Drought-Hardening Improve Waterlogging Tolerance of Maize at Seedling Stage

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Abstract

This study aimed to investigate the stress tolerance of maize by exploring the changes in abscisic acid (ABA) concentration, biomass accumulation, and transpiration rate of maize exposed to drought and waterlogging stress; The experiment was conducted in a controlled greenhouse by setting up a total of 17 treatments of water stress, waterlogging stress, and drought stress followed by waterlogging. A completely randomized block design was employed; Waterlogging limited the formation of maize biomass more than that by water stress. Waterlogging alone (W) inhibited more strongly the growth of the aboveground part than of the underground part, causing a decrease in the canopy-to-root ratio. However, the canopy-to-root ratio increased under waterlogging after drought. Under drought and waterlogging stress, the ABA concentrations of maize leaves and roots changed gradually, decreasing from the leaves to the root base, then middle root, and finally root tip. Early water stress had a greater effect on leaf ABA concentration than on root ABA concentration, and leaves were the most sensitive to drought stress. Root system was more sensitive to drought stress followed by waterlogging; Moderate controlled drought at the seedling stage can improve their resistance to subsequent waterlogging stress, but the subsequent water-logging stress should not last more than 7 days.

1. Introduction

Environmental stresses restrict agricultural development worldwide, which are therefore perpetual topics for discussion. Drought, flood and their secondary disasters are the top issues restricting agricultural development and seriously decrease crop growth and yield [1–5]. Drought stress in early crop growth can promote the emergence of certain metabolites and structural functions in later crop growth, which is beneficial to the improvement of crop stress resistance [6]; for example, it enhances the ability of crop roots to extend into deeper soil layers [7], adjusts the stomatal opening to reduce water loss owing to transpiration [8], and changes the biological properties [9, 10]. One important physiological response of crops after a drought is the change in the abscisic acid (ABA) concentration, which is considered a characteristic indicator of drought stress in crops. Under drought stress, ABA is synthesized and transported in crop tissues, where it synergistically interacts with water to mediate crop stomatal opening and maintain water balance in crop plants [8, 11]. The degree of damage brought by drought to crops depends on the soil water holding capacity, crop type, growth stage, etc. Timely replenishment of water after a drought will enable the crops to recover their growth, whereas excessive water supply after a drought will easily cause waterlogging. Waterlogging weakens the respiration of crop roots and impairs or prevents early stomatal conductance in crops, which is therefore not conducive to stress hardening of crops [11]. Under controlled conditions, crops can receive appropriate amounts of water supply in a timely manner after a drought. However, under the current frequent global extreme climate events, spring drought is often accompanied by rainy weather. The seedling stage of maize coincides with spring droughts and rainy weather, and the seedlings are thus exposed to damaging effects of rainwater logging. Humans are still unable to eliminate the risks of rainwater logging in a timely manner, i.e., they are often able to quickly eliminate waterlogging, but it takes some time for field waterlogging to drop to

safe water levels. Therefore, sustainable and efficient agricultural production in dry areas urgently requires a solution to keep and moderate field drought and waterlogging under real-time control in extreme weather to stimulate the stress resistance of crops and reduce the damage to their growth. This study aimed to investigate the tolerance of maize seedlings to drought and waterlogging stress. To that end, maize seedlings grown in a greenhouse under constant temperature were exposed to drought and waterlogging stress to determine ABA concentrations and physiological responses.

2. Results

2.1. Biomass changes

Leaf area is directly related to crop respiration, photosynthesis, and biomass. Too large or too small leaf area will affect the improvement of crop yields. This study showed that for maize at the seedling stage, 65%-Wi and 75%-Wi treatments had no significant effect on leaf area. In contrast, waterlogging after severe water stress (55%) affected leaf area development, and waterlogging alone (W) significantly inhibited leaf extension (Figure 1).

The most direct effect of stress on plants is the inhibition of crop growth and biomass reduction. In this study, the effects of waterlogging after drought on maize biomass accumulation at the seedling stage varied. The leaf dry matter in different treatments after one day of post-drought waterlogging were ranked as follows: 65%-W1 > 55%-W1 > 75%-W1 > W. After three days of post-drought waterlogging, the leaf mass in treatment 55%-W3 quickly increased. After five days of post-drought waterlogging, the leaf mass in 65%-W5 was close to the control level. Treatment W showed a significant inhibitory effect on leaf mass accumulation (Figure 2 (a)). Waterlogging-alone (W) treatment showed a significant inhibitory effect on stem and root biomass accumulation, whereas post-drought waterlogging had no significant effect on stem biomass accumulation (Figure 2 (b)). Different degrees of drought and waterlogging stress had a greater impact on the root system when compared with that of stem and leaves of maize at the seedling stage. In Phase I, root biomass increased with water stress: the biomass of the root system under water stress was higher than that under waterlogging-alone (W) stress.

