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Effects of drought and rehydration on the growth and physiological characteristics of mustard seedlings

Peipei JIA[1,2], Andrii MELNYK[2] (✉), Lijie LI[1], Xiangjun KONG[1], Haifang DAI[1], Zhiyong ZHANG[1], Sergey BUTENKO[2]

[1] School of Life Science and Technology, Henan Institute of Science and Technology, Hualan St. 90, 453003, Xinxiang, People's Republic of China

[2] Department of Agronomy and Agricultural Technology, Sumy National Agrarian University, Herasyma Kondratyeva St. 160, 40021, Sumy, Ukraine

✉ Corresponding author: melnyk_ua@yahoo.com

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ABSTRACT

The mustard variety Felicia was used to analyze the response and compensation effects of growth and physiology under drought stress and rehydration conditions at the seedling stage. The seedlings were exposed to different levels of drought stress simulated by polyethylene glycol (PEG). The growth parameters, fresh weight, chlorophyll fluorescence, and antioxidant system were measured. The results showed that drought stress inhibited the growth of roots and shoots and reduced the performance of photosystem II (PS II). After rehydration, the root length and fresh weight of plants rapidly increased, and the performance index (PI_{ABS}) was found to be higher compared with the control, which suggested a compensative effect. The chlorophyll content was significantly reduced under moderate and severe drought stress. However, it increased under mild stress conditions. After rehydration, the chlorophyll content under moderate and severe stress did not return to the levels of control, and there was no significant difference between mild stress and the control. Under drought stress, the activities of antioxidant enzymes and content of malondialdehyde (MDA) increased significantly in the leaves. After rehydration, MDA and the activities of antioxidant enzyme were higher than those of the control group, particularly under moderate and severe stress. Therefore, these results suggest that mustard is strongly adapted to mild drought stress through the efficient activities of antioxidant enzymes activity and photosynthesis, as well as its rapid recovery after rehydration.

Keywords: mustard, drought stress, rehydration, chlorophyll fluorescence, antioxidant enzyme activity

INTRODUCTION

In the current scenario of global climate change, drought stress has become a challenging problem and is threatening sustainable agricultural productivity worldwide. Water deficit disturbs various physiological and biochemical traits and adversely affects the growth and productivity of crop plants (Maevskaya and Nikolaeva, 2013; Furlan et al., 2014). Under natural conditions, plants are often exposed to an environment in which they are subjected to alternating drought and rehydration. Plant adaptability includes not only drought tolerance but also a process of recovery after rehydration that improves growth and physiological metabolism (Dong et al., 2019). Therefore, studying the dynamic growth and physiological responses of plants under drought and rehydration conditions can facilitate a better understanding of the adaptive mechanism of plants.

Although drought restricts plant growth and development, plants exhibit growth compensation or overcompensation after some level of drought stress and rehydration (Dong et al., 2019; Iovieno et al., 2016; Bu et al., 2009; Jin et al., 2015). The plant compensation effect usually makes up for the loss caused by stress. A PS II study of maize leaves found that the rehydration compensation effect reached its maximum on the sixth day after drought treatment (Gao et al., 2016). Studies of soybean (Dong et al., 2019) and *Brassica carinata* (Husen et al., 2014) showed that plants can exhibit compensation on the root length, leaf area, and the number of leaves after some level of drought stress and rehydration. An increase in the number of tillers after rehydration is necessary for the adaptation of rice to drought–prone environments (Okami et al., 2015). In sorghum, the chlorophyll content, water potential, and osmotic potential recovered to or even exceeded the level of control after rehydration (Liu et al., 2018). Antioxidant enzymes play a crucial role in scavenging the reactive oxygen species (ROS) generated by stress conditions. The synthesis and increase of antioxidant enzymes can reduce the damage to plant cells from ROS, and enable the plants to quickly recover after rehydration (Men et al., 2018). In *Artemisia halodendron*, the chlorophyll content, membrane permeability, activities of superoxide dismutase (SOD) and catalase (CAT), and the contents of the three osmoregulatory substances began to recover under moderate drought stress and rehydration (Chen et al., 2019). As a product of membrane lipid peroxidation, the content of malondialdehyde (MDA) can reflect the degree of damage to the cell membrane. The decrease in hydrogen peroxide (H_2O_2) and content of MDA during the post-drought recovery of tea seedlings indicated that rehydration reduced the negative effects of drought stress (Upadhyaya and Panda, 2004).

