



Metabolic and growth responses of maize to successive drought and re-watering cycles



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ABSTRACT

In light of an increase in the severity and frequency of episodic drought predicted due to climate change, the mechanisms underlying plant responses to repeated drought and recovery cycles need to be understood. Maize (*Zea mays* L.) plants of two inbred lines were subjected to two cycles of drought and re-watering and then compared with plants that were watered daily. Changes in the metabolome and growth were monitored at multiple time points during the experiment. The extent of recovery in plant growth after re-watering strongly depended on the plant lines and drought cycles. Both full and partial recovery was observed. The variation in the pattern and extent of the metabolomic profile and in metabolite levels initiated by re-watering during two drought cycles was complex and diverse. Correlation-based network analysis indicated that maize plants required more coordinated and extensive metabolic shifts to cope with drought in the second cycle than in the first cycle. Metabolic pathways in the maize plants returned to their normal status at different rates during recovery. The results provide valuable insight into the growth, biochemical, and metabolic mechanisms used by maize to adapt to cyclic drought. The analysis is also useful in indicating specific traits to be targeted in breeding programs aiming to better adapt the crop to climatic changes.

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1. Introduction

Soil drought because of inadequate rainfall and fluctuations in soil moisture has become an acute problem that constrains plant growth and productivity, in numerous regions worldwide, particularly in growing regions that already have a tendency to water deficits (Boyer, 1982; Ahuja et al., 2010; Dawson et al., 2011). Plants respond to water deficit through complex mechanisms, which include differential gene expression, changes in biochemical metabolism and morphological adaptation (Chaves et al., 2003; Harb et al., 2010; Pinheiro and Chaves, 2011; Lipiec et al., 2013). To cope with drought, plants can enhance their capacity for acquiring water or conserve water by increasing their root-to-shoot ratios

Abbreviations: BA, biomass allocation; BAS, ratio of shoot dry mass to total dry mass; BAR, ratio of root dry mass to total dry mass; BM, biomass weight; C1, control in the first cycle; C2, control in the second cycle; D1, drought stress in the first cycle; D2, drought stress in the second cycle; D-W, drought and re-watering treatment; LA, total leaf area per plant; PCA, principal component analyses; NMR, nuclear magnetic resonance spectroscopy; W1, re-watering in the first cycle; W2, re-watering in the second cycle.

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under water deficits. This route has been considered an adaptive strategy because a larger investment in roots improves water absorption and a decrease of leaf area reduces the area for transpiration (Blum, 1996; Bargali and Tewari, 2004; Xu et al., 2010). In addition, plants could also improve their ability for osmotic adjustment and alter metabolic pathways to tolerate or resist water deficits (Shulaev et al., 2008; Pinheiro and Chaves, 2011). Multiple metabolic processes are widely recognized to be involved in the adaptive response to water stress (Mahajan and Tuteja, 2005; Verslues and Juenger, 2011; Krasensky and Jonak, 2012). Drought disrupts metabolic processes, including CO₂ assimilation and metabolic impairment, and ultimately decreases the rate of biomass accumulation (Flexas et al., 2004). Moreover, turgor is maintained by osmotic adjustment under drought conditions and requires the transport and synthesis of functionally important osmolytes and compatible solutes, such as proline, soluble sugars, glutamate, polyols, and glycine-betaine (Foyer et al., 1998; Chaves et al., 2003; Sicher et al., 2012; Sun et al., 2015). Several compounds that are involved in primary metabolism are key precursors of stress-related metabolites, such as flavonoids, phenylpropanoids, and proteins (Dixon and Pavia, 1995). Another function of primary metabolites in stressed plants is the mitigation of oxidative stress because of the formation of reactive oxygen

species in plants in response to water stress (Shen et al., 1997; Dixon, 2001; Ramakrishna and Ravishankar, 2011). Using rapidly developing metabolomic techniques, recent studies have identified different types of metabolites that are associated with drought stress responses in plants, and understanding these adjustments in plant metabolism is important in enhancing plant performance under water-stressed conditions (Fiehn, 2002; Shulaev et al., 2008; Obata and Fernie, 2012).

In the field context, soil drought and rainfall often occur alternately, implying that repeated drought-recovery cycles are considerably more common than a prolonged drought event. With the changing climate due to the buildup of greenhouse gases in the atmosphere and diversion of irrigation water from agriculture to other purposes, an increase in the occurrence of episodic drought, in which plants will be repeatedly exposed to drought, may be likely (IPCC, 2007; Xu et al., 2010; Gallé et al., 2011; Sun Y. et al., 2013). Drought stress and recovery following re-watering may follow different adaptive mechanisms where plants are exposed to episodic drought (Gazanchian et al., 2007; Izanloo et al., 2008). The rate and degree of recovery to pre-stress levels varies among plant species and can exert a substantial impact on plant fitness (Loewenstein and Pallardy, 2002). Thus, in addition to drought resistance/tolerance, drought recovery ability is another important component in the plants ability to cope with predicted increases in the severity and frequency of episodic drought (Vankova et al., 2012).

Numerous studies consider the effects of episodic drought on plant growth as one of the most fundamental processes in the life cycle of plants. Rapid and complete growth recovery following re-watering is likely the key to preventing significant declines in plant production after episodic drought (Chaves et al., 2009). Several studies showed that plant growth measured as leaf area and biomass was stimulated by re-watering following drought (Reynolds et al., 2004; Siopongco et al., 2006). Xu et al. (2009) found that new plant growth in perennial grass, *Leymus chinensis*, was enhanced by re-watering. It may overcompensate for the loss of the grass's net primary production due to the effect of previous drought. In other studies it was found that plant growth characteristics recovered gradually after re-watering (Miyashita et al., 2005; Shi et al., 2014). By contrast, Yahdjian and Sala (2006) found that previous drought limitation to growth existed in the Patagonian steppe. This limitation, which is due to previous drought, may be portrayed as a plant memory behavior based on past drought stress (Xu et al., 2010). Notably, limitations to previous drought and recoveries by subsequent re-watering may influence biochemical metabolism and signal cascades (Fortunati et al., 2008; Xu et al., 2010). Toscano et al. (2014) recently demonstrated that Mediterranean ornamental shrubs could employ various mechanisms, such as the differential partitioning of dry matter between root and shoot parts, as well as the reduction of leaf area, to allow them to tolerate repeated cycles of drought. Furthermore, whether plant growth exhibits complete recovery after re-watering and the extent of recovery may depend on previous drought intensity or duration, plant species, variety, and number of consecutive drying cycles (Flexas et al., 2004; Miyashita et al., 2005; Xu et al., 2009; Shi et al., 2014). Thus, the effect of previous drought and re-watering on plant growth and plant function must be further clarified.

Technological innovation over the past decade has made measuring changes in metabolite levels on metabolome-wide scales possible (Urano et al., 2010), enabling an unprecedented overview of the global metabolic changes occurring under drought stress and re-watering. Plant recoveries from drought stress include shifts in specific metabolic pathways and changes in metabolite levels (An et al., 2013). The degree of recovery from drought has been associated with various biochemical mechanisms, including maintenance of membrane stability, osmotic adjustment, phytohormone

accumulation, increased carbon partitioning and carbohydrate storage in plant organs, as well as accumulation of sugars and organic solutes (Xu et al., 2009; Gechev et al., 2013; Sicher et al., 2012; Sun C. et al., 2013; Foster et al., 2015). For example, in addition to regulating gene expression and sustaining growth, sugars have been implicated in stabilization of membrane structures and cell osmotic adjustment during drought stress and in providing carbon skeletons for recovery during the rehydration process (Suguiyama et al., 2014).

Although physiologically and ecologically significant, the recovery period of the plant in response to drought has received considerably less attention than the response to the developing drought. Drought recovery mechanisms have been already described for shrubs and trees (Marron et al., 2003; Gallé et al., 2007; Echevarria-Zomeno et al., 2009; Gallé et al., 2011; An et al., 2013; Cao et al., 2014; Correia et al., 2014; Toscano et al., 2014), and grasses (Siopongco et al., 2006; Xu et al., 2009; Kang et al., 2011; Meyer et al., 2014; Suguiyama et al., 2014; Zhang et al., 2014; Foster et al., 2015), but evidence of the capacity for recovery from previous drought and the underlying metabolic processes remain largely unknown in crop plants. Especially, in most maize (*Zea mays* L.) growing regions, irrigation and rainfall patterns dictate episodic drought that can exist at any of the growth stages during the plant life cycle. Maize, which is one of the most important crops worldwide, is used as food, feed, and an energy source and can be planted in diverse ecosystems. Understanding how maize plants respond to episodic drought, as well as the underlying mechanism will indicate specific traits to be targeted in breeding/selection programs and is likely to help in implementing crop management practices during climatic changes. In this study, we attempt to provide an insight into the mechanism of maize plant responses to two successive drought and re-watering cycles in terms of plant growth and metabolome profiles. We also try to explore if various metabolic pathways in maize recover from the effects of previous drought to the same extent and if any differences exist between responses to repeated drought-recovery cycles in maize.

2. Materials and methods

2.1. Plant growth conditions and treatments

In this experiment, we used two maize inbred lines: PH4CV (with the Lancaster background; subsequently abbreviated as line L) and PH6WC (with the Reid background; subsequently abbreviated as line R). These two lines that were developed for high yield and extensive adaptability are parents of popularly planted hybrids and are divided into two major germplasm groups, which are available for breeding and research programs in China. The seeds were sown in pots containing 4 kg of soil and then grown side-by-side in a greenhouse at the Experimental Station of Northeastern University, Shenyang, Liaoning (123°4'E, 41°8'N), at 30 ± 2 °C/20 ± 2 °C (day/night), with a 14 h light/10 h dark cycle at a photon flux density of 700 μmol m⁻² s⁻¹ and with approximately 65 ± 5% relative humidity. The soil in this experiment is a brunisolic soil having pH 5.72, organic matter 2.52 g kg⁻¹, total N 1.22 g kg⁻¹, total P (P₂O₅) 1.12 g kg⁻¹, total K (K₂O) 24.24 g kg⁻¹. Fertilizer consisted of 180–75–75 kg ha⁻¹ of N–P₂O₅–K₂O incorporated before planting. Water stress was minimized with timely irrigation during plant culture. After about one month of growth (the fourth leaf stage), the seedlings were randomly assigned to either the control group or subjected to drought and re-watering (D-W) treatments (Fig. 1). For the experiment described in this study, 40 plants from each line were subjected to two consecutive cycles of D-W, whereas another 40 plants from each line received water every day (control). For each treatment cycle, the degree of soil drying was controlled by measuring the pot weight for 7 days, after which the plants were

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