During the post-drought waterlogging stress in Phase II, the root biomass accumulation rate in treatment 65%-Wi increased significantly, the highest root biomass was measured in 65%-W10 treatment, followed by that in 55%-W10. However, the root biomass under waterlogging-alone (W) stress and higher water content (75%) was relatively small, showing that waterlogging alone or high-water content was not conducive to root development, drought treatments followed by waterlogging inhibited the root biomass accumulation (Figure 2 (c)). The canopy-to-root ratios in different treatments at the end of Phase I were reduced gradually with reducing soil water content from 75% to 55% field capacity.

After 10 days of waterlogging in Phase II, the canopy-to-root ratio was the lowest in waterlogging-alone (W) treatment and the highest in 75%-W10, whereas those in 65%-W10 and 55%-W10 treatments did not significantly differ from the control (Figure 2 (d)).

2. 2. Changes in ABA concentration

Soil water stress can change the physiological properties of crops and thereby increase the ABA concentration in xylem sap of crops. The change in ABA concentrations can be adjusted or corrected via different irrigation methods to optimize the water use efficiency of crops [12, 13]. Under the stress of drought followed by waterlogging, the ABA concentrations of maize leaves and roots decreased gradually from the leaves to the root base, middle root, and root tip (Figure 3). The greater the water stress, the higher the foliar ABA concentration and the larger the difference between the treatments ($P < 0.05$). ABA concentration of the root system did not significantly differ between the treatments in Phase I ($P < 0.05$), but it was more affected by water stress than by waterlogging. In Phase II, different durations of waterlogging had different effects on the ABA concentrations of maize. The plant ABA concentration in 75%-Wi treatment gradually decreased with prolonged waterlogging. The leaf and root ABA concentrations under 75%-W1 treatments were significantly higher than those after 3 to 7 days of waterlogging. There was no significant difference in leaf and root ABA concentrations after 3, 5, and 7 days of waterlogging. From the first to fifth day of waterlogging, the plant ABA concentrations in 55%-Wi and 65%-Wi treatments decreased with prolonging the waterlogging. During the same period, the ABA concentration of the plant segment from leaves to the root base significantly varied with different durations of waterlogging, whereas that of the segment from the middle root to the root tip did not significantly vary with different waterlogging periods. The seventh day of waterlogging resulted in the lowest leaf ABA concentrations but the highest root ABA concentration in 55%-W7 and 65%-W7 during the waterlogging period, especially, the ABA concentration increased significantly in the segment from the middle root to the root tip in 65%-W7. The leaf ABA concentration in the waterlogging-alone (W) treatment decreased as the duration of waterlogging increased from 1 to 5 days but rebounded to the highest value on day 7 of waterlogging. In the waterlogging-alone environment, the leaves responded after 7 days of waterlogging stress, whereas the root ABA concentration did not respond to waterlogging stress.

It can be observed from the gradients of ABA concentrations that the leaf ABA concentration increased with the increase in early water stress and so did the ABA concentration of the plant segment from the leaves to roots. The ABA concentration of the leaves was more sensitive to the water environment than that of the roots.

2. 3. Changes in leaf stomata and plant transpiration

Figure 4 shows changes in leaf stomata and plant transpiration under drought and waterlogging stress. Stomatal conductance of leaves under moderate and low water control (65% and 55%) and waterlogging-alone (W) stress was inhibited in Phase I. Stomatal conductance under treatments of waterlogging after drought stress increased on the first to third day of Phase II, and then showed a downward fluctuating trend. In 65%-Wi treatment, the stomatal conductance fluctuated the most from days 3 to 7 of waterlogging. On the fourth to fifth day of waterlogging, the stomatal conductance gradually decreased, whereas the transpiration gradually reached a peak. The stomatal conductance in 75%-Wi treatments

fluctuated greatly within a short period and lagged behind the stomatal conductance observed in 65%-Wi treatment. The stomatal conductance in other treatments fluctuated slightly (Figure 4 (a)).

3. Discussion

Drought and waterlogging are frequent natural disasters in spring and summer. The most direct effect of stress on crops is to inhibit crop growth and reduce biomass [14, 15]. Therefore, biomass is often used as an important measure of crop resistance to stress. In this study, watering at 65% field capacity had the most prominent advantage in terms of the leaf, stem, and root dry matter. Waterlogging alone (W) showed a significant inhibitory effect on the biomass of maize stems, leaves, and roots, indicating that maize at the seedling stage was more resistant to waterlogging stress after one week of water stress hardening (Fig. 1). Therefore, early moderate drought helps to alleviate or improve the effect of subsequent waterlogging on crop biomass, thereby improving crop resistance to subsequent waterlogging. This, in turn, lays a good foundation for promoting crop yield and ensuring economic benefits [16–18]. The canopy-to-root ratio can reflect the sensitivity of crops to stress. The ratio depends on the duration of the stress, and it is considered an adaptation mechanism to stress [19]. Research has revealed that some crop growth characteristics recovered to the control levels in 7 days after a continuous drought followed by waterlogging [20, 21], and another study showed that ABA synthesis induced by water stress is related to the canopy-to-root ratio [19]. Therefore, the canopy-to-root ratio is another important measure in studies of crop response to environmental stress. The results of the present study showed that in Phase I, greater water stress had a greater effect on the growth of shoots and leaves above ground and generated a more developed root system; on the seventh day of waterlogging after drought (65%-Wi and 55%-Wi) in Phase II, the canopy-to-root ratio was close to the control level (Fig. 1 (d)). The canopy-to-root ratio reflected the physiological regulation effect of crops under stress of drought followed by waterlogging. The main hazard of waterlogging is the inhibition of root function. The early water stress promoted the growth of the root system and expanded the extent of the root functional zone, which laid a good physiological foundation for the hardening of crop viability under later waterlogging stress and had a buffering and regulating effect on later maintenance of waterlogging damage to the root zone. Increasing dry matter accumulation is the main way to improve the crop harvesting potential [22]. In contrast, soil moisture regulation is an important means to interfere with crop product formation. Excessive irrigation or waterlogging stress will cause obvious changes in crop morphology, which is the most intuitively characterized by the deterioration of leaf photosynthesis and corresponding reduction of transpiration [14]. The present study found that maize transpiration was related to the level of drought and waterlogging. The transpiration of maize under drought stress followed by waterlogging was higher than that under waterlogging alone (W). When there was no significant change in stomatal conductance, the daily plant transpiration decreased by 28.41% on the fifth day and by 30.13% on the seventh day of the waterlogging-alone (W) treatment at the seedling stage of maize. The small leaf area under waterlogging alone resulted in a small number of stomata and thereby low transpiration rate. In 65%-Wi, the stomatal conductance gradually decreased on the fourth to fifth day of waterlogging, while at the same time the transpiration gradually reached a peak. The difference in plant transpiration among

different treatments under drought stress followed by waterlogging become insignificant starting from day 7 in Phase II, reflecting the hardening of maize to water stress. The physiological stress resistance function manifested itself within 7 days of waterlogging after a drought.