Mustard is widely cultivated for its prominent economic value and unique flavor (Husen et al., 2014). In recent years, abiotic stresses, including a limited supply of moisture, high transpiration, and continuous high temperature, have been detrimental to the healthy growth of mustard. Previous studies primarily focused on assessing the effects of drought stress on the growth and physiology of *Brassica* (Alam et al., 2013; Hossain and Fujita, 2013). However, few studies have been reported on the physiological responses that occur after rehydration. This study was designed to examine the effects of drought stress and rehydration on growth, photosynthesis, and antioxidant system of mustard. These results should provide a better theoretical basis for the ability of mustard to adapt to drought stress.

MATERIALS AND METHODS

Plant materials and stress treatments

The mustard variety Felicia was used in the experiment, and was provided by the Department of Agronomy and Agricultural Technology of Sumy National Agrarian University, Sumy, Ukraine. The mustard seedlings were grown in a plastic container (40×28×14 cm) with 5 L Hoagland's solution in an artificial climate chamber at the Henan Institute of Science and Technology, Xinxiang, China. The temperature was set to 28/23 °C and a light cycle of 14/10 h (day/night) with a relative humidity of 40 to 50%. Drought stress was induced by the addition of PEG. The following treatments were used: (1) control (CK) – Hoagland's solution; (2) mild drought –10% PEG + Hoagland's solution; (3) moderate stress – 15% PEG + Hoagland's solution; (4) severe stress – 20% PEG + Hoagland's solution. After 9 days, all the drought treatments were transferred into Hoagland's solution and cultured for 6 days after they were rehydrated to the CK treatment level. Samples were measured 3, 6, and 9 days after drought treatments and 6 days after rehydration.

Plant growth parameters

The roots and shoots of the seedlings were separated and washed with tap water. After blotting with a clean towel, the fresh weight (FW) and length of the roots and shoots of five plants in each treatment were measured manually.

Chlorophyll content and chlorophyll fluorescence

A Dualex chlorophyll meter (Force-A, Orsay, France) was used to measure the relative chlorophyll content of the intact expanded leaf on bottom of the plant. A portable fluorometer (PEA, Hansatech Instruments Ltd, King's Lynn, UK) was used to determine the maximal photochemical efficiency (F_v/F_m) and performance index (PI_{ABS}). The expanded leaves of five plants were measured after half an hour of dark adaptation per treatment.

Enzyme assays and the determination of lipid peroxidation

All leaf samples were excised from the third or fourth fully expanded leaves at the bottom of the plant, and roots were collected from the tips of taproot. Lyophilized leaf (0.50 g) and root (0.50 g) powder were homogenized with 5 mL of 100 mM potassium phosphate buffer (pH 7.5) that containing 1 mM EDTA and 1% polyvinylpolypyrrolidone (PVPP). The homogenate was centrifuged at 12,000 g for 20 min at 4 °C, and the supernatant was used as a crude extract for protein, enzyme activity, and lipid peroxidation assays. The entire extraction procedure was conducted at 4 °C.

The soluble protein content was detected using Coomassie brilliant blue G250 (Bradford, 1976). A total of 30 µl supernatant and 170 µl of 0.12 mM Coomassie brilliant blue G250 were mixed, and the absorbance was read at 595 nm. Bovine serum albumin was used as the standard. The activity of SOD was assayed by its ability to inhibit the photochemical reduction of nitroblue tetrazolium chloride (NBT) at 560 nm. The activity was expressed as U/g FW*min (Beauchamp and Fridovich, 1971). The activity of peroxidase (POD) was determined using the guaiacol oxidation method (Kochba et al., 1977). The absorbance of the mixture was determined within 3 min at 470 nm. The activity of CAT was determined as described by Neto et al. (2006) with modifications. The activity of CAT was calculated based on the rate of disappearance of H_2O_2, which was followed as a decline in the absorbance at 240 nm measured 4 min after the addition of H_2O_2. The activity of ascorbate peroxidase (APX) was determined as described by Nakano and Asada (1981). The absorbance of the mixture was measured at 290 nm. Lipid peroxidation was determined as described by Rao and Sresty (2000). The content of MDA was calculated as nmol/g FW.

Statistical analysis

All the collected data are shown as the mean values ± SD (standard deviations). A statistical analysis was performed using SPSS 22.0 (IBM, Inc., Armonk, NY, USA), and significant differences were analyzed using a one-way analysis of variance (ANOVA) with Duncan’s multiple range tests ($P<0.05$).

RESULTS

The effect of drought stress and rehydration on mustard growth

The growth parameters of mustard seedlings treated with different levels and durations of drought stress were investigated. Table 1 shows that drought stress inhibited seedling growth in terms of length and fresh weight. Moreover, the inhibitory effect significantly increased with an increase in the level and duration of drought. Compared with the control plants, all the drought treatments for 9 days significantly reduced the root length by 16.18%, 22.55%, and 28.67%, and the shoot length by 6.93%, 10.39%, and 18.48%, respectively. The relative growth rate of root and shoot lengths decreased significantly after 9 days of drought treatment, particularly under severe drought conditions. After 6 days of rehydration, the stressed plants partially recovered. For the growth rate of root length, the compensation effect under mild (2.46%) and moderate (11.77%) stress was greater than that of control (0.25%). However, the compensation effect in shoot lengths was not apparent after rehydration.

Drought stress significantly affected the fresh weight (FM) of roots and shoots compared with the control (Table 1). In all of the treated plants, 9 days of drought stress decreased the root fresh weight by 51.19%, 82.29%, and 85.31%, and the fresh weight of shoots by 60.18%, 86.09%, and 88.73%, respectively. The relative growth rate of fresh weight of root and shoot decreased rapidly under moderate and severe stress. After 6 days of rehydration, growth rates of fresh weight in roots and shoots were higher than before rehydration. Under normal growth conditions, the relative growth rates of root and shoot fresh weight were only 36.5% and 3.82%, but there was an overcompensation of roots (82.93% and 191.19%) and shoots (172.55% and 347.58%) under moderate and severe stress, respectively.

Table 1. Effects of drought stress and rehydration on the growth and fresh weight of mustard seedlings

Growth parameters	Treatment	D0 Mean±SD	D3 Mean±SD	D6 Mean±SD	D9 Mean±SD	R6 Mean±SD	Growth rate% (D9 VS D0)	Growth rate% (D9 VS R6)
Root length(cm)	CK	37.67±3.06	38.75±3.5a	50.67±3.75a	51±2.65a	51.13±4.8a	35.40	0.25
	10%		39.13±9.82a	44.25±11.09ab	42.75±6.3a	43.8±2.08ab	13.50	2.46
	15%		38.88±3.47a	41.5±3.42ab	39.5±8.96a	44.15±6.11ab	4.87	11.77
	20%		37.38±7.18a	36.13±5.04b	36.38±5.94a	36.53±5.93b	-3.42	0.41
Shoot length(cm)	CK	3.46±0.50	3.43±0.83a	3.17±0.29b	4.33±0.67a	4.43±0.82a	24.90	2.31
	10%		3.75±0.5a	3.98±0.21a	4.03±0.53ab	4.1±0.47a	16.25	1.74
	15%		3.45±0.58a	3.88±0.63a	3.88±0.22b	3.95±0.91a	11.92	1.8
	20%		3.25±0.65a	2.45±0.42c	3.53±0.29b	3.55±0.46a	1.83	0.57
Root fresh weight(g)	CK	0.85±0.06	2.11±0.36a	4.27±0.18a	4.63±0.35a	6.32±0.81a	441.94	36.5
	10%		0.86±0.08b	1.95±0.76b	2.26±0.31b	2.42±0.57b	164.53	7.08
	15%		0.86±0.2b	1.21±0.39b	0.82±0.04c	1.5±0.52b	-4.02	82.93
	20%		1.1±0.13b	1.41±0.32b	0.68±0.1c	1.98±0.62b	-20.41	191.18
Shoot fresh weight(g)	CK	2.42±0.33	3.89±1.22a	5.84±1.04a	11±0.9a	11.42±1.29a	391.95	3.82
	10%		2.76±0.3ab	4.06±0.64b	4.38±0.43b	6.2±1.09b	95.89	41.55
	15%		2.84±0.51ab	3.2±0.22b	1.53±0.23c	4.17±0.87c	-31.57	172.55
			2.15±0.49b	3.65±0.5b	1.24±0.44c	5.55±0.42bc	-44.54	347.58

Mustard seedlings were measured on the 0, 3, 6, and 9th days of drought stress (D0, D3, D6, and D9), and the 6th day after rehydration (R6). Means ± SD, n = 5. Values in a column followed by different lowercase letters are significantly different at P<0.05 according to Duncan′s multiple range test

Changes in chlorophyll content and chlorophyll fluorescence

The chlorophyll content could reflect the level of photosynthesis to some extent and could further affect plant growth. The chlorophyll content changed in varying manners under different stress levels and stress times (Figure 1). Exposure to drought stress for 3 days resulted in an increase in chlorophyll content, particularly under mild and moderate stress by 25.74% and 11.87%, respectively. After 9 days of drought stress, the chlorophyll content decreased significantly by 12.84% and 21.95% under moderate and severe stress, respectively, but it was 14.69% higher than the control under mild stress. After 6 days of rehydration, the chlorophyll content of moderate and severe stress did not return to the control level. The leaf chlorophyll content after subjection to mild stress was lower than that before rehydration and did not differ from the control level.

Drought stress decreased the F_v/F_m and PI_{ABS} (Figure 2), and there was no significant difference between the drought-treated groups on day 3. With the extension of the stress to 9 days, the F_v/F_m and PI_{ABS} of the stressed plants were still lower than those of the control plants. Rehydration led to an increase in the PI_{ABS}, particularly under mild and moderate stress comprised 52.17% and 98.47%, respectively. However, the F_v/F_m did not return to control levels.

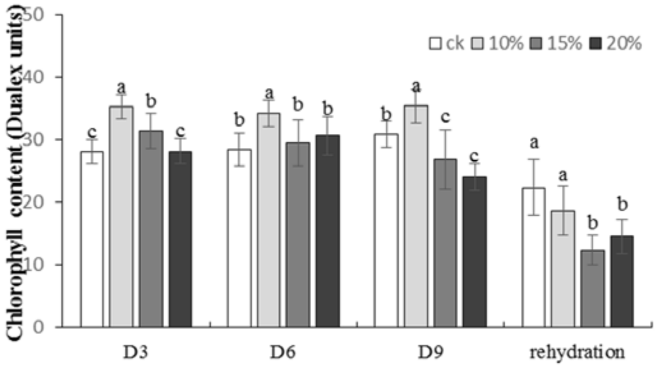

Figure 1. Effect of drought stress (D3: day 3 of drought, D6: day 6 of drought, D9: day 9 of drought) and rehydration on the leaf chlorophyll content. Values are means ± SD (n = 5). Means followed by different lowercase letters are significantly different at P<0.05 according to Duncan's multiple range test

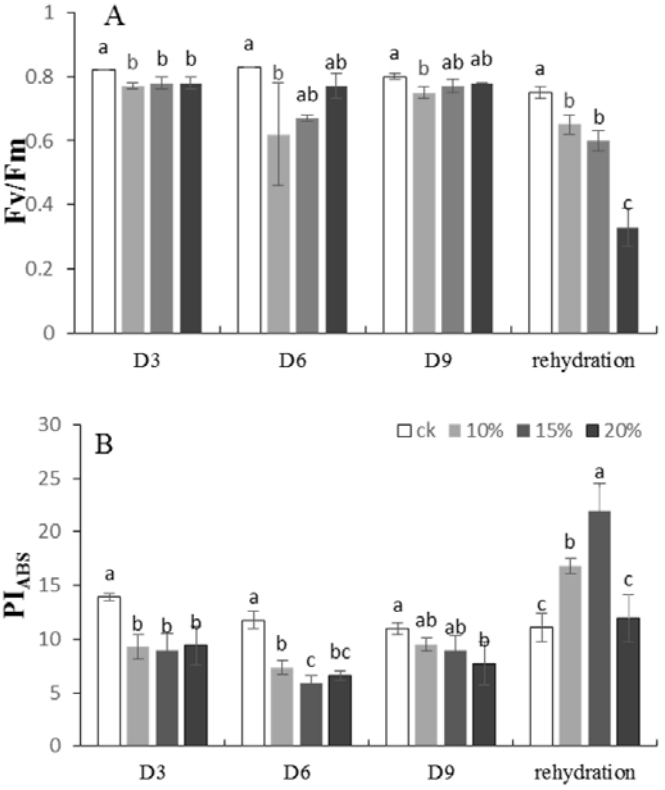

Figure 2. Effects of drought stress and rehydration on A: F_v/F_m, the maximal photochemistry of PS II; B: PI_{ABS}, performance index on absorption basis. Values are means ± SD (n = 5). Means followed by different lowercase letters are significantly different at P<0.05 according to Duncan's multiple range test

Changes in contents of soluble protein and malondialdehyde content

The results shown in Figure 3 indicate that 9 days of drought stress increased the soluble protein content in the roots and leaves. After rehydration, the soluble proteins in roots and shoots changed in different manners. The protein content of all treatments in the roots was significantly higher than that of the control by 42.68%, 70.89%, and 35.62%, while the protein content of mild and moderate stress in the leaves was 35.07% and 13.30% lower than that of the control.

In response to drought stress for 3 days, the content of MDA in treated leaves rapidly increased by 124.61%, 197.37%, and 303.29% compared with the control (Figure 4). With the prolongation of the stress period, the MDA content of all the stressed leaves decreased slightly, but it was still significantly higher (71.57%, 94.11%, and 131.68%) than the control level on the ninth day of stress.

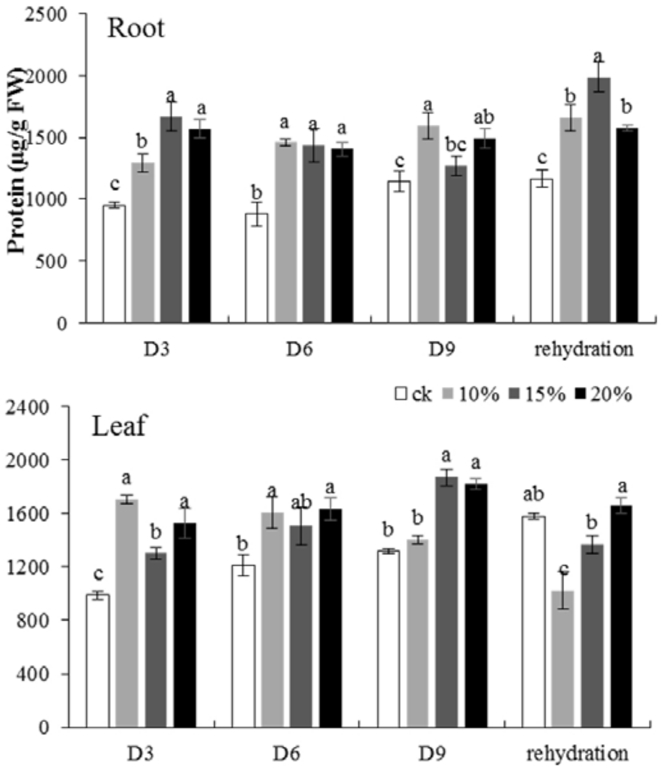

Figure 3. Effects of drought stress and rehydration on the soluble protein

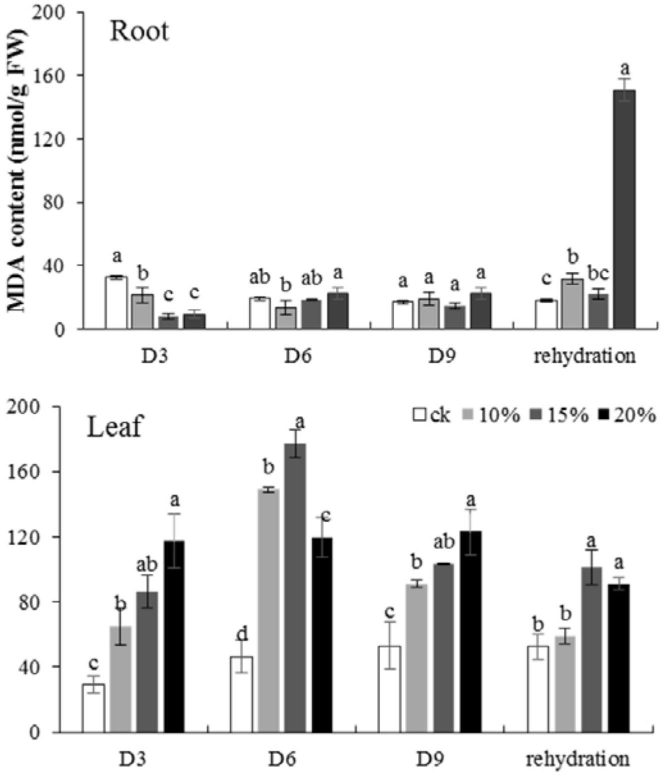

Figure 4. Effects of drought stress and rehydration on MDA content of mustard seedlings. Means ± SD, n = 3. Values in a column followed by different lowercase letters are significantly different at P<0.05 according to Duncan's multiple range test

After rehydration, the content of MDA under moderate and severe stress was higher than that of the control by 92.07% and 73.38%, respectively, and the content of MDA returned to the control level under mild stress. The change in content of MDA in the roots was completely different from that in the leaves. Compared with the plants under normal conditions, the content of MDA in the roots, that had been subjected to drought, decreased by 34.68%, 76%, and 71.79% after 3 days. There was no significant change in the content of MDA in roots after 9 days of drought treatment. However, rehydration caused a significant increase in the content of MDA in roots compared with untreated plants. The effect was particularly strong in the plants under severe stress, resulting in an increase as high as 731.99%.

Changes in antioxidant enzyme activities

As shown in Figure 5, the activity of SOD in the roots increased significantly by 20.41%, 29.77%, and 35.21% during the initial 3 days of drought stress, respectively. With the increase in duration and intensity of drought, the activity of SOD in the roots under moderate and severe drought was both dramatically higher (143.26% and 152.90%) than in the control on the sixth day of drought. On the ninth day, the SOD activity under severe drought was significantly higher than that in the control and other stress treatments. After rehydration, the SOD activity of the three drought treatments was higher than that of the control. The change in activity of SOD in leaves occurred later than that in the roots. The activity of SOD in leaves under moderate and severe stress did not significantly increase until the sixth day after drought. Among the treated groups in leaves, the activity of SOD was greater in the treated leaves than in controls by 36.10%, 47.93%, and 8.84% on the ninth day. After rehydration, the SOD of the severe stress treatment was 19.76% higher than that of the control, and the activities of other treatments recovered to the control level.

The drought-induced changes in the activity of POD in the roots and leaves are shown in Figure 5.

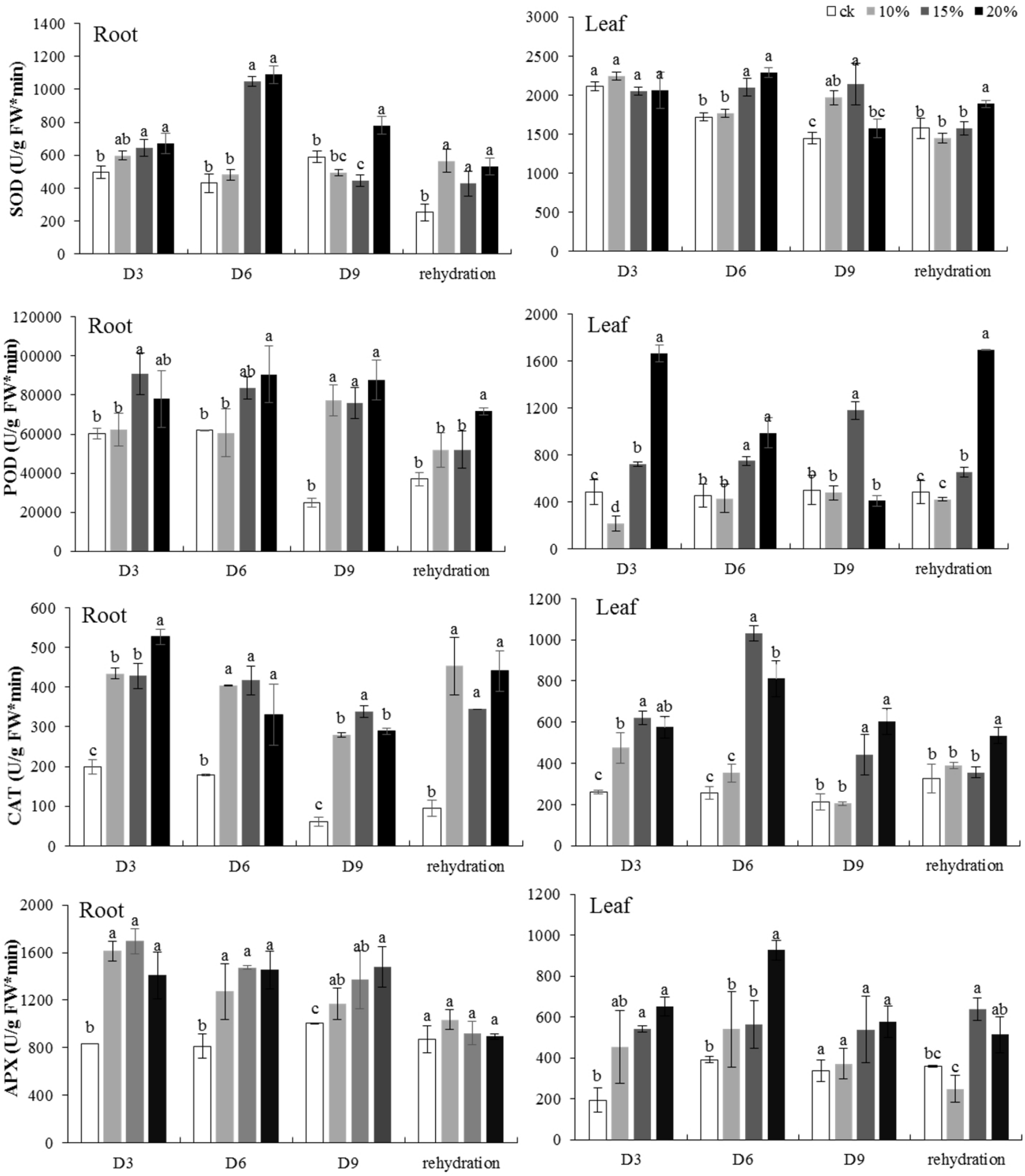

Figure 5. Effects of drought stress and rehydration on enzyme activities in mustard seedlings. Means ±SD, n = 3. Values in a column followed by different lowercase letters are significantly different at P<0.05 according to Duncan′s multiple range test

The activity of POD in roots increased remarkably and maintained a high level of activity under moderate and severe drought throughout the treatment period. The activity of POD increased dramatically by 209.35%, 203.97%, and 251.55% with the extension of stress time, and reached its maximum value on the ninth day of drought stress. The activity of POD of all treatments was lower than that before rehydration, and the activity of POD of severe drought was higher than that of the control and other treatments. After 3 and 6 days of drought treatment, the activity of leaf POD under moderate and severe stress was higher than that under the control and mild stress. After 9 days of leaf stress, the activity of POD increased significantly from 65.99% to 135.92% under moderate stress, and there was no difference between the other treatments and the control. After rehydration, the activity of POD returned to the control level under mild stress, while the activity of POD was higher than that under the control by 35.36% and 250.47% under moderate and severe stress, respectively.

Figure 5 illustrates different effects of stress levels and times on the activity of CAT in roots and leaves. Drought stress induced a rapid increase in the activity of CAT in roots during all treatment days and reached its maximum on the 9th day by 354.26%, 451.68%, and 368.88%. After rehydration, the activities of CAT in roots under all drought treatments were still higher than that of the control by 382.06%, 266.94%, and 368.88%. The activity of CAT increased dramatically in the leaves compared with the treatment without drought stress on the third day. The activity of CAT in the leaves under moderate and severe stress was notably higher than that of the control, and the activity reached its maximum on the sixth day by 303.09% and 217.04%, respectively. After rehydration, the activity of CAT did not differ from that of the control under mild and moderate stress, but the activity under severe stress was 63% higher than that of the control.

The drought-induced APX maintained a high level in the roots during the experimental period (Figure 5). The activity of APX in all the drought-treated roots on the 9th day was lower than that on the third day and gradually decreased. After rehydration, the activity of APX of all the treatments recovered to the control level. The APX activity in leaves increased substantially after 3 and 6 days of stress and reached the maximum value of 134.07%, 178.86%, and 236.01% on the third day. On the ninth day of drought stress, there was no difference between all the treatments compared with the control. After rehydration, the activity of APX decreased by 30.58% under mild stress and increased by 77.62% and 43.26% under moderate and severe stress, respectively.

DISCUSSION

Drought is a major limiting abiotic stress factor during the growth and development of crop plants. Changes in growth, photosynthesis, and physiology after drought and rehydration can affect the growth status and stress tolerance in plants to some extent. Therefore, the assessment of mustard stress resistance and the ability to recover from water deficit is an important task of modern crop production.

The growth rate is an important index of the plant growth status. Drought stress inhibited plant growth and reduced the growth rate. However, timely rehydration after drought stress can induce the drought-resistant ability of plants and result in a compensation effect. Compensation is an important self-regulatory mechanism adapted by plants to defend against environmental stresses or injuries (Dong et al., 2019). Previous studies have suggested a growth compensation effect after drought stress and rehydration in terms of the root length, shoot length, leaf area, and number of leaves (Chen et al., 2001; Dong et al., 2019; Husen et al., 2014). The results of this study showed that the growth rate of root length decreased by 61.86%, 85.76%, and 109.66% compared with the control under drought stress. After rehydration, the root length grew rapidly, and the growth rate of mild and moderate stress (2.46% and 11.77%, respectively) was greater than that of control (0.25%), indicating that there was growth compensation in the root length. However, there was no compensating effect for shoot length. The results suggested that the growth compensation of root and shoot lengths differed after drought stress and rehydration.

The accumulation of plant biomass was reduced by abiotic stress and preferentially supplies to the root system, which led to an increase in the root-shoot ratio (Ren et al., 2020; Tang et al., 2020). In this study, the root-shoot ratio of plants under three drought levels increased by 56.70%, 99.65%, and 48.05% compared with controls after 9 days of drought stress. After rehydration, the fresh weight of seedlings rapidly recovered. The growth rates of root fresh weights under moderate and severe stress were 82.93% and 191.19%, respectively, and the shoot fresh weights were 172.55% and 347.58%, respectively. However, under normal conditions, the fresh weight of the root and shoot was only 36.5% and 3.82%, respectively. These results indicated that the fresh weight of roots and shoots had a compensating effect after rehydration. In addition, the shoot allocated more assimilates after rehydration, which resulted in a decrease in the root-shoot ratio of stressed plants. Compensation growth effects after drought and rehydration were observed in the studies of Chen et al. (2001) and Guan et al. (2019), who concluded that explosive growth was an effective strategy to compensate for the carbon deficit. The compensation effect was related to the degree and duration of stress periods. In a study of soybeans, mild and short-term stress can lead to more compensation (Dong et al., 2019). *Artemisia halodendron* was able to tolerate a longer period under moderate drought and recovery to pre-drought levels after rehydration (Chen et al., 2019). The results of this study indicated that under moderate and severe drought stress, the fresh weight of plant benefitted from more compensation. These results may indicate variations in the resistance to drought stress among plants.

Chlorophyll is the main photosynthetic pigment, and its content is positively correlated with photosynthetic carbon fixation and drought resistance (Husen et al., 2014). Previous studies of *Brassica* species and cultivars had reported that the chlorophyll content decreased under drought stress (Kauser et al., 2006; Lada, 2012), which is different from the results of this study. In the early stage of drought, the chlorophyll content was significantly higher than that of the control by 12% and 15% under mild and moderate drought, respectively. In the late stage of stress treatment, the chlorophyll content under mild stress was 12% higher than that of the control, but the chlorophyll content decreased by 12% and 13% under moderate and severe stress, respectively. These results suggested that mustard can more effectively adapt to mild and short drought by maintaining high chlorophyll content. Moreover, the decrease in leaf water content with drought increased the chlorophyll concentration per unit area to some extent, which led to the increase in chlorophyll content. The excessive accumulation of ROS under severe stress accelerated the degradation of chloroplasts and then inhibited chlorophyll synthesis (Anjum et al., 2003). After rehydration, under moderate and severe stress, the chlorophyll content was still significantly lower than that under normal conditions, indicating that the damage of chloroplasts under moderate and severe stress could not be recovered and it may cause yellowing of the leaves.

Chlorophyll fluorescence is a useful tool to quantify the effect of abiotic stress on photosynthesis (Hooks et al., 2019). PI_{ABS} and F_v/F_m can reflect the reaction center activity of PS II, particularly since PI_{ABS} has been suggested to be a better parameter at reflecting the effect of stress on photosynthetic apparatus compared with F_v/F_m (Appenroth et al., 2001; Heerden et al., 2003). PIABS and F_v/F_m decreased significantly in the drought-treated plants compared with plants without stress, indicating that the reaction center of PS II was inactivated, and the performance of PS II decreased. After rehydration, the PIABS was recovered or was higher than the control level, which indicated a recovery in PS II performance and a compensatory effect. However, F_v/F_m failed to recover even after the release of the stress by the added water. One of the reasons for this difference could be the fact that PIABS was more sensitive to stress than F_v/F_m.

Abiotic stress tolerance in crop plants depends on the enhancement of the antioxidative defense system, which includes antioxidant compounds and several antioxidative enzymes (Neto et al., 2006). In this study, drought stress induced a notable increase in the activities of SOD, POD, APX, and CAT in roots and leaves compared with the wellwatered control plants, which indicated the activation of the antioxidant system. SOD is one of the ubiquitous enzymes in aerobic organisms and is a key ROS scavenger by converting O_2.– to H_2O_2, while other enzymes, such as POD, APX, and CAT, have the main function of detoxifying H_2O_2 (Mittova et al., 2004). Thus, SOD constitutes the first line of defense against the superoxide-derived oxidative stress in the plant cells. In the stressed leaves, although the activities of POD, CAT, and APX significantly increased, the activity of SOD was not different from that of the non-stressed leaves, which further led to the accumulation of ROS and the peroxidation of membrane lipid. This hypothesis can be proven by the increase in content of MDA in stressed leaves. In the root, the increase in SOD activity accompanied by the increase in the activities of POD, APX, and CAT can decrease the excessive accumulation of ROS, which was consistent with the low content of MDA in roots. The synergistic effect of antioxidant enzymes is a good indication of plant tolerance. The same result was obtained in drought-tolerant cotton (Gossett et al., 1994) and sesame (Koca et al., 2007). After rehydration, the activities of CAT, POD, and SOD in the stressed roots were higher than in the control plants. The activities of SOD, POD, CAT, and APX in the leaves under severe stress were significantly higher. Previous studies have shown that after drought and rehydration, the antioxidant enzymes in wheat (Zhang et al., 2004) and glycyrrhiza (Zhou et al., 2011) remain highly active, which was consistent with the results in this study. The reason for the high level of enzyme activity after rehydration could be to maintain the balance of ROS and mitigate the damage to membranes.

CONCLUSIONS

This study demonstrated that drought stress significantly affected the growth of mustard seedlings, inhibited photosynthetic activity, and activated the antioxidant enzyme system. After rehydration, seedling growth and PIABS recovered quickly and had a compensating effect. However, the contents of chlorophyll and MDA did not recover to the control level under moderate and severe stress. In addition, drought stress and rehydration increased the activity of antioxidant enzymes, but the changes in antioxidant enzymes in roots and leaves differed. After rehydration, the activities of SOD and CAT in all three treatments of roots were significantly higher than in the control. The activities of SOD and CAT in the leaves were only higher than those in the control group under severe stress, but no significant difference was found between the other treatments. There was no difference in the activity of APX in roots after rehydration. However, the activity of APX in leaves under moderate and severe stress was higher than in the controls. These results suggest that there are specific enzymes in roots and leaves that removed excess ROS. The drought resistance of mustard is a complex physiological process, which is closely related to its variety and living environment. To better evaluate the drought resistance and the drought resistance mechanism of mustard, more varieties and other aspects merit further study.

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