAD values), light-saturated photosynthetic rate (A_{sat}), and photosystem II actual quantum yield (Φ_{PSII}), maximum quantum yield (F_v'/F_m') decreased at lower leaf positions and with plant development. Episodic drought effects on plant growth, leaf morphological traits and photosynthetic processes at both vegetative and reproductive stages were severely remarked, particularly at late development stage and with longer drought duration. The recovery of leaf functional traits of the plants experienced historical-drought following re-irrigating was not fully restored to the level of the plants subjected to ample and normal water status; and the strength of recovery was proportional to the persistence of pre-drought episodes. The relationship of A_{sat} with SPAD depends on water status and plant development. A principal component analysis can well denote the change patterns in responses to water status treatments with plant development. The results may give an insight into how to understand the maize traits' responses to drought episode and rewatering, and this also might assist the drought-stricken crops to cope with future climatic change.

1. Introduction

Climate change results in abnormal changes in precipitation pattern in terms of both its total amounts and episodic drought frequencies (Alley et al., 2003; Trenberth et al., 2014; IPCC, 2014). Water shortage is a crucial constraint to crop growth, yield, physiological processes in many areas around world, including rain-fed and deficit-irrigation regions; meanwhile the abnormal occurrences of drought episodes usually fluctuate at various spatial-temporal scales (Boyer, 1982; Battisti and Naylor, 2009; IPCC, 2014; Rurinda et al., 2014; Myers et al., 2017). Intensifying drought also may reduce and even eliminate the expected benefits from some fewer favorite factors due to climate change such as elevated CO_2 and enhanced anthropogenic nitrogen (N) deposit (Iversen and Norby, 2014; Gray et al., 2016; Xu et al., 2016), and climatic warming may exacerbate drought disaster by further reducing soil moisture availability (Lobell et al., 2011, 2014; Iversen and Norby, 2014). As reported, due to potentially adverse climate change, since 1950s, agricultural drought-inducible disaster area also had an increasing trend in China—the drought-induced grain loss reached approximate 25–30 billion kg, accounting for 60% of total loss of natural disasters (Jiao et al., 2014; Zhou, 2014). It has been notable that China's agricultural drought becomes more serious mainly due to the adverse climate change and rapid social-economic development.

Maize is one of the most important three staple crops—maize, wheat, and rice, the main resources of the feed, industrial raw materials (Campos et al., 2004; Long et al., 2006; Ribaut et al., 2009), recent years it has ranked first place among the three staple crops (FAO, 2017). In China, it also plays a critical role in food security and husbandry industry development among agricultural and even entire economic sectors at both regional and national levels (Meng et al., 2013; Ma and Ma, 2017; PINC, 2017). Drought is one of major limitations to maize production (Boyer, 1982; Sharp et al., 2004; Xu et al., 2008; Lobell et al., 2014; Avramova et al., 2015), resulting in a yield reduction of 25–30%, even with no harvest in those years of extremely severe drought (Campos et al., 2004; Zhang et al., 2011). In the major maize production zone of USA, the drought sensitivity in maize production in

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recent two decades has been also reported to increase, despite cultivar improvements and the agronomic practices with higher sowing densities (Lobell et al., 2014). Climatic warming is projected to further exaggerate drought's negative impact, leading to huge loss of maize production (Ribaut et al., 2009; Lobell et al., 2014). Drought stress leads to reductions in maize (*Zea mays* L.) and other crops' yields mainly by (i) reducing plant growth and reproductive activities, (ii) reducing photosynthetic potentials and thereby radiation use efficiency (RUE), and (iii) reducing harvest index (HI) (Saini and Westgate, 1999; Earl and Davis, 2003; Barnabás et al., 2008; Xu et al., 2008). Contrastingly, if a maize cultivar root system and its ear growth are not completely limited, and leaf survival is enhanced despite water deficit, the cultivar may be recognized as high drought-tolerant one (Ribaut et al., 2009). Nevertheless, the intermittent drought imposition, and then following rewatering effects on crop plants grown in field still receive a relatively scant attention.

Based on cyclic drought experiment using *Catalpa bungei* species, the accumulative functional effects of progressive drought and subsequent re-watering on plant growth, leaf and root parameters have been found as a useful adaptive mechanism to successive drought and subsequent rewatering (Zheng et al., 2017). As recently reported by Abid et al. (2016), the adaptability to drought, and recovery rate and capacity were closely associated with wheat cultivars. The accumulation of effective metabolites such as sugars, and some amino acids like proline and leucine may exert an adaptive mechanism in response to the drought cyclic patterns (Meyer et al., 2014; Sun et al., 2016; Zheng et al., 2017). In plants of *Lupinus albus*, the new leaves can be produced more as quickly re-watered, although restoration of other metabolites (e.g. sugar content) was lagged (Pinheriro et al., 2004). Maize leaf length undergone one or several days of drought can restore completely following rewatering, but its growth rate could not reach the control level, suggesting that the growth resumption may be only a postponed event, no overcompensation occurrence (Acevedo et al., 1971). It is implied that the magnitude and rate of resumption might depend on pre-drought intensity and its duration (Hsiao, 1973; Xu and Zhou, 2007; Xu et al., 2009, 2010). Thus, the extent of compensation for the limitation of pre-drought by promoting plant growth as rewatering might determine the final plant biomass or crop yield, which may link to drought severity and its duration. Nevertheless, whether plant growth and physiological activities completely recover following rewatering, what are the rate and degree of recovery, and the ability of the adaption to the drying-rewetting cycles might strongly depend on previous drought strength and persistent duration, species and genetic types, and drying-rewetting cycle patterns, which the underlying mechanism is elusive so far (Loewenstein and Pallardy, 2002; Marron et al., 2003; Flexas et al., 2004; Yahdjian and Sala, 2006; Xu et al., 2009, 2010; Sun et al., 2016; Zheng et al., 2017). Thus, responses of plant growth and leaf functional processes to drought history and subsequent rewatering remain to be clarified further, particularly *in situ* crop field.

As stated above, drought effects on plant/crop growth, photosynthesis, and other crucial eco-physiological process have been investigated extensively (e.g., Ne Smith and Ritchie, 1992; Yordanov et al., 2000; Chaves et al., 2002; Harrison et al., 2014). However, as just recently stated by Abid et al. (2016), "studying plants' capability to adapt and recover from drought stress is essential because of the ever-changing nature of drought events". Herein, the objectives of this present study were to: (1) examine the effects of drought episode and rewatering on photosynthetic capacity and chlorophyll fluorescence; (2) compare the leaf functional responses to drought episode and rewatering at different leaf positions from most bottom to upmost leaves, at various plant growth developments; (3) determine changing patterns in responses to drought episode and recovery after rewatering on photosynthetic capacity and chlorophyll fluorescence with the leaf developments; and (4) elucidate the indices for drought adaptability and recovery ability following a pre-drought episode. Our hypotheses are expected: i) drought-episode-induced negative responses may depend on leaf ages/positions and leaf/plant development; ii) the amelioration of drought-induced negative responses by rewatering in field grown maize plants may mainly result from gas exchange behaviors relative to the chlorophyll fluorescence performances—photosystem II (PSII) photochemical processes; iii) the morphological and physiological functional traits may closely interacted, coordinately representing the adaptive responses to episodic drought and following rewetting.

2. Materials and methods

2.1. Site descriptions

The present two-year field experiment was carried out directly *in situ* at an agricultural ecosystem research station during 2015–2016 (41°49′N, 121°12′E, 27.4 m a.s.l.), Jinzhou Ecology and Agricultural Meteorology Center, Jinzhou, Liaoning, a northeastern Chinese province on the renowned northeastern maize production belt (PINC, 2017). This region is located in the northeast of the Eurasian areas, belongs to the warm temperate semi-humid monsoon climate, and atmospheric circulation mainly composes of westerlies and subtropical systems, with clear four seasons. The mean annual temperature is 7.8–9.0 °C, with the extreme maximum temperature of 41.8 °C and the extreme minimum temperature of −31.3 °C; annual frost-free period is 144–180 days; average annual rainfall is 540–640 mm, with 60%–70% of rainfall concentrated in summer. The soil is the typical brown soil, with a soil pH value of 6.3. The soil bulk density, soil field capacity, and wilting coefficient of the soil moisture were 1.61 g cm^{-3}, 22.3%, and 6.5% (gravimetric), respectively. The organic matter and total nitrogen content is 6.41–9.43 g kg^{-1} and 0.69 g kg^{-1}, respectively. The staple crop in this region is maize (Han et al., 2007).

2.2. Experimental design

This study, a maize water-controlled field experiment, was conducted by using a huge mobile rain-proof shelter during two growth seasons of 2015–2016. The two-year experimental design and its results were similar; thus, here the 2016-year results were mainly reported (for 2015-year experimental design and its results, see the Supporting Information File: Table S1 and S2, and Figs. S1–S3). In the 2016-year experiment, the five irrigation treatments were designed: T_1, T_2, T_3, T_4, and T_5 treatments, which denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire developmental stage, respectively (Table 1).

There were three replicates in each treatment and 15 plots in total. Each plot is 5 m long and 3 m wide, surrounded by a cement layer to avoid water permeation. The large mobile water-proof shelter is 4 m in height, which is used for simulating precipitation to avoid the rainfall entrance. Maize used in this experiment was a hybrid cultivar, named as Danyu 405, which has been planted widely in recent years in Northern China. Seeds were sowed with 5.3 plants m^{-2} of planting density on 23 May, and the plants were harvested on 25, September 2016. Controlled release fertilizer (N, P_2O_5, and K_2O accounting for 26%, 12%, 12% of the total mass, respectively), was used with 600 kg hm^{-2}.

2.3. Environmental variables and maize traits measurements

2.3.1. Soil relative water content (SRWC) measurements

We used weighing method to measure the soil relative water content. Methods with soil auger were used to retrieve soil samples (0–50 cm), then put the samples to the aluminum specimen box, and weighed the samples to obtain the wet weight. Later, the samples were dried in an oven at 105 °C until a constant weight, and then the dried soil samples were weighed. There were three replicates in each treatment. The SRWC was calculated by the equation below: