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Dynamic responses of root vigor, lipid peroxidation and antioxidant enzymes in *Artemisia selengensis* to long-term drought and re-watering

Hui-xiong Huang · Yun Cao · Kai-jing Xin · Rong-hua Liang · Yi-ting Chen · Jia-jun Qi

Abstract *Artemisia selengensis* is a typical wetland plant with valuable nutritional and medical purposes, and its growth and field distribution is highly dependent on water conditions. However, wetland hydrology is becoming more complex due to global climate change, and the future response of *A. selengensis* to water deficits and rehydration is uncertain. We here conducted simulations to investigate physiological variations in *A. selengensis* in response to varying degree of soil moisture (85–90%, 60–65%, 45–50%, and 30–35%) and re-watering. Results show that drought boosted root vigor and increased water and soil nutrient absorption in *A. selengensis*. As drought conditions progressed, the superoxide anion (O_2^-) and malondialdehyde content significantly increased. This led to increased activity of antioxidant enzymes, which significantly inhibited O_2^- content. Root vigor and peroxidase (POD) activity were fully recovered after rehydration. The O_2^- and MDA content, and catalase (CAT) activity also fully recovered under moderate and mild drought, although full recovery can take longer under severe drought. Superoxide dismutase (SOD) activity decreased significantly after rehydration, but SOD activity in drought conditions has not yet recovered to the control level. *A. selengensis* is drought tolerant due to its high root vigor and the regulation of antioxidant enzyme system. Our results may provide guidance for the future population dynamics of wetland ecosystems under climate change.

Keywords *Artemisia selengensis* · Water deficit · Rehydration · Malondialdehyde · Antioxidant enzyme

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Introduction

Abiotic and biotic stresses are common challenges in the life history of plants (Gechev and Petrov 2020), such as drought, flooding, salinity, temperature extremes, light conditions, chemical toxicity, and pathogen attacks (Gill and Tuteja 2010; Atapaththu and Asaeda 2015; Garssen et al. 2015). Among these stress factors, drought is one of the most severe abiotic challenges that plants face (Mahajan and Tuteja 2005). Drought causes water loss in plant cells,

leading to major changes in plant morphology (Eziz et al. 2017), physiology and biochemistry (Zhanassova et al. 2021), and limits the ecological niche and survival space of many plants (Gaviria et al. 2017). Various evidence shows that global warming and climate change have been exacerbated by the impact of human activities, and subsequently has increased the amplitude of climate system variability (IPCC 2021). This can be observed in the increased frequency and intensity of extreme heat events, extreme precipitation events, and agricultural and ecological droughts in some regions (Ummenhofer and Meehl 2017). Water within these regions is unevenly distributed both spatially and temporally, where plants usually undergo cycles of drought and rehydration throughout their life cycle. Therefore, the study of plant adaptation and tolerance mechanisms to drought, as well as recovery ability after re-watering, is critical in predicting the impacts of ongoing climate change (John et al. 2018).

There have been many studies on plant response mechanisms to abiotic stress (Bornette and Puijalon 2011; Li et al. 2013; Das et al. 2016), and part of those results show that drought stress induces excess reactive oxygen species (ROS) and causes damage to the membrane system of plant cells (Voss et al. 2013; Guan et al. 2015). ROS are also produced continuously as by-products of various metabolic pathways that are localized in different cellular organelles such as chloroplast, mitochondria and peroxisomes (Navrot et al. 2007). Under stress, the balance of intracellular ROS production and scavenging is disrupted, and excessive accumulation of ROS can directly or indirectly trigger membrane lipid peroxidation, of which malondialdehyde (MDA) is the final product (Cