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Correlation of the corn compensatory growth mechanism after post-drought rewatering with cytokinin induced by root nitrate absorption

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ABSTRACT

The mechanism of compensatory growth in corn after post-drought rewatering at the seedling stage was explored by investigating the levels and effects of several plant hormones. This study consisted of two treatment conditions: nitrate (NO_3^-) addition to the roots and cytokinin addition to the leaves. Results showed that drought stress reduced the biomass of aboveground parts and the whole plant, but increased root soluble carbohydrate concentration and root activity. Post-drought rewatering under the addition of NO_3^- to the roots increased corn growth. Biomass values of the aboveground parts and the whole plant were similar between the rewatering and wetness at 10 days after rewatering conditions. Upon addition of NO_3^- to roots, post- drought rewatering increased the cytokinin contents of leaves and its delivery rate from roots to leaves. Addition of cytokinin to leaves without the addition of NO_3^- to roots increased the growth rate of corn seedlings upon post-drought rewatering and simultaneously caused high leaf cytokinin concentration. Thus, increase in concentration of root-derived cytokinin concentration in leaves was closely related to compensatory growth in corn upon post-drought rewatering at the seedling stage.

1. Introduction

In recent years, regulated deficit irrigation and deficit irrigation, which are important measures of agricultural water-saving, have been widely adopted in crop, vegetable and fruit production (Cui et al., 2009; Pèrez-Pèrez et al., 2008; Ballesteret al., 2013; Intriglioloet al., 2013; Shao et al., 2010; Rufat et al., 2011; Jensen et al., 2014). The theoretical basis for benefits of regulated deficit irrigation and deficit irrigation is that plants can undergo compensatory growth upon post-drought rewatering. In other words, plants display reduced growth under drought stress but increases their growth rate when water supply becomes available. The reduced growth caused by drought stress is compensated or exceeded by rapid growth under sufficient water supply. Plant roots are vitally important to growth because they play a key role in organic substance storage, water and inorganic nutrient absorption and abscisic acid (ABA) and cytokinin synthesis (Bano 2010; Shi et al., 2007; Veselova et al., 2005; Yang et al., 2004). Thus understanding how roots affect compensatory growth upon post-drought rewatering in plants and the factors involved may provide useful information for improving agricultural water-saving.

Although some scholars have reported that roots can affect auxin and gibberellic acid concentration in aboveground organs such as shoots and leaves (Bacaicoa et al., 2011; Coelho et al., 2013), few have reported that auxin and gibberellic acid are produced by roots and then transferred to aboveground organs. Cytokinin and ABA are produced by roots (Bano, 2010; Yang et al., 2004). These hormones are transferred to aboveground organs of leaves and stems, thereby affecting their growth and development. However, cytokinin stimulates plant growth, whereas ABA inhibits it. Since plant compensatory growth upon post-drought rewatering is also inherently a growth process, cytokinins may play an important

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role in this process. Wang et al. (2014) reported that root-derived cytokinin concentration in leaves influences ryegrass regrowth at different clipping heights. Ghanem et al. (2011a,b) also found that root-derived cytokinin in leaves plays a key role in increasing tomato production and shoot biomass. In addition, nitrate (NO_3^-) has been reported to be the direct factor inducing variations in cytokinin content of many plants (Criado et al., 2009; Lu et al., 2009; Tamaki and Mercier, 2007). However, little is known about the relationship between plant growth upon post-drought rewatering and root-induced cytokinin and root NO_3^- absorption. Investigation of these relationships should provide a better understanding of the mechanism underlying crop compensatory growth upon post-drought rewatering.

Corn (*Zea mays* L.) is the third most important cereal food crop worldwide after wheat and rice. Corn ranks first among cereals in terms of planting area and production in China. Water deficit is a critical issue limiting corn growth and production in China (Han et al., 2013; Jin et al., 2010). Efficient use of water must be increased to improve corn production in the region. Corn seedlings grow quickly, and their growth variations can easily be detected because of their small size. In addition, corn seedlings are sensitive to drought, and the seedling stage is an important phase in corn growth and production. Therefore, corn seedlings were selected as the subject in the present study. We first explored the relationship between cytokinin production and the addition of NO_3^- to roots, as well as that between cytokinin production and direct addition of cytokinin to leaves by spraying. The mechanism of compensatory growth upon post-drought rewatering induced by root-produced cytokinin was investigated by studying growth-related factors, including the amount of soluble carbohydrates, and contents of indole-3-acetic acid (IAA), gibberellic acid (GA_3), ABA, zeatin ribosid (ZR) and NO_3^- in newly grown leaves and xylem sap.