As a stress hormone, ABA plays a very important role in regulating the growth and development of plants, especially in many physiological processes of abiotic stress response (such as high salt, low temperature, and drought) [20]. Studies suggest that a variety of abiotic stresses can cause increased ABA concentrations in plants [19, 23]. Under water stress, the root system is the first part to sense changes in soil moisture. The plant ABA concentration originates from the root system, and its change is, therefore, stimulated by soil water stress [13]. Therefore, the change in plant ABA concentration is usually regulated or corrected through different irrigation methods to optimize crop water use efficiency [12]. In this study, water control followed by waterlogging led to a gradual change in the ABA concentration of maize leaves and roots. Specifically, the ABA concentrations decreased from leaves to the root base, then middle root, and finally root tip. The root system is the source of drought stress signals. Such signals accumulate and spread to the leaves along with the sap flow. Therefore, the leaf becomes the end point of ABA signal accumulation and witnesses the highest ABA concentration. The root system had higher ABA concentrations in 65%-Wi and 55%-Wi than under waterlogging alone (W) on day 7 of waterlogging in Phase II, indicating that drought followed by waterlogging elicits root production of stress signal and changes the physiological properties of the root system. Early water stress awakened the physiological response of maize to the subsequent waterlogging stress. Drought stress had a mediating effect on the physiological functions of maize, and this effect manifested itself in the subsequent stress. Studies on other plants have found that stomatal conductance and transpiration rate of plants are slightly or significantly reduced by drought stress and recover to varying degrees within 15 days of re-hydration [9, 24]. Drought stress inhibits the increase in leaf area. After rehydration starts, the leaf area shows a short and rapid increase, and the dry matter accumulation rate increases, resulting in compensatory growth effects [9, 25–28]. In the present study, the ABA concentration of leaves under water stress (55% and 65% field capacity) was significantly higher than that under non-stress treatments (75% field capacity). With the increase in water stress, the ABA concentration of leaves increased, the leaf stomatal conductance and plant transpiration decreased, but the inhibitory effect of water stress on leaf area and dry matter was not significant. On day 1 to 5 of waterlogging, the ABA concentration in the stem between the leaves and the root system increased with increasing water stress. In this period, the leaf stomatal conductance, plant transpiration, and dry matter under 65%-Wi treatment was also recovered and increased, whereas the recoverability of these indexes in 55%-Wi treatment was relatively weak. On day 7 of waterlogging, while the leaf ABA concentration continued to decrease, the physiological function of the root system was induced and stimulated, resulting in increased root ABA concentration. Consequently, the ABA concentration gradient between leaves and roots decreased, and the ABA concentrations of leaves and roots were relatively balanced. The leaf stomatal conductance and plant transpiration in 65%-W7 and 55% -W7 treatments slowly decreased. The dry matter accumulation rate in 65%-W7 slowed down, and that in 55%-W7 decreased significantly. Rehydration effects occurred within 5 days of waterlogging after moderate drought stress (65% field capacity), and each parameter increased to the compensation point. A

more severe water stress (55% field capacity) reduced the compensation effect, which is not conducive to biomass formation. After 7 days of waterlogging following drought stress, the negative effects of waterlogging stress began to appear. Therefore, waterlogging stress after a drought period at the seedling stage of maize should not exceed 7 days.

4. Materials And Methods

4.1. Experimental design

The experiment was conducted in a temperature-controlled greenhouse with PPFD of $400 \sim 600 \mu\text{mol m}^{-2}\cdot\text{s}^{-1}$, 14 h photoperiod, and day and night temperature of $19 \sim 24^\circ\text{C}$. Maize variety sweet corn F1 Early Sunglow, a commercialized seeds acquired from the lab in Environment Centre, Lancaster University, was planted in black cylinders made of PVC plastic, with an outer diameter of 6.6 cm, thickness of 2 mm, and height of 24.5 cm. The bottom of each cylinder was sealed with a stainless-steel net to facilitate drainage and stabilize the cylinder. The cultivated organic loam John Innes No. 2 was used as experimental soil. This soil type is traditional British soil compost containing loam, sphagnum peat, grit, humus, and fertilizers that promote healthy growth of plants. Owing to its good performance, John Innes No. 2 has been widely used in the UK for more than 60 years. Each cylinder was filled with 1050 g of the experimental soil. The soil was filled and compressed in layers so that the soil bulk density in each cylinder was the same. Each cylinder was filled with soil to about 2.5 cm below its edge. Two maize seeds were sown in each cylinder and watered with 50 mL of water. The water amount was determined with a measuring cup. During the waterlogging test, the soil in each pot was covered with a plastic to prevent water from seeping out.

Soil water was controlled from the three-leaf stage of maize, and the experiment was divided into two phases, i.e., Phase I (7 days) and Phase II (10 days). In Phase I, the soil water content was kept at 55%, 65%, and 75% of the field capacity; in the waterlogging-alone (W) treatment, a water layer of 1 cm was maintained on soil surface. In Phase II, the treatments from Phase I were subjected to waterlogging for 1, 3, 5, 7, and 10 days (55%-Wi, 65%-Wi, and 75%-Wi, where i is the number of days a plant was subjected to waterlogging; Table 1). The treatment of water control at 75% field capacity (optimal soil water content for growth of maize) was used as a control. There were 17 treatments in total, each repeated three times.

