

Morphological and Physiological Responses of Maize Seedlings under Drought and Waterlogging

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ABSTRACT

Waterlogging and drought are severe constraints that limit maize seedling growth in tropical and subtropical regions. It is significant to determine the differences in morphological and physiological responses of maize to drought and excess soil water, with a view toward better breeding and field management. In the present experiment, different levels of soil water availability were initiated at the one-leaf (V1) stage of two maize cultivars (Denghai9 and Yidan629): Control (CK), Severe Drought (SD), Light Drought (LD), Severe Waterlogging (SW), and Light Waterlogging (LW). The results indicated that waterlogging had more discernible impact on the seedling growth of both cultivars than drought stress. The Relative Growth Rate (RGR) of shoots and roots, along with root length, volume, and surface area were all markedly decreased in both cultivars under waterlogging stress. The malondialdehyde content increased significantly in roots and leaves under waterlogging treatment. In both cultivars, SuperOxide Dismutase (SOD) was mostly activated in roots and leaves at the three-leaf (V3) stage by waterlogging stress, while the Catalase (CAT) activity apparently increased under drought stress. The activity of Peroxidase (POD) distinctly enhanced in both cultivars under drought and waterlogging stress. Ascorbate Peroxidase (APX) showed constant activity with prolongation of waterlogging stress, and Glutathione Reductase (GR) activity notably increased in roots under waterlogging conditions at the six-leaf (V6) stage. We concluded that SOD, POD, APX, and GR were the most important antioxidant enzymes under waterlogging conditions, whereas CAT and POD appeared to play key roles under drought stress.

Keywords: Antioxidant enzyme activity, Excess soil water, Peroxidase (POD), Soil water availability.

INTRODUCTION

Maize (*Zea mays* L.) is one of the most important crops in the world and it accounts for more than 34% of cereal production worldwide (FAO, 2012). The popularity of maize cultivation extends from tropical to

cooler temperate regions. However, maize yield in tropical and subtropical rainfed environments is affected by an array of abiotic and biotic stresses, limiting maize yield to 1–3 tons per hectare, whereas the global average is around 5 tons per hectare (Prasanna, 2016). Two major abiotic stresses limiting maize production in these areas are drought and

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excess soil water stress (AICRP, 2006). In the lowland tropics or subtropical regions, specifically, these stresses account for almost 28% of the losses in maize crops (Edmeades *et al.*, 2006), and drought alone account for approximately 17% of losses (Edmeades *et al.*, 1992). Furthermore, in Southeast Asia, approximately 18% of the total growing area of maize is affected by floods and waterlogging, which cause 25–30% yield losses annually (Cairns *et al.*, 2012). Moreover, with increase in unpredictable rain patterns attributable to global climate change causing both drought and flooding, the amount of crop yield losses is expected to increase (Cairns *et al.*, 2012). Therefore, understanding the responses of maize to soil moisture-related stresses with regards to growth, development, and yield, is important for developing improved genotypes that are tolerant to both drought and excess moisture stresses.

Tolerance to soil water stress is important for the successful growth of maize hybrids in regions prone to drought or waterlogging. Previous studies have demonstrated that both drought and excess moisture stress induce adverse changes in morphological, physiological and biochemical parameters in maize plants. In particular, photosynthesis, plant height, dry matter production, and leaf area, as well as final grain yield, are known to be affected (Earl and Davis, 2003; Zaidi *et al.*, 2004; Ge *et al.*, 2012; Saeidi and Abdoli, 2015). Water-logging and drought stress continue to cause crop production losses in various parts of the world (Li *et al.*, 2009; Li and Lascano, 2011). Drought or waterlogging cause significant decrease in both shoot and roots dry matter and changes in roots distribution in the soil profile (Grzesiak *et al.*, 2014). Inhibition of plant growth is mostly attributed to reduced rooting volume (Fageria *et al.*, 2006). Decreases in the root number and length of plants grown under waterlogging have previously been shown to be greater than in plants under drought (Grzesiak *et al.*, 2014). A previous study evaluating tolerant maize cultivars showed elongation of the youngest adventitious roots and formation of more aerenchyma in roots (Lizaso *et al.*, 2001).

Oxidative stress caused by an increase in Reactive Oxygen Species (ROS), such as singlet Oxygen (1O_2), superoxide radical (O_2^-), Hydrogen peroxide (H_2O_2), and hydroxyl radical (OH \cdot), is a common consequence under drought and waterlogging (Waraich *et al.*, 2011). To cope with ROS and maintain redox homeostasis, plants have developed a well-integrated antioxidant defense system, which is composed of antioxidant molecules and antioxidant enzymes, such as superoxide dismutase, catalase, and enzymes involved in the ascorbate–glutathione cycle (Mittler, 2002). Comparison of the activities of SuperOxide Dismutase (SOD), Ascorbate Peroxidase (APX), Glutathione Reductase (GR), Catalase (CAT), and guaiacol Peroxidase (POD) between waterlogging-tolerant and waterlogging-sensitive genotypes has shown that CAT is the most important H_2O_2 -scavenging enzyme in leaves, whereas APX appears to play a key role in roots (Tang *et al.*, 2010). Although drought and excess moisture stress commonly coexist within individual crop cycles, most studies regarding the morphological and physiological responses of maize to water stress have only examined single types of stress. Few studies have investigated crop responses to these stresses simultaneously.

Therefore, the aim of the present study was to gain a better understanding of differences in the mechanisms of drought and excess moisture stress tolerance in maize seedlings by comparing their morphological and physiological attributes. It is anticipated that the findings will provide a basis for the breeding and management of maize that is exposed to both drought and waterlogging in subtropical regions.

MATERIALS AND METHODS

Experimental Design and Management

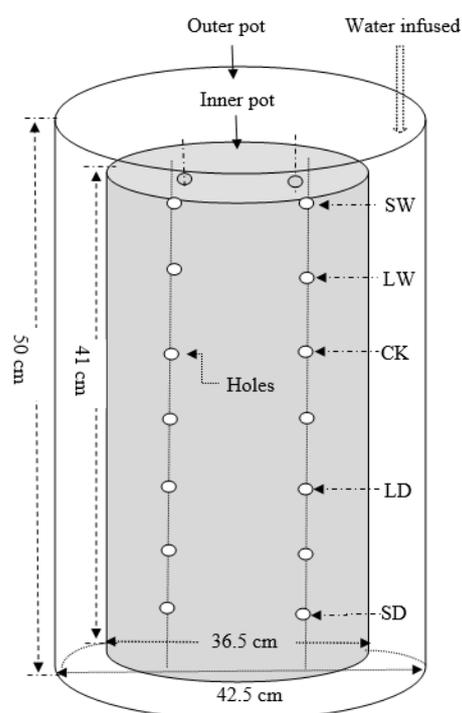
The pot experiment was conducted in a greenhouse, in order to avoid the influence

of rainfall on soil water treatment, at the Huazhong Agricultural University, Wuhan, China. Pots of two sizes were used in this study. The small pots were 36.5 cm in diameter and 41 cm in height, and larger pots were 42.5 cm in diameter and 50 cm in height. Four symmetrical rows of holes were made in the side walls of the small pots at 5-cm intervals from the bottom, and a total of seven holes were made along each row. The pots diagram has shown in supplementary figure 1. Each small pot was filled with 17.5 kg of sieved dry field soil that were amended with 0.14 g urea, 0.14 g diammonium phosphate, and 0.18 g potassium chloride per kg soil. The experimental soil had the following composition: Organic matter, 54.95 g kg⁻¹; total N, 0.69 g kg⁻¹; total P, 0.274 g kg⁻¹; available P (Olsen-P), 1.86 mg kg⁻¹; and available K, 107.1 mg kg⁻¹ (extracted with CH₃COONH₄). Soil pH was 6.22 (extracted with H₂O; Soil: Water= 1:2.5).

Small pots filled with soil were placed within the larger pots. Water was infused

through the interspace between the small pot and the larger pot, and the water passed through the holes into the soil within the small pot. This arrangement of outer and inner pots with holes was convenient for homogenizing the soil water content horizontally and for generating a continuous soil moisture gradient vertically. By using this setup, the following five soil water treatments were established: (1) Severe Drought (SD), (2) Light Drought (LD), (3) Suitable water status (CK), (4) Light Waterlogging (LW), and (5) Severe Waterlogging treatment (SW). These five levels of soil water content were achieved by maintaining the water level at the respective position of the hole along the numbers on the sidewall of the small pot. That is, the water level in the interspace between the two size pots was maintained at the position of the first hole numbered from the bottom under the SD treatment; likewise, the third hole for the LD treatment, the fifth hole for the CK treatment, the sixth hole for the LW, and the seventh hole for the SW treatment.

We used two maize varieties, Denghai9 and Yidan629, in this study, based on their popularity in Hubei Province, China, where the experimental site was located. Before sowing, the healthy seeds of both maize varieties were sterilized by soaking in 1% (v/v) sodium hypochlorite for 30 minutes, and then kept in the incubator for germination at 28°C in darkness for about 3 days. Uniformly-germinated seeds were selected and sown in soil in pots, which had been prepared 10 days before and had already reached the appropriate soil water content for maize emergence. Six germinated seeds were sown in each pot, and seedlings were thinned to three plants per pot at the one-and-a-half-leaf stage. Water treatments were initiated after the one-leaf stage (V1). During the experimental period, soil water content levels for each treatment were maintained following the method described above. The soil water content of each treatment was monitored at a depth of 12 cm, using probes of a Field Scout TDR 200 Soil Moisture Meter



Supplementary Figure 1. Pots design for different soil moisture treatments.



(Spectrum Technologies, Inc., Aurora, IL, USA). The relative soil water content fluctuated at 30–42%, 50–62%, 70–78%, 82–90%, and > 90% of the saturated soil (100%) under the SD, LD, CK, LW, and SW treatments, respectively. All measures against diseases and insect infestation were deployed at the appropriate time for maize seedlings during the experimental period.

Plant Sampling and Measurements

At the one-leaf (V1), three-leaf (V3), and six-leaf (V6) stages, nine maize seedlings were carefully removed from three pots in each treatment and then separated into root and shoots. The roots were gently washed with running water, and minimum root loss was ensured during cleaning. One of the plant roots was immediately stored at -80°C for physiological indicator analysis. The roots and shoots of six plants were rapidly transferred to ovens, dried at 105°C for 30 minutes, and then dried at 80°C to a constant mass and weighed for dry matter determination. Further, the plant roots were used to assess the total length, surface area, and volume of the roots, using a root scanning analysis system WinRHIZO (Pro 2.0 Version 2005; Regent Instruments, Quebec, QC, Canada).

All the biochemical analyses were carried out by using fresh leaves and root samples and the seminal parts of root were used for these analyses. MalonDiAldehyde (MDA) content was measured as described by Chen and Zhang (2006). 0.2 g and 0.5 g ground roots and leaves were homogenized in 5 mL 10% TriChloroAcetic acid (TCA) with a chilled mortar and pestle, and then centrifuged at 4,000 rpm for 10 minutes. Then, 2 mL supernatant was mixed with 2 mL solution containing 0.6% TBA in 10% TCA. The mixture was heated in a boiling bath for 15 min, quickly cooled and then centrifuged at 4,000 rpm for 10 minutes. Absorbance of the supernatant was determined at 532 and 600 nm. The MDA concentration was calculated after

subtracting nonspecific absorbance at 600 nm using the extinction coefficient of 155 mM cm^{-1} (Monferrán *et al.*, 2009), and expressed in $\mu\text{mol per gram fresh weight}$. The blank was 2 mL distilled water in 2 mL 0.6% TBA in 10% TCA without the extract.

The Antioxidant enzyme analysis was performed as described by Tang *et al.* (2010). The roots and leaves were homogenized in 100 mmol L^{-1} potassium phosphate buffer (pH 6.8) containing 0.1 mmol L^{-1} EDTA and 100 mg of polyvinyl pirolidone. The homogenate was filtered through muslin cloth and centrifuged at $15,000\times g$ for 20 minutes at 4°C , and the supernatant was used for the following enzyme assays.

SuperOxide Dismutase (SOD) activity was analyzed by monitoring inhibition of the photochemical reaction of Nitro Blue Tetrazolium (NBT) according to the method of Giannopolitis and Ries (1977). Peroxidase (POD) activity was determined as described by Hao *et al.* (2004). The activity of catalase (CAT) was determined by monitoring the disappearance of H_2O_2 at 240 nm ($\epsilon = 40\text{ mM cm}^{-1}$) as described by Aebi (1983). Ascorbate Peroxidase (APX) activity was assessed as described by Nakano and Asada (1981). Total GR (EC 1.6.4.2) activity was determined as described by Schaedle and Bassham (1977).

Calculations and Statistical Analysis

The Relative Growth Rate (RGR) based on shoot and root dry weights was calculated from stages V1 to V3 and V3 to V6 using the equations reported by Radford (1967). The Root/Shoot mass Ratio (RSR) was calculated as the ratio of root dry mass to shoot dry mass.

The data were analyzed using a complete randomized design applying SAS 9.0 statistical software (SAS Institute Cary, NC) for analysis of variance with the generalized linear model procedure (2-factors). Significant differences among treatments were identified at the 0.05 probability level

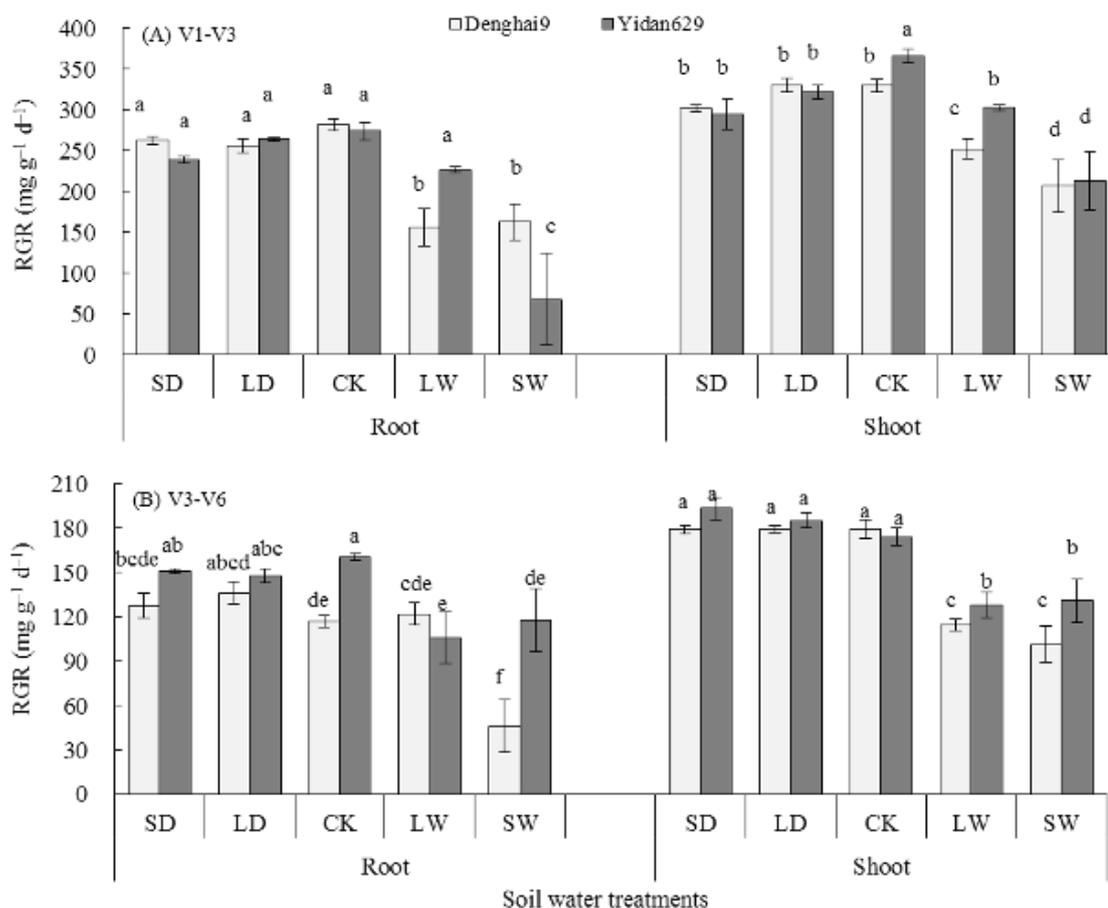


Figure 1. Effects of water stress on the Relative Growth Rate (RGR) of shoots and roots of maize seedlings of two cultivars, Denghai9 and Yidan629.

using the Student–Newman–Keuls test, and the results are presented as the means of three replications.

RESULTS

Effects of Soil Water Stress on Maize Seedling Growth

As shown in Figure 1, waterlogging stress treatments had more adverse effect on the Relative Growth Rate (RGR) of maize seedlings than drought stress treatments. Compared with CK treatments, both drought treatments had no significant impact on root RGR of both cultivars and shoot RGR of the Denghai9 cultivar in each of the growth stages assessed (Figures 1-A and -B). While,

the shoot RGR of the Yidan629 was significantly restrained at the V1-V3 stages of growth ($P < 0.05$). Notably, SW treatment significantly decreased the RGR of the roots and shoots of both cultivars at two observed stages (Figures 1-A and -B).

In response to drought and waterlogging conditions, we found that both varieties exhibited significant changes in morphological parameters, when compared to seedlings under the CK treatment (Table 1). Soil water treatments and their interactions with the cultivars had a significant effect on the shoot and root biomass of maize seedlings ($P < 0.05$). Moreover, both waterlogging treatments decreased shoot biomass significantly ($P > 0.05$) in both cultivars. However, the results indicated that the light drought treatment



significantly increased shoot biomass by 0.72% at V3 and 0.70% at V6, whereas it declined by 69.7 and 91.6% under severe waterlogging treatment in Denghai9, respectively. Nevertheless, all water stress treatments considerably reduced shoot biomass of Yidan629 in both stages. Root biomass of Denghai9 at V3 stage apparently decreased under SD and LD treatments ($P < 0.05$), but it recovered to a level similar to that in CK plant at V6 stage, which significantly increase 2.51 and 13.1% under severe and light drought treatments. In both maize varieties, waterlogging treatments exhibited more severe stress on shoot and root biomass of both maize seedling as compared to drought stress treatment. At the V3 stage in the maize seedlings, all water stress treatments markedly reduced the root length of both cultivars ($P < 0.05$; Table 1). However, at the V6 stage, the root length of the Denghai9 and Yidan629 seedlings was remarkably 46.9 and 60.7% higher in response to the LD treatment compared to the control plants. All water stress treatments had significant impact on the root volume and surface area of Yidan629 ($P < 0.05$). At the V3 stage, the root volume significantly decreased in Denghai9 (81.7%) and Yidan629 (90.2%) in response to the SD and SW treatments compared to CK treatment. Moreover, the SW treatment showed more severe decline than the other water stress treatments at the V6 stage of Yidan629. The root volume of Denghai9 at the V3 stage was not affected by the LD treatment, whereas a noticeable decline was observed under other stress treatments (Table 1). The root volume of Denghai9 at the V6 stage significantly decreased under all water stress treatments ($P < 0.05$). The root surface area of Denghai9 was significantly reduced by exposure to waterlogging stress at the two growth stages ($P < 0.05$; Table 1). However, in comparison with the control plants, Denghai9 had comparative less root surface area at V3 and V6 stage under LD, and at V6 stage under SD treatment.

Effect of Water Stress on MDA Content

The MDA content varied between the roots and leaves of both cultivars across the profile of soil water treatments (Figure 2). In comparison with the respective Control plants (CK) at the V3 stage of Yidan629 (Figure 2-A), the MDA content in the roots under SW treatment was significantly increased by 57.10%, while, MDA content in the leaves was markedly reduced by 49.56% under SD treatment. Under the LD and SD treatments, the MDA content in the roots of Denghai9 was significantly lower, but the MDA content in the leaves increased significantly by 280.31 and 151.11%, respectively. At the V6 stage, the MDA concentrations in roots and leaves significantly increased in both cultivars under the LW and SW treatments ($P < 0.05$; Figure 2-B). The MDA values in roots were significantly decreased by 45.74% in Denghai9 and by 44.13% in Yidan629 in response to the LD treatment. There were apparently no changes in MDA content in leaves at the V6 stage under the drought treatments.

Effect of Water Stress on Antioxidant Enzyme Activity

Experimental findings relating to the antioxidant system in roots and leaves indicate that the two maize genotypes responded differently to normal water supply and water stress conditions (Table 2). In comparison with the CK treatment, SOD activity in roots and leaves remarkably increased in both cultivars under the waterlogging treatments ($P < 0.05$), whereas the drought treatments did not induce a significant change in SOD activities in the roots and leaves of either cultivar at the V3 stage. However, at the V6 stage, a significant increase in SOD activities was detected in the roots of Denghai9 and Yidan629 cultivars under LD treatment. In contrast, there were apparent decreases in

Table 1. Morphological indexes of Denghai9 and Yidan629 maize seedlings grown under different water-stress treatments.^a

Water treatment	Variety	Shoot biomass	Root biomass	Root length	Root volume	Root surface area
V3 stage						
SD	Denghai9	0.61 cd	0.28 bc	1378 c	1.58 bc	182.9 cd
	Yidan629	0.57 d	0.22 d	1512 c	2.33 bc	163.8 cd
LD	Denghai9	0.82 b	0.26 c	2406 b	7.48 a	417.2 ab
	Yidan629	0.75 bc	0.28 bc	1516 c	4.56 b	303.9 bc
CK	Denghai9	0.81 b	0.34 a	3151 a	8.67 a	518.7 a
	Yidan629	1.17 a	0.31 ab	2328 b	7.27 a	459.8 a
LW	Denghai9	0.37 e	0.10 e	1240 c	1.67 bc	158.4 cd
	Yidan629	0.62 cd	0.19 d	1377 c	3.18 bc	221.3 cd
SW	Denghai9	0.24 e	0.10 e	997 c	2.64 bc	131.9 cd
	Yidan629	0.26 e	0.04 f	861 c	0.71 c	79.5 d
F values						
Water Treatment		65.8**	166.7**	15.9**	26.9**	22.7**
Variety		30.3**	3.92	2.61	0.09	0.06
Water×Variety		11.0**	28.2**	3.43*	6.38**	2.25
V6 stage						
SD	Denghai9	22.06 c	3.57 c	6482 de	46.47 c	3351.3 c
	Yidan629	30.52 b	4.44 c	7780 d	50.47 c	4434.2 b
LD	Denghai9	29.43 b	3.94 c	9332 c	47.80 c	3511.6 c
	Yidan629	27.32 b	5.36 b	20665 a	54.05 c	3605.9 c
CK	Denghai9	29.22 b	3.49 c	6355 de	93.04 b	3547.1 c
	Yidan629	38.02 a	7.62 a	12860 b	114.38 a	6760.3 a
LW	Denghai9	3.68 e	1.08 de	5406 ef	15.36 e	2225.0 d
	Yidan629	8.06 e	1.69 d	4538 f	26.52 d	2445.4 d
SW	Denghai9	2.45 e	0.31 e	1720 g	3.62 f	787.1 e
	Yidan629	5.13 de	0.59 e	4230 f	3.44 f	2063.7 d
F values						
Water Treatment		322.7**	83.9**	193.5**	166.5**	110.5**
Variety		1.35	30.0**	22.34**	.366	94.5**
Water×Variety		8.41*	6.40**	18.3**	2.6	22.5**

^a SD: Severe Drought; LD: Low Drought; LW: Low Waterlogging, SW: Severe Waterlogging. * $P < 0.05$; ** $P < 0.01$. Within each column, different lower-case letters indicate significant differences ($P < 0.05$) in treatments.

SOD activities in the roots of Yidan629 and Denghai9 under SD and SW treatments.

Significant changes were observed in POD activities in the roots and leaves of both cultivars under different water stress treatments. At the V3 stage, POD activities in the roots of both cultivars were markedly higher under LW and LD treatments (Table 2), whereas they were lower under SW and

SD treatments. Furthermore, at the V6 stage, levels of POD activity in the roots of both cultivars were still markedly higher under water stress treatment ($P < 0.05$). The POD activities in the leaves of both cultivars were, in most cases, lower than the roots under the same water stress treatment (Table 2). A significant increase in POD activity in the leaves of Denghai9 was observed at the

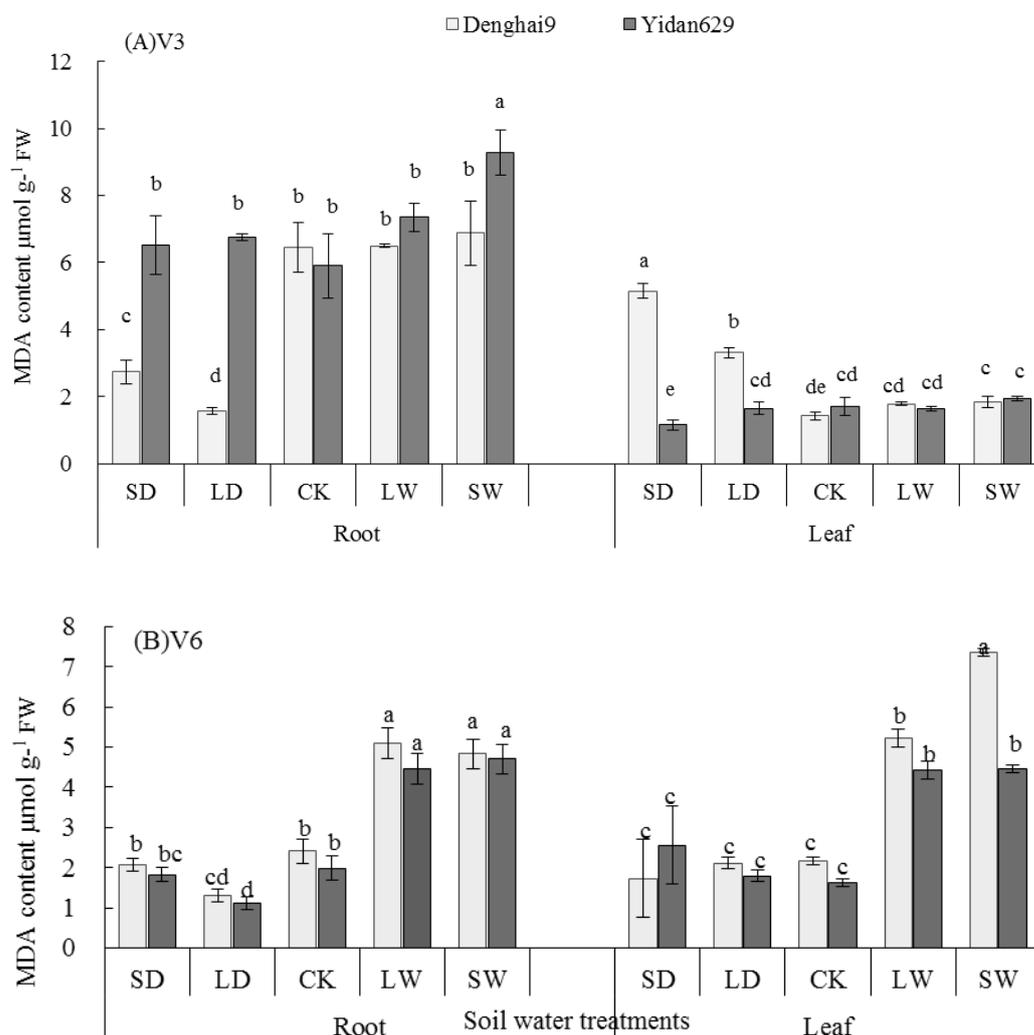


Figure 2. Effect of water stress on the MalonDiAldehyde (MDA) content of maize seedlings of two cultivars, Denghai9 and Yidan629.

V3 stage under LD and LW treatments, while at V6 stage the POD activities were increase in SD and SW treatment, and the POD activities continuously at the same trend V6 stage under all water stress. In contrast, in Yidan629, all the water stress treatments produced significant decreases in leaf POD activity at the V6 stage.

Both drought treatments caused significant increase in CAT activities in roots at the V3 stage in Denghai9 (Table 2). However, at the V6 stage of Denghai9, both SD and SW treatments, but not the LD treatment, apparently decreased CAT activity in the roots. Under water stress, the Yidan629

showed a root CAT activity response at the V3 stage comparable to that observed in the CK plants. However, a considerable increase in CAT activity in root at the V6 stage was observed under the drought and LW treatments ($P < 0.05$). A marginal increase in CAT activity in the leaves of LD- and SW-treated plants at the V3 stage was observed in both cultivars ($P < 0.05$). Moreover, at the V6 stage, CAT activity in the leaves of Denghai9 was still higher under drought and LW treatments ($P < 0.05$). In contrast, with the exception of the LD treatment, there was no significant increase in CAT activity in the

Table 2. Activities of antioxidant enzymes in the roots and leaves of Denghai9 and Yidan629 maize seedlings grown under different soil water treatments.^a

Water treatment	Variety	Root							Leaf						
		SOD (U min ⁻¹ g ⁻¹ FW)	POD (U min ⁻¹ g ⁻¹ FW)	CAT (mg min ⁻¹ g ⁻¹ FW)	APX (U min ⁻¹ g ⁻¹ FW)	GR (U min ⁻¹ g ⁻¹ FW)	SOD (U min ⁻¹ g ⁻¹ FW)	POD (U min ⁻¹ g ⁻¹ FW)	CAT (U min ⁻¹ g ⁻¹ FW)	APX (U min ⁻¹ g ⁻¹ FW)	GR (U min ⁻¹ g ⁻¹ FW)				
V3 stage															
SD	Denghai9	20.0 c	364.9 f	80.78a	18.3 bc	8.4 b	16.6 c	62.0 de	18.3 c	61.7 c	12.2 c				
	Yidan629	31.8 c	136.0 g	10.48c	17.7 bc	9.5 b	21.3 c	48.1 e	32.3 c	61.9 c	9.01 d				
LD	Denghai9	38.6 c	698.0 d	56.25b	16.6 bc	14.3 a	46.6 c	153.2 b	49.5 b	59.4 c	11.0 c				
	Yidan629	29.4 c	862.8 b	24.25c	11.9 c	13.5 a	40.4 c	135.5 bc	80.7 a	62.1 c	8.26 d				
CK	Denghai9	32.1 c	532.7 e	30.44c	20.0 abc	12.3 a	44.2 c	73.7 de	27.1 c	57.0 c	24.9 a				
	Yidan629	42.8 c	687.4 d	15.02c	12.6 c	14.3 a	35.7 c	98.8 cd	26.1 c	48.1 c	12.1 c				
LW	Denghai9	108.6 b	787.0 c	20.83c	26.4 ab	12.0 a	100.3 b	124.8 bc	21.0 c	88.8 bc	12.7 c				
	Yidan629	113.9 b	1003.6 a	20.83c	29.1 a	6.28 c	57.1 c	280.9 a	21.0 c	111.0ab	18.5 b				
SW	Denghai9	154.6 a	300.5 f	24.78c	14.7 c	0.55 e	162.8 a	103.1 cd	55.7 b	122.6 a	3.65 e				
	Yidan629	172.5 a	155.6 g	20.45c	29.7 a	2.52 d	182.4 a	110.4 bed	55.2 b	85.4 bc	2.41 e				
V6 stage															
SD	Denghai9	27.3f	525.5 d	25.5 d	12.5 d	1.56 f	34.6 c	206.7 a	42.7 cd	41.1 b	4.71 d				
	Yidan629	11.0 g	656.3 b	101.3 a	15.3 cd	0.34 g	30.9 c	148.9 d	67.1 b	28.8 c	1.35 e				
LD	Denghai9	77.5 c	570.2 c	76.2 b	24.4 bed	5.56 c	67.8 b	163.8 c	109.7 a	42.5 b	13.7 b				
	Yidan629	117.6 a	598.9 c	41.7 c	22.3 bed	1.37 f	97.5 a	132.8 e	124.5 a	29.2 c	2.50 de				
CK	Denghai9	39.6 e	169.8 h	48.1 c	27.4 bc	2.57 e	29.1 c	23.3 i	20.9 d	26.2 c	11.7 c				
	Yidan629	97.7 b	379.2 f	27.9 d	20.1 bed	1.64 f	101.8 a	175.6 b	68.6 bc	32.2 c	2.51 de				
LW	Denghai9	66.1 d	383.3 f	40.4 c	31.3 b	7.79 a	44.9 c	47.3 g	84.1 b	97.0 a	15.4 b				
	Yidan629	40.0 e	462.2 e	46.9 c	25.0 bed	7.51 a	48.1 c	74.8 f	78.0 b	58.7 b	18.4 a				
SW	Denghai9	33.3 ef	1202 a	21.5 d	16.6 cd	6.80 b	35.7 c	181.1 b	35.6 d	80.82 a	5.06 d				
	Yidan629	24.0 f	245.0 g	24.8 d	46.5 a	3.79 d	33.6 c	35.5 h	44.1 cd	104.3 a	4.04 d				

^a SOD: SuperOxidase Dismutase; POD: Guaiacol Peroxidase; CAT: Catalase; APX: Ascorbate Peroxidase; GR: Glutathione Reductase; SD: Severe Drought; LD: Light Drought; CK: Control; SW: Severe Waterlogging; LW: Light Waterlogging.



leaves of Yidan629 at the V6 stage under water stress.

Different effects on APX activities in roots and leaves were observed under different water stress treatments at different growth stages of both varieties (Table 2). Except that the SD treatment significantly reduced root APX activity in Denghai9 at the V6 stage, other water stress treatments had no effects as compared with the CK plants. However, APX activities in the root of Yidan629 markedly increased at the V3 stage under waterlogging treatments and at V6 stage under SW treatment. A significant increase in APX activity was also detected at the V3 stage in the leaves of Denghai9 under SW treatment and in the leaves of Yidan629 under LW treatment ($P < 0.05$). At the V6 stage, all water stress treatments induced marked increases in APX activities in the leaves of Denghai9, whereas only the two waterlogging treatments apparently enhanced APX activities in the leaves of Yidan629 ($P < 0.05$).

The GR activities in the roots and leaves of both cultivars at V3 stage were significantly inhibited in both cultivars, particularly under the SD and SW treatments ($P < 0.05$, Table 2). No notable change in GR activity was detected in roots, but a significant decrease in leaves was noted at the V3 stage in both cultivars. GR activities in the roots and leaves of both cultivars were maintained at lower levels during the V6 stage under SD treatment than under CK treatment. However, at the V6 stage, significant increases in GR activity were observed in the roots and leaves of both cultivars under LW and SW treatments ($P < 0.05$).

In order to understand the functional patterns of antioxidant enzymes under a certain water stress condition, we summarized the antioxidant enzymes and their physiological activities (change index in Figure 3). Significant changes in their activities were noted in comparison with the respective CK plants. At the V3 stage, SOD and POD activities were substantially higher

in the roots and leaves of both cultivars under waterlogging treatment than in the control ($P < 0.05$). Also, the POD, CAT, and GR activities were stimulated in the roots of Denghai9 under the LD treatment, whereas the CAT activity in the leaves of both cultivars was significantly higher in response to drought and waterlogging treatments. However, at the V6 stage, significant increases in POD, CAT, and GR activities were detected only in the roots of both cultivars under the LD treatment, only the POD activity was also markedly higher in roots under water stress treatment. Moreover, the CAT and POD activities were slightly greater in the leaves of both cultivars under SD and LW treatments, respectively. Yet, the prominent antioxidant activities were detected in both growing stages of Denghai9 under both drought and waterlogging stress conditions. Although the increase in activity of these antioxidant enzymes was greater under waterlogging condition in both growth stages, most prominently, different antioxidant enzymes came into play in root and leaf along with the duration of water stress.

DISCUSSION

Maize may frequently be subjected to both drought and waterlogging stress during its growing period in tropical and subtropical regions (Prasanna, 2016). Few previous studies have evaluated the similarities and differences in responses of maize genotype under both drought and waterlogging stress, an understanding of which may benefit the selection of adaptive varieties in these regions. Previous studies have revealed that maize seedlings alter their physiological processes and growth depending on the extent of drought or waterlogging (Zhang *et al.*, 2003; Li *et al.*, 2013; Mejri *et al.*, 2016). In our study, compared with the controls, waterlogging conditions were observed to have more pronounced effects on root and shoot growth in both cultivars than drought stress (Figure 1 and Table 1). Malondialdehyde contents, an indicator of possible oxidative damage of

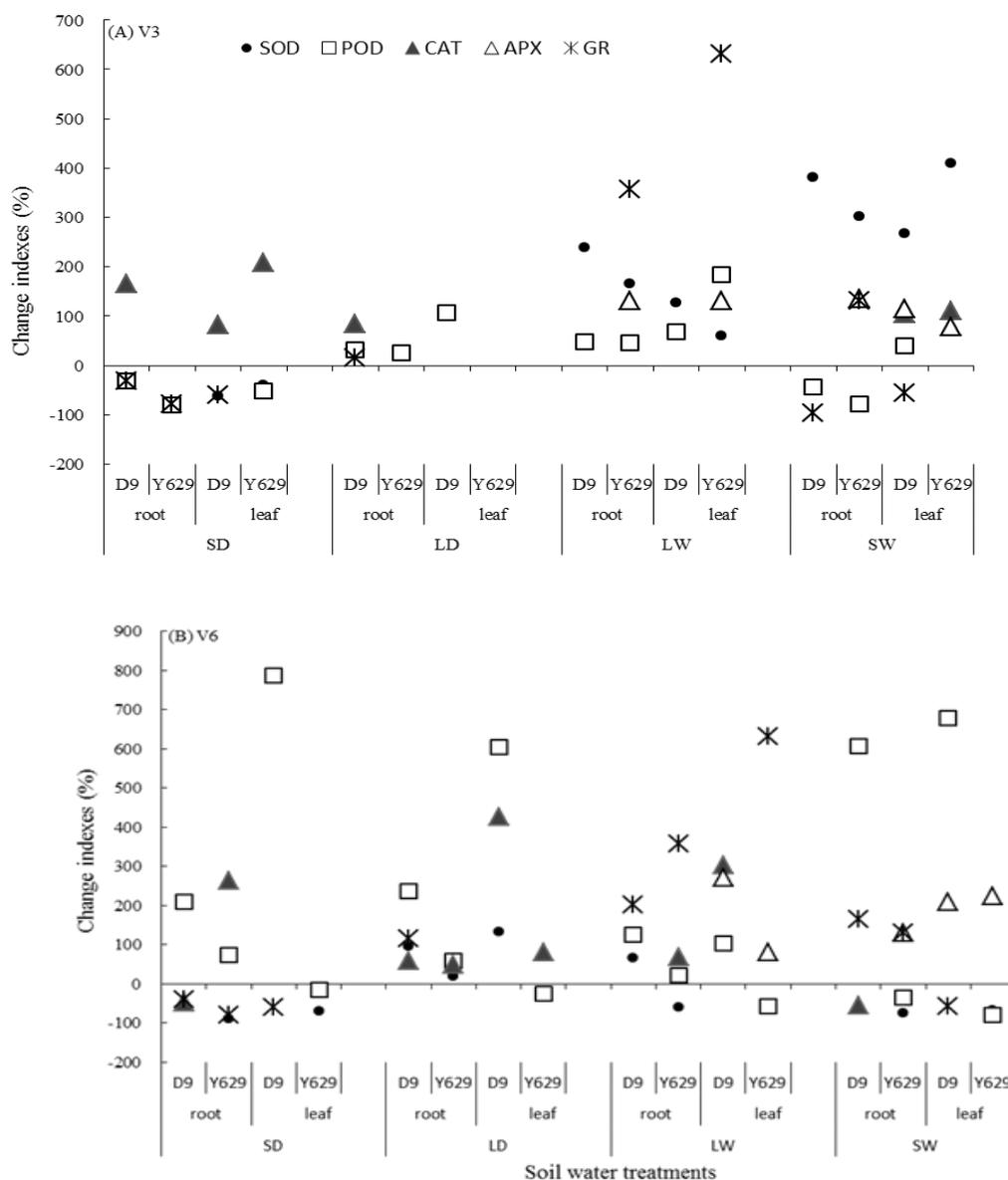


Figure 3. Effects of water stress on significant changes in antioxidant activities on roots and leaves of maize seedlings.

membrane lipids, which are dependent upon the intensity and duration of stress (Mafakheri *et al.*, 2011; Zhang *et al.*, 2011; Sharma *et al.*, 2012), have been shown to increase in leaves and roots under soil water stress conditions (Tang *et al.*, 2010). Our data showed that the relatively marked increase in root and leaf MDA induced by waterlogging was detected at the V6 stage. These results may help to explain the lower biomass and RGR of maize seedlings under waterlogging. Previous studies have shown that growth inhibition was more

pronounced in roots than in shoot under waterlogging stress (Liu *et al.*, 2010; Zaidi *et al.*, 2003). However, in our study, the shoots of maize seedlings showed a reduction in biomass similar to that observed in roots under these conditions, as indicated by the Change Index (CI) (Table1). Compared with waterlogging, drought stress had a comparatively less severe impact on the RGR and biomass accumulation of maize seedlings. Comparable findings have been reported in wheat crops that waterlogging had a more adverse effect than the drought



condition (Malik *et al.*, 2001). Our study further confirmed that waterlogging in tropical or subtropical regions is a greater potential threat to maize seedlings than drought stress (Grzesiak *et al.*, 2014).

In maize, the root is considered the primary sensor and the most important plant part with respect to tolerance to drought and waterlogging (Pearson *et al.*, 2013; Loades, 2013; Grzesiak *et al.*, 2014). In the present study, waterlogging had a more pronounced effect on root length, volume, and surface area than did drought in both maize cultivars (Table 1). However, in our study, the root morphological traits of the two maize cultivars displayed distinct responses to drought stress. In spite of inhibition of root length at the V3 stage, both cultivars under LD treatment surpassed their respective CK plants in terms of root length at the V6 stage (Table 1). Other researchers also found that drought stress significantly increased root length (Tuna *et al.*, 2010; Kavas *et al.*, 2013; Comas *et al.*, 2013), while root volume of maize seedlings were not affected by light drought condition. Similar behavior of root volume in maize under water-deficient conditions has been reported previously (Andrade *et al.*, 2002; Earl and Davis, 2003). Root surface area was noticeably reduced in eggplant grown under ambient and elevated CO₂ environment by water stress (Sarker and Hara, 2010). In our study, the constant decrease in root surface area in both cultivars under waterlogging treatments was observed. Huang *et al.* (2012) reported that root surface area was significantly increased under drought conditions. However, in the present study, root surface area under drought stress responded inconsistently in both cultivars. Denghai9 gained comparative value in root surface area as its CK plants under LD stress, while Yidan629 cultivar showed a consistently lower root surface area under drought.

Previous studies have revealed that SOD, APX, POD, and GR enzymes trigger the plant antioxidative defense system under soil water stress conditions (Hongbo *et al.*, 2005; Yang *et al.*, 2008). However, few studies have reported the temporal patterns and relationships of these antioxidative enzymes under soil water stress conditions. Among the antioxidant enzymes, SOD constitutes the first line of defense that

facilitates the detoxification of superoxide radicals, thereby maintaining the membrane integrity of plant tissue (Nagy *et al.*, 1995; Sairam and Saxena, 2000; Lin *et al.*, 2006; Qadir *et al.*, 2004; Zhang *et al.*, 2014). Our results indicated that SOD activity was increased in the roots and leaves of both varieties at the V3 stage under waterlogging conditions (Table 2 and Figure 3), whereas, dully activated in the roots of Yidan629 at the V6 stage. Under water stress, the leaves are highly capable of increasing the number and intensity of POD isoforms (Abedi and Pakniyat, 2010). Noticeably, in both maize cultivars, POD showed a consistent level of activity at the two growth stages under light drought and waterlogging, particularly in roots (Table 2 and Figure 3). This contrasts with the results reported by Ekmekci *et al.* (2008), who observed that POD activity in the leaves of maize crops increases with the accumulation of high levels of toxic compounds and decreases with low levels. Previous studies have reported inconsistent findings regarding CAT activity, which variously being observed to increase, decrease, or remain constant under drought conditions (Zhang and Kirkham, 1996). In our study, CAT activity was increased markedly at the V3 stage in both cultivars under SD conditions (Table 2 and Figure 3), and similar findings were reported in previous studies (Gechev *et al.*, 2006; Kavas *et al.*, 2013). High CAT concentrations induced by drought stress may lead to the removal of O₂ and H₂O₂ (Sairam *et al.*, 2000; Dat *et al.*, 2001) and reduction in the levels of reactive oxygen species under stress conditions (Willekens *et al.*, 1997); however, effective removal of these toxic products was not observed under waterlogging stress. APX activity has been shown to confer flooding tolerance in roots and leaves (Lin *et al.*, 2006). Moreover, an increase in APX activity under increasing levels of stress suggests that it plays an important role in scavenging H₂O₂ (Tang *et al.*, 2010), particularly since APX has a higher affinity for H₂O₂ than CAT or POD (Wang *et al.*, 1999). However, in the present study, higher APX activity was only consistently detected in leaves under waterlogging stress, whereas it did not show activity in roots under drought stress or waterlogging. Badawi *et al.* (2004) suggested

that CAT and APX, in conjunction with SOD, play a central protective role in the O₂⁻ and H₂O₂ scavenging process and that the activity of these enzymes is related, at least in part, to waterlogging-induced oxidative stress tolerance in maize seedlings.

CONCLUSIONS

In conclusion, the present study demonstrated that both drought and waterlogging conditions strongly inhibit the vegetative growth of maize seedlings and the scale of impact depends upon the level and duration of stresses. This study revealed that waterlogging had a more discernible impact on the seedling growth of both cultivars than drought stress. The Relative Growth Rate (RGR) and root morphological traits dramatically decreased with the duration of waterlogging stress. However, RGR of root under drought conditions was not suppressed as compared to the control. Although root morphological traits significantly decreased under SD treatment before V3 stage, root length and surface area recovered to the similar level in the control at V6 stage. The MalonDiAldehyde (MDA) content increased significantly in both cultivars when plant was subjected to waterlogging treatment, but greater membrane damage was observed in V6 than in V3 stage. Our results suggested that waterlogging had greater potential threat in tropical and subtropical regions than drought on maize seedling. Antioxidant enzymes exhibited different functional pattern under drought and waterlogging stress. Joint working of SOD, POD, APX, and GR were found at V3 stage of maize seedling, while POD, APX, and GR more active at V6 stage. However, only CAT and POD activities were observed enhanced under drought stress. We conclude that SOD, POD, APX, and GR are the most important antioxidant enzymes under waterlogging, while CAT and POD seemed to play key role under drought stress. Additional information is needed to deeply understand physiological and morphological responses of maize cultivars to varying stresses and facilitate further study.

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واکنش های مرفولوژیکی و فیزیولوژیکی گیاهچه ذرت در شرایط خشک و ماندابی

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چکیده

ماندابی و خشکی محدودیت های شدیدی برای رشد گیاهچه ذرت در مناطق استوایی و نیمه استوایی ایجاد میکند. به منظور انجام بهنژادی و اصلاح نژاد و مدیریت مزرعه ای بهتر، بسیار مهم است که تفاوت های مرفولوژیکی و فیزیولوژیکی واکنش های ذرت به خشکی و زیادی رطوبت خاک تعیین شود. در پژوهش حاضر، سطوح مختلف آب قابل دسترس خاک در مرحله تکبرگی (V1) دو کولتیوار ذرت (به نام های Denghai9 و Yidan629) به این صورت اجرا شد: شاهد (CK)، خشکی شدید (SD)، خشکی کم (LD)، ماندابی شدید (SW)، و ماندابی کم (LW). نتایج حاکی از آن بود که ماندابی تاثیر شدیدی از تنش خشکی روی رشد گیاهچه هر دو کولتیوار ذرت داشت. نرخ نسبی رشد (RGR) شاخساره و ریشه همراه با طول ریشه، حجم و سطح ریشه هر دو کولتیوار همگی به طور قابل ملاحظه ای در تنش مانداب کم شد. در تیمار مانداب، محتوای مالون دی آلدنید در برگ و ریشه به طور چشمگیری افزایش یافت. در هر دو کولتیوار در تنش مانداب، سوپراکسید دیسموتاز (SOD) اکثرا در ریشه و برگ در مرحله سه برگی (V3) فعال شد در حالیکه فعالیت کاتالاز (CAT) ظاهرا در تنش خشکی افزایش یافت. در تیمار های تنش خشکی و ماندابی، فعالیت پراکسیداز (POD) به طور چشمگیری افزایش یافت. آسکوربات پراکسیداز (APX) با طولانی شدن تنش ماندابی فعالیت ثابتی نشان داد و فعالیت گلوکاتایون ردوکتاز (GR) در شرایط ماندابی در مرحله شش برگی (V6) افزایش چشمگیری در ریشه نشان داد. نتیجه اینکه SOD، POD، APX، و GR مهمترین آنزیم های آنتی اکسیدان در شرایط مانداب بودند در حالیکه به نظر می رسد CAT و POD در شرایط خشکی نقش کلیدی بازی میکنند.