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Research article

Abscisic acid and aldehyde oxidase activity in maize ear leaf and grain relative to post-flowering photosynthetic capacity and grain-filling rate under different water/nitrogen treatments

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ABSTRACT

This study investigated changes in leaf abscisic acid (ABA) concentrations and grain ABA concentrations in two maize cultivars and analyzed the following relationships under different water/nitrogen treatments: leaf ABA concentrations and photosynthetic parameters; leaf ABA concentrations and grain ABA concentrations; leaf/grain ABA concentrations and grain-filling parameters; and aldehyde oxidase (AO, EC 1.2.3.1) activities and ABA concentrations. The ear leaf average AO activities and ABA concentrations were lower in the controlled release urea treatments compared with the conventional urea treatments. The average AO activities in the grains were higher in the controlled release urea treatments, and the ABA concentrations were significantly increased at 11–30 DAF. The Pn and ABA concentrations in ear leaves were negatively correlated. And the Gmean were positively correlated with the grain ABA concentrations at 11–30 DAF and negatively correlated with the leaf ABA concentrations at 20 and 40–50 DAF. The grain ABA concentrations and leaf ABA concentrations were positively correlated. Thus, the Gmean were closely related to the AO activities and to the ear leaf and grain ABA concentrations. As compared to other treatments, the subsoiling and controlled release urea treatment promoted the uptake of water and nitrogen by maize, increased the photosynthetic capacity of the ear leaves, increased the grain-filling rate, and improved the movement of photosynthetic assimilates toward the developing grains. In the cultivar Z958, higher ABA concentrations in grains at 11–30 DAF and lower ABA concentrations in ear leaves during the late grain-filling stage, resulted in higher grain-filling rate and increased accumulation of photosynthetic products (relative to the cultivar D3).

1. Introduction

Abscisic acid (ABA) acts as a signal that regulates plant growth and development relative to changes in water and nitrogen qualities and quantities [1,2]. Changing ABA concentrations in leaves and grains signal and regulate plant photosynthetic machinery and grain filling. A suitable ABA concentration is essential for improving the photosynthetic machinery in leaves and for promoting the transport of photosynthates to grains [3,4]. In higher plants, ABA is ubiquitous and potentially plays an important role in the adaptation of these plants to different environmental stresses [5,6]. On the one hand, ABA acts as an endogenous messenger that regulates the water status of plants to initiate adaptive responses to changing water availability during their life cycle [7,8]. On the other hand, ABA concentration in tissue is affected by nitrogen availability [9]. Thus, the quantities of water and nitrogen in the soil are important for regulating the biosynthesis of ABA in plants [10,11].

Aldehyde oxidase (AO, EC 1.2.3.1) catalyzes the final step of ABA biosynthesis and is expressed in both leaves and grains. The presence of AO confirms that ABA can be produced in leaves and grains [5,12]. The delivery of AO from the roots and the biosynthesis of AO in the leaves contribute to the local accumulation of ABA in

Abbreviations: ABA, abscisic acid; AO, aldehyde oxidase; Z and Z958, Zhengdan 958; D and D3, Denghai 3; R, rototilling for stubble breaking; S, subsoiling after rototilling for stubble breaking; C, 225 kg N hm^{-2} controlled release urea; U, 225 kg N hm^{-2} conventional urea; Pn, net photosynthetic rate; gs, stomatal conductance; WUE, water use efficiency; PNUE, photosynthetic nitrogen use efficiency; R_0, initial filling potential; Gmax, max grain-filling rate; Gmean, mean grain-filling rate; DAF, days after flowering.

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response to nitrogen status. The accumulation of ABA in maize during nitrogen deficiency is caused, in part, by the up-regulation of AO [9]. Moist soil conditions are beneficial for nitrogen uptake. Thus, both the soil nitrogen concentration and water status play important roles in plant AO activity.

Water and nitrogen management are two of the most important factors for crop production [13]. However, water shortages occur around the world and are serious problems. China is one country that must cope with water shortages, particularly in the north and northwest regions. It is widely believed that increasing agricultural water use efficiency will mitigate water shortages and reduce environmental problems [14]. Subsoiling may break up the plow pan and significantly increase the rainfall storage capacity of soils [15,16]. In addition, subsoiling may also increase rooting depth and promote water uptake by crop roots [17]. Thus, compared to conventional tillage, crop yields and water use efficiencies are greater after subsoiling [18]. In addition, nitrogen (N) fertilizer plays an important role in improving maize yields. However, excessive applications of N fertilizer to crops can decrease the nitrogen use efficiency [19,20] and degrade soil and water quality by increasing NO_3–N concentrations in the topsoil and groundwater [21]. Controlled release urea has many advantages over conventional fertilizers. For example, controlled release urea results in more efficient N uptake by plants compared to conventional fertilizers [22,23]. In addition, controlled release urea can reduce environmental pollution by matching nutrient release with plant demand [21,24]. Thus, subsoiling and controlled release urea are new and important water/nitrogen regulation technologies with broad application prospects. However, several questions exist regarding leaf and grain ABA regulatory mechanisms in plants following subsoiling and in the presence of controlled release urea.

The mechanism of ABA concentrations on photosynthesis and grain filling in response to soil water and nitrogen levels is unknown. Furthermore, the relationships between AO activities and ABA concentrations as well as the relationships between leaf ABA concentrations and grain ABA concentrations are not clear. Therefore, the objectives of this study were to investigate the effects of subsoiling and controlled release urea treatments on the abovementioned parameters and relationships as well as to determine if different responses occur between two cultivars with different water/nitrogen use efficiencies.

2. Results

2.1. Gas exchange, WUE, and PNUE

At the same nitrogen level, the controlled release urea (C) significantly increased the net photosynthetic rate (Pn) and the stomatal conductance (gs) after flowering relative to conventional urea (U) (Fig. 1). Subsoiling after rototilling (S) also significantly increased the Pn and gs in the Z958 and D3 cultivars.

The controlled release urea treatments decreased the water use efficiency (WUE) significantly between 10 and 30 days after flowering (DAF) in the Z958 and D3 cultivars. However, no significant changes between 40 and 50 DAF occurred in the Z958 cultivar (except for ZR at 50 DAF). In addition, no significant changes between 40 and 50 DAF occurred in the D3 cultivar, except for the DR. At the same nitrogen level, subsoiling after rototilling decreased the WUE relative to rototilling for stubble breaking in the Z958 and D3 cultivars, however, there were no significantly differences in ZC at 10 and 50 DAF, in DC at 50 DAF, and in ZU and DU at 20 and 30 DAF (Fig. 2A–D).

In the same crop system, controlled release urea treatments significantly increased the photosynthetic nitrogen use efficiency (PNUE) for the Z958 and D3 cultivars (Fig. 2E–H). At the same nitrogen level, subsoiling treatments increased PNUE in the both cultivars, however, no significant differences for PNUE were noted in the ZU treatments at 10 and 40 DAF, in the ZC treatments at 50 DAF, and in the DC treatments between 10 and 50 DAF.

2.2. ABA concentration

The leaf ABA concentrations in both cultivars increased in the growth stages after flowering (Fig. 3A–D). In the same crop system, the ABA concentrations significantly decreased in response to controlled release urea treatments in both cultivars. When the same type of nitrogen fertilizer was used, the ABA concentrations significantly decreased for subsoiling treatments in both cultivars, except for ZSU.

Grain ABA concentrations in the controlled release urea treatments were higher than in the conventional urea treatments for both cultivars. When the same type of nitrogen fertilizer was used, the grain ABA concentrations of the subsoiling treatments were significantly higher than the rototilling treatments at 21–30 DAF, the results were opposite at 41–50 DAF in both cultivars (Fig. 3E–H).

2.3. Aldehyde oxidase (AO) activity

In ear leaves, the conventional urea treatments significantly increased the average AO activities relative to the controlled release urea treatments in both cultivars after flowering (Fig. 4A–D). The average AO activities under rototilling were greater than that of subsoiling for both cultivars, except for ZRC $<$ ZSC. The average AO activities of the Z958 cultivar were significantly higher than that of the D3 cultivar, except for ZRC $<$ DRC.

In grains, the conventional urea treatments resulted in lower average AO activities compared to the controlled release urea treatments in both cultivars after flowering, except for ZRC $<$ ZRU (Fig. 4E–H). In addition, the average AO activities under the rototilling treatments were greater than under the subsoiling treatments for both cultivars. The average AO activities in the Z958 cultivar were significantly lower than those in the D3 cultivar.

2.4. Relationships between grain and leaf ABA concentrations

A positive correlation ($P < 0.001$) between grain and leaf ABA concentrations was observed in both cultivars and across all cropping systems and nitrogen treatments (Fig. 5).

2.5. Relationships between Pn/gs/PNUE/WUE and ABA concentrations

In ear leaves, the ABA concentrations were inversely correlated with the Pn and gs in all treatments for both cultivars. The correlation coefficient reached a significance level of 0.01 for all treatments (Table 1). In addition, significant inverse correlations occurred between ABA concentrations and PNUE. Furthermore, both cultivars reached a significance level of 0.01 across all treatments, expect for ZSC and DSU (DSU reached a significance level of 0.05). However, no significant correlations between ABA concentrations and WUE occurred, except in the ZRC and ZSC treatments.

2.6. Relationships between gs/PNUE/WUE and Pn

Positive correlations between the gs and Pn in both cultivars were observed in all cropping systems and nitrogen treatments (Fig. 6). However, the slopes of these correlations were greater in the Z958 cultivar than in the D3 cultivar. The correlations of ZRU, ZRC, ZSU, ZSC and DRU reached a significance level of 0.001, and the correlations of DRC, DSU, and DSC reached a significance level of