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No post-drought compensatory growth of corns with root cutting based on cytokinin induced by roots

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ABSTRACT

The effect of shallow and deep roots on compensatory growth of potted corn seedlings during post-drought rewatering was investigated on the basis of leaf cytokinin induced by roots. Two treatment conditions, namely, root cutting and nitrate (NO_3^-) addition, were used in the study. Results showed that drought stress retained corn growth. In the absence of root cutting, rewatering increased the net photosynthetic rates of corn and induced compensatory growth. However, under root cutting, no compensatory growth occurred in the rewatered corns. In the absence of root cutting, significantly higher zeatin riboside (ZR) concentrations in the leaves and xylem saps were recorded under rewatering treatment than under wet treatment. However, these results were not observed under root cutting owing to loss of deep roots. Furthermore, corns with deep roots added with NO_3^- showed significantly higher ZR concentration in the leaves and xylem saps than those with shallow roots added with NO_3^-. High leaf cytokinin concentration is known to induce rapid corn growth. Thus, no compensatory growth occurred during post-drought rewatering in corns with few deep roots, likely due to lack of leaf cytokinin enhancement induced by deep roots.

1. Introduction

Plants adapt to drought stress by reducing growth and then accelerating growth when sufficient water becomes available. Consequently, the reduced growth is offset or even surpassed under sufficient water supply. This is central to the theory of plant compensatory growth during post-drought rewatering. Given this theory, regulated deficit irrigation and deficit irrigation technologies have been extensively used in water-saving agriculture (Cui et al., 2009; Pèrez-Pèrez et al., 2008; Ballester et al., 2013; Intrigliolo et al., 2013; Shao et al., 2010). Therefore, compensatory growth of post-drought rewatering is highly important for water-saving agriculture.

Many scholars have explored the mechanism underlying crop compensatory growth during post-drought rewatering in cotton, wheat, maize, and Kentucky bluegrass. Various factors, including photosynthetic rate, stomatal conductance, fertiliser use and anti-aging properties, have been found to play a role (Luo et al., 2016; Wang et al., 2011; Yao et al., 2012; Ghahfarokhi et al., 2015; Xu et al., 2011). Some studies have revealed that cytokinin is closely related to plant growth, photosynthesis, anti-aging, leaf stomatal conductance and nitrogen fertiliser use (Rubio-Wilhelmi et al., 2014; Tamaki and Mercier 2007; Lu et al., 2009; Aloia et al., 2011). Therefore, exploring the mechanism of cytokinin-induced compensatory growth may be a worthwhile endeavor. Indeed, Wang et al. (2016a) studied plant growth hormones and found that leaf cytokinin levels, which are influenced greatly by roots, contribute to corn compensatory growth during post-drought rewatering.

Kirkegaard et al. (2007) conducted a field experiment on wheat water use and demonstrated that a relatively small amount of subsoil water is highly valuable for grain yield. Liu et al. (2015) investigated the combined effects of soil moisture and physical parameters on winter-wheat production. Similarly, the group observed that roots growing in deep soil layers improve the water-use efficiency as well as drought resistance of winter wheat. However, Zhou et al. (2009) found that two ridges and furrows mulched by one plastic film with maize planted in the furrow could increase maize yield. This observation was associated with enhanced topsoil moisture in the planting zone. Li et al. (1999) also reported that plastic-film mulching could partly increase the yield of spring wheat because of increased moisture in the upper 5 cm of the soil. Roots in the topsoil or deep soil both hold a close

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relationship with crop water use. However, no study has explored the relationship between crop compensatory growth mechanism of post-drought rewatering and topsoil or deep soil roots. Investigating the effect of cytokinin on corn growth on the basis of shallow and deep roots should provide further insight into this mechanism.

In the present study, corn (Zea mays L.) at the seedling stage was selected for studying compensatory growth of post-drought rewatering in pots. Corn, the world's third largest and China's principal crop, consumes large quantities of water. For this reason, corn productivity in Northern China is usually constrained by water shortage. Augmenting water-use efficiency is the key to improving corn production in the region. To achieve our research object, which is to determine the effect of deep roots on corn compensatory growth of post-drought rewatering on the basis of leaf cytokinin induced by roots, root cutting in corns was conducted to allow shallow roots to secret cytokinin. Then, we compared the effects of cytokinins secreted by shallow roots and the whole roots on corn growth of post-drought rewatering, to determine the connection between cytokinins secreted by deep roots and compensatory growth. Concentrations of gibberellic acid (GA_3), abscisic acid (ABA), indole-3-acetic acid (IAA) and zeatin riboside (ZR) in the leaves, ZR and ABA concentrations in the xylem saps, and the net photosynthetic rate (P_n), transpiration rate (T_r), and stomatal conductance (G_s) were also determined to attain our goal.