Table 1
Experimental settings

Treatment No.	Treatment count	Phase I (7 days)	Phase II (≤ 10 days)
75%	1	75% field capacity	75% field capacity(10 days)
75%-Wi	5	75% field capacity	Waterlogging after 7 days of water control at 75% field capacity, $i = 1, 3, 5, 7, 10$ d
65%-Wi	5	65% field capacity	Waterlogging after 7 days of water control at 65% field capacity, $i = 1, 3, 5, 7, 10$ d
55%-Wi	5	55% field capacity	Waterlogging after 7 days of water control at 55% field capacity, $i = 1, 3, 5, 7, 10$ d
W	1	Waterlogging	Waterlogging(10 days)

W_i is the waterlogging at specific days and W is the waterlogging alone.

4.2. Methods

During the experiment, the top of each cylinder was sealed with tin foil to expose only the maize plants. The total mass of the cylinders was weighed every morning from 8:00 to 9:00 to calculate the daily water loss owing to plant transpiration. The lost water was then supplemented. Maize was harvested at the end of the experiment. Aboveground parts of the seedlings were cut and separated into stem and leaves in each pot. The soil from each pot with the root zone was divided into four segments: 0 ~ 5 cm, 5 ~ 10 cm, 10 ~ 15 cm, and 15 ~ 22 cm from the soil surface. The roots in each segment were then washed.

Leaf area was measured by an automatic leaf area meter. Stem, leaf, and root samples were dried at 65 °C for 72 h, and their dry matter was then determined.

ABA concentration in leaves and roots was measured by radioimmunoassay using the monoclonal antibody AFRC MAC 252 [29]. The youngest and fully expanded leaflet was harvested for ABA measurement. The sampling was conducted at the same time (10:00 ~ 10:30) on each harvesting day to avoid diurnal effects on foliar ABA concentration. Leaflets and roots (of the same plant) were sampled, frozen in liquid nitrogen, freeze-dried for 48 h, and then finely ground. Small amounts of samples (10 ~ 15 mg dry weight for leaflets, and 30 ~ 40 mg dry weight for roots) were used for ABA analysis. The powdered samples were diluted with deionized, distilled water (1:70 for leaflets, and 1:25 for roots) and placed on a shaker in a cold room (4°C) overnight to extract ABA. A standard curve was determined with standards in a serial dilution of synthetic unlabeled ($\pm$)-cis, trans-ABA (Sigma Let., Dorset, UK). ABA concentration was calculated by reference to the standard curve after linearization using the 'logit' transformation.

4.3. Statistical analysis

All data were analyzed by one-way analysis of variance (ANOVA). Less significant difference (LSD) and Student's t-test were carried out ($P < 0.05$) using Statistica 10.0 (StatSoft, Inc., Tulsa, OK, USA).

5. Conclusions

At the seedling stage of maize, early moderate water stress (65% field capacity) promoted leaf biomass accumulation under subsequent waterlogging stress. The canopy-to-root ratio under drought stress followed by waterlogging was higher than that under waterlogging alone (W). The solid matter foundation improved the stress resistance of maize under drought stress followed by waterlogging. Under drought and waterlogging stress, the ABA concentration of maize leaves and roots gradually decreased from leaves to the root base, then middle root, and finally root tip. Maize leaves were the most sensitive to drought stress, and the root system had a certain response to post-drought waterlogging. At the seedling stage, moderate drought stress on maize had a mediating effect on its physiological functions, and this effect manifested itself under later stress. Physiological rehydration effects occurred in maize crops within 5 days of waterlogging after moderate drought (65% field capacity), and the biomass witnessed a compensatory increase. A more severe stress (55% field capacity) reduced the compensatory effect. Starting from day 7 of waterlogging that was conducted after water stress, damage to maize crop owing to waterlogging stress began emerge. Therefore, the waterlogging stress should not exceed 7 days after a drought at the seedling stage of maize.

Declarations

Author Contributions: Conceptualization, C.L., methodology, J.S., software, G.W. and Q.H, formal analysis, C.L. and A.K.M.H., investigation, C.L., data curation, H.N., writing—original draft preparation, C.L., writing—review and editing, A.K.M.H., funding acquisition, J.S. and Z.L. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Conflicts of Interest: The authors declare no conflict of interest.

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Figures

Figure 1

Effects of drought and waterlogging stress on maize leaf growth

Figure 2

Changes in maize biomass under drought and waterlogging stress

Figure 3

Changes in ABA concentrations under drought and waterlogging stress

(a) Stomatal conductance

(b) Transpiration

Figure 4

Changes in stomatal conductance and plant transpiration under drought and water-logging stress