2. Materials and methods

2.1. Experimental design

The study was conducted under rain-shelter at the experimental farm of the College of Agronomy at Henan University of Science and Technology in Luoyang City of Henan Province (34°32′N, 112°16′E, altitude 138 m). The experimental site was representative of the warm temperate continental monsoon climate, with an annual rainfall of 601 mm and annual temperature of 14.2 °C. The corn cultivar 'Zhendan-958′ exhibits drought resistance and wide adaptability and currently has the highest planting areas in china. For this reason, this cultivart was selected for the current study. On 1 June 2013, corn seeds were planted in 200 plastic pots (15 cm in diameter, 14 cm in height and 2.5 L in volume) filled with sand, with 6 seeds in each pot. Sand was used in the study because the mineral nutrients in sand are easy to rinse. Each pot was watered daily with an average volume of 20–30 mL of modified Hoagland solution to ensure normal corn growth. The modified Hoagland solution contained 5 mM K, 8 mM Ca, 1 mM P, 1 mM Mg, 89 μM Fe, 18 μM Mn, 0.9 μM Cu, 1.75 μM Zn and 10 mM NO_3^-. Seedling emergence occurred after 7 days. Only the two seedlings showing strong growth were selected, and the other seedlings were pulled out. The two remaining seedlings were grown for 25 days; 99 pots with uniformly grown seedlings were selected for the study. These 99 pots were divided into two groups of 72 and 27 pots. The group containing 72 pots was used for the experiment in which NO_3^- was added to the roots (Exp-1), while the other group of 27 pots was used for the addition of cytokinin to leaves (Exp-2).

The pots of Exp-1 were divided into four groups with 18 pots each, and the pots of Exp-2 were divided into three groups with nine pots each. Two growth periods of drought stress and rewatering, both lasting 10 days, were established in Exp-1 and Exp-2. In the drought stress period, the first and second groups in Exp-1 and the first group in Exp-2 received ample water supply; the third and fourth groups in Exp-1 and the second and third groups in Exp-2 were put under drought stress. In the rewatering period, all pots in Exp-1 and Exp-2 received sufficient water supply. At the end of the drought stress period, they were also all rinsed with distilled water to remove any traces of inorganic nitrogen in the sand. During the rewatering period, the first and third groups in Exp-1were watered with modified Hoagland solution without 10 mM NO_3^-, whereas the second and fourth groups were watered with modified Hoagland solution containing 10 mM NO_3^-. By contrast, all groups in Exp-2 were watered with modified Hoagland solution without 10 mM NO_3^-. In addition, the third group in Exp-2 was also sprayed once daily with cytokinin (8 mg/L6-benzylaminopurine, concentration based on preliminary experiments) during the rewatering period.

Thus, Exp-1 had four treatment conditions with 18 pots each as follows: (1) wetness without the addition of NO_3^- to the roots (WT), (2) wetness with the addition of NO_3^- to the roots (WN), (3) rewatering without addition of NO_3^- to the roots (DT) and (4) rewatering with addition of NO_3^- to the roots (DN). On the other hand, Exp-2 had three treatment conditions with nine pots each as follows: (1) wetness (WB), (2) rewatering (DB) and (3) rewatering with cytokinin sprayed to the leaves (DC).

By maintaining the soil water content (SWC) at 75–80% or 50–55% of field water capacity (FWC), wetness or drought stress were provided to the plants, respectively. SWC was determined gravimetrically every 5 h by weighing pots from six o'clock in the morning to nine o'clock in the evening. When SWC reached below 75% of FWC, the appropriate amount of water was added to the soil to maintain SWC in the 75–80% range in the wetness treatment conditions. In the rewatering treatment condition with drought stress, no water was added to the soil during the first 2–3 days to allow water to dissipate from the soil. Then SWS was maintained at 50–55% of FWC by weighing pots and adding appropriate amounts of water.

SWC at each treatment hour was calculated based on the following formula (1):

$$\mathrm{SWC} = \frac{W_t - W_d - W_e - W_p}{W_d \times \mathrm{FWC}} \times 100\% \quad (1)$$

where W_t is the temporary whole pot weight, W_d is the net weight of dried sand in the pot, W_e is the weight of empty pot, W_p is the estimated fresh weight (FW) of all plants in the pot and FWC is the field water capacity. The estimated FW of all plants in one pot was determined in advance using extra pots in each test period.

In Exp-1, six pots from each treatment group were taken to the laboratory at the end of the drought stress period. Three pots from each treatment condition were used to measure biomass, root soluble carbohydrate content, xylem sap quantity of roots and plant hormones before rewatering. The other three pots were used to measure the transpiration rate. During the rewatering period, the remaining 12 pots from each treatment group were further divided into two subgroups of six pots each. At 5 days and 10 days after rewatering, one subgroup from each treatment group was taken to the laboratory. Three pots of each subgroup were used to measure biomass, root soluble carbohydrate content, xylem sap quantity of roots and plant hormones before rewatering. A set of three other pots were used to measure the transpiration rate. In Exp-2, three pots from each treatment group were taken to the laboratory to measure biomass and the ZR concentration in leaves before rewatering at the end of the drought stress period. During the rewatering period, at 5 and 10 days after rewatering, three pots from each treatment group were used to measure biomass and the ZR concentration in leaves. One pot was used as a replicate in this study.