2. Materials and methods

2.1. Experimental design

The study was carried out in the experimental farm of Henan University of Science and Technology. The farm (34°32′ N, 112°16′ E, altitude 138 m) was located in Luoyang City of Henan Province and experiences a warm temperate continental monsoon climate. Its annual rainfall and temperature are 601 mm and 14.2 °C, respectively. The corn cultivar 'Zhendan-958', which is widely planted in China, was used in the study because of its high drought resistance and wide adaptability. Given their rapid growth and easily detectable growth variation, the present study adopted corns at the seedling stage as test material to investigate the compensatory growth mechanism. Specifically, root growth in corn seedlings is also easily detectable and controlled. The study was conducted under a rain shelter with potting filled with sand, and two experimental setups, which involved root cutting (Exp-1) and NO_3^- addition (Exp-2), were prepared. Sand was employed to allow water solution to permeate easily and rinse the mineral nutrient content.

The pots used in Exp-1 were 20.0 cm in pot-mouth diameter, 16.5 cm in pot-floor diameter, 22.3 cm in height and 20 cm in sand height. Meanwhile, nested pots were used for Exp-2, with pot B placed inside pot A (Fig. 1). Pot A was 28, 23 and 14 cm in pot-mouth diameter, pot-floor diameter and height, respectively. By contrast, the floor of pot B was removed, and the pot-mouth diameter, pot-floor diameter and height were 22,12 and 14.5 cm, respectively. The filled sand in pot A had a height of 10 cm. The sand height was 12 cm when measured from the top sand level in pot B to the floor of pot A.A 4 cm height separated pot B from the floor of pot A. Twelve evenly distributed small holes were punched through the floor of pot A to allow water to flow through. In Exp-1 and −2, the pots were watered daily with 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 15 mM NO_3^-.

In April 2017, a total of 200 and 150 pots were prepared for Exp-1 and Exp-2, respectively. The experiment was carried out from April 20 to June 3, for a total of 44 days. On 20 April, six corn seeds each were planted in both Exp-1and Exp-2. After 6 days, seedlings emerged. Then, 6 days after emergence, only two seedlings with strong growth were selected from the two setups, and the other seedlings were pulled out. The two remaining seedlings were grown for 12 days, and 36 and 27 pots with uniformly grown seedlings were selected for Exp-1 and Exp-2, respectively.

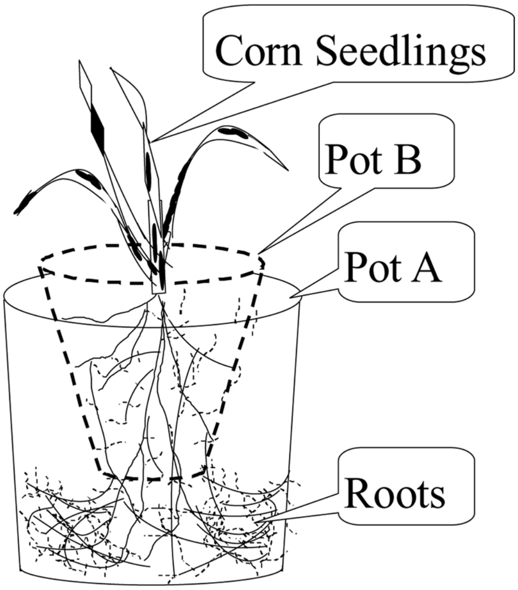

Fig. 1. A schematic diagram showing the experimental design for Exp-2.

2.1.1. Exp-1 design

In Exp-1, the 36 pots were divided into four groups with 9 pots each. Two growth periods of drought stress and rewatering were established in these pots for 10 days each. At the beginning of rewatering, the corn seedlings were at 28 days after seedling emergence. In the drought-stress period, the first and second groups received sufficient water supply, and the third and fourth groups were under drought stress. In the rewatering period, all groups received sufficient water supply. At the end of the drought-stress period, root cutting was conducted in the second and fourth groups. Thus, Exp-1 involved four treatments of 9 pots each designated as follows: (1) wetness (WT), (2) wetness with cut roots (WC), (3) rewatering (DT) and (4) rewatering with cut roots (DC).

Root cutting was performed in order to decrease root length by removing relatively deep roots at the bottom of the pot. The procedure was performed as follows: the pots were cut transversely through roughly the middle into halves using a thin-back knife with 10 cm sand height in the upper half and 10 cm sand height in the lower half (Fig. 2). During root cutting, the pots were kept stable to avoid sand disturbance. And then the upper and lower halves of roots were kept in place using transparent adhesive tape.

Fig. 2. Photographs showing root cutting for Exp-1.