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Chemical signals and their regulations on the plant growth and water use efficiency of cotton seedlings under partial root-zone drying and different nitrogen applications



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Abstract Partial root-zone drying during irrigation (PRD) has been shown effective in enhancing plant water use efficiency (WUE), however, the roles of chemical signals from root and shoot that are involved and the possible interactions affected by nitrogen nutrition are not clear. Pot-grown cotton (*Gossypium* spp.) seedlings were treated with three levels of N fertilization and PRD. The concentrations of nitrate (NO₃⁻), abscisic acid (ABA) and the pH value of leaf and root xylem saps, biomass and WUE were measured. Results showed that PRD plants produced larger biomass and higher WUE than non-PRD plants, with significant changes in leaf xylem ABA, leaf and root xylem NO₃⁻ concentrations and pH values, under heterogeneous soil moisture conditions. Simultaneously, high-N treated plants displayed larger changes in leaf xylem ABA and higher root xylem NO₃⁻ concentrations, than in the medium- or low-N treated plants. However, the WUE of plants in the low-N treatment was higher than that of those in the high- and medium-N treatments. PRD and nitrogen levels respectively induced signaling responses of ABA/NO₃⁻ and pH in leaf or root xylem to affect WUE and biomass under different watering levels, although significant interactions of PRD and nitrogen levels were found when these signal molecules responded to soil drying. We conclude that these signaling chemicals are regulated by interaction of PRD and nitrogen status to regulate stomatal behavior, either directly or indirectly, and thus increase PRD plant WUE under less irrigation.

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1. Introduction

Soil water availability is one of the major environmental factors limiting crop growth and yield formation (Wu et al., 2008; Gonzalez-Dugo et al., 2010). The plant hormone abscisic

acid (ABA) has been suggested many physiological roles in the plant when the soil water potential dropped below optimum levels, including control of stomatal behavior and limiting ineffective water use (Davies and Zhang, 1991; Tardieu and Davies, 1993; Dodd, 2003; Verslues et al., 2006; Pinheiro and Chaves, 2011).

The increase of ABA biosynthesis in both root and shoot and the enhancement of ABA transportation as a root-to-shoot or shoot-to-root signal, accompanied with the subsequent weakening of gas exchange capacity and decrease of growth rate, have been observed in many studies when water availability decreased from optimal level (Davies and Zhang, 1991; Schurr et al., 1992; Tardieu and Davies, 1993; Comstock, 2002; Chaves and Oliveira, 2004; Verslues et al., 2006; Jia and Davies, 2007; Qin et al., 2011; Wang et al., 2012). However, except the effect of ABA on plant shoot phenotype, the elongation of root length and increase of the root surface area were improved by ABA (indicating an indirect role) to ensure the growth-based water and (nitrogen) nutrition uptake (Wittenmayer and Merbach, 2005; Dodd et al., 2009). ABA-deficient mutants (e.g. *flacca*, *aba-1* and *aba-2* etc.) and/or grafted technique have been used to explain the physiological role of shoot-synthesized and root-sourced ABA in plants under suboptimal environmental conditions (Dodd et al., 2008). These studies suggested that the movement of ABA between symplast and apoplast can be inhibited by the alkalization of the xylem sap and the decrease of pH gradients over the cells membrane in stem, leaf or root tissues when the soil dries (Wilkinson et al., 2007; Xue et al., 2014; Dodd et al., 2008), eventually leading to ABA accumulation in mesophyll cells, the guard cells dehydration and then stomatal closure (Jia and Davies, 2007; Netting et al., 2012).

As a signaling molecule, ABA regulates plant physiological behaviors under suboptimal environmental conditions, for example the increased ABA levels weakens gas exchanges capability, declines stomatal conductance and transpiration rates as well as maintains leaf water potential and root water-uptake ability by increasing root: shoot ratio and decreasing leaf surface etc. under drought stress (Wittenmayer and Merbach, 2005; Dodd et al., 2009). However, due to convenience of measurement, many researches focused on shoot growth and regulation of shoot-synthesized ABA.

Additionally, stomatal closure regulated by ABA can be caused by soil nitrogen (N) deficiency, a same mechanism induced by drought (Wilkinson et al., 2007). It has been suggested that N deficiency increases tissue ABA concentrations (Rahayu et al., 2005). It is also well known that water fluxes in the xylem sap are generally reduced by limited water supply. Mineral N fluxes are also declined because N uptake by plants is limited under these conditions; this alters plant N nutrition and can even lead to N deficiency (Wilkinson et al., 2007; Haeefe et al., 2008; Wu et al., 2008; Gonzalez-Dugo et al., 2010). NO_3^- is one of the main forms of nitrogen (N) uptake and utilization by plants, and its changes in the xylem sap can alter the pH of xylem sap (Dodd, 2003; Wilkinson et al., 2007). Therefore, NO_3^- concentration in the xylem sap can be reduced under water stress situation (Dodd, 2003; Wilkinson et al., 2007).

Studies indicated that the concentration of NO_3^- in the xylem sap affected stomatal sensitivity to both ABA and soil dryness (Jia and Davies, 2007; Wilkinson et al., 2007), leading

to stomatal opening/closure and even changes in WUE, as the apoplastic pH changed (Davies and Zhang, 1991; Haeefe et al., 2008; Qin et al., 2011). It has been proved that the effects of NO_3^- on plant growth were mediated by pH-based ABA redistribution (Wilkinson et al., 2007). It is recently reported that the nitrate transporter 1/peptide transporter (NRT1/PRT) family comprises two ABA transporters (Yann et al., 2013), which suggests the close relationship of ABA and NO_3^- . Therefore, much work should be focused on the available interaction between ABA and supplied N/NO_3^- . Furthermore, numerous studies have been focused on ABA not only because of its key regulation to leaf stomatal conductance especially during the early stages of plant response to water deficit, but also its role in increasing water use efficiency (WUE) in agriculture (Schachtman and Goodger, 2008). An innovative partial root-zone drying model (PRD) has been used to remarkably increase the WUE of various crops including grape, fruit trees, and maize, in the regions of limited water supply (Wang et al., 2009; Jovanovic et al., 2010; Wang et al., 2010, 2012). In the field-grown grapevines study, the use of PRD or deficit irrigation increased WUE by about 40% with a yield decreasing by only 15% (Schachtman and Goodger, 2008).

It has been confirmed that PRD can promote the increase of xylem sap ABA concentrations as compared with full irrigation, which can be explained by the changes of root water potential (Dodd et al., 2010; Puértolas et al., 2014) and other physiological parameters (Dodd, 2009; Sepaskhah and Ahmadi, 2010). Therefore, the increase of WUE and reductions in stomatal conductance are correlated with increased ABA concentrations under PRD treatment (Schurr et al., 1992; Gonzalez-Dugo et al., 2010; Dodd et al., 2010). On the other hand, studies on N fertilization effect under water stress have indicated that N supply can reduce the negative effects of drought stress on plant growth (Wu et al., 2008; Haeefe et al., 2008; Cramer et al., 2009; Gonzalez-Dugo et al., 2010). A typical example is that *Sophora davidii* seedlings subjected to severe water deficit under low nitrogen conditions had a higher WUE than well-watered seedlings under high nitrogen conditions (Wu et al., 2008). Most experiments showed positive effect of WUE after supplying of N fertilizer, while few results reported about N effect to WUE (Brueck, 2008). Therefore, although PRD or N supply plays a role in enhancing plant WUE, the involved root-sourced chemical signals (ABA, pH and NO_3^-) and the possible interaction between N nutrition and PRD remain unclear.

The aim of this study is to examine how cotton (*Gossypium* spp.) seedling growth and WUE are affected by the interaction of PRD treatment and different nitrogen levels via cooperatively regulating root-sourced ABA signal and NO_3^- under soil water change. The cotton seedlings supplied with different N levels were subjected to a drought-rewatering treatment, with PRD or full water supplying before drought and after rewatering. The xylem sap in both shoot and root was collected for the analysis of ABA, NO_3^- , and pH, and for the measurement of the biomass, leaf water potential and whole plant water consumption. These results can illustrate the mechanism(s) by which plants adapt to changes in water availability. It is also important to explore how to improve WUE with appropriate N supply, especially for crops cultivated in drought-prone areas or in alternating wet-dry growth conditions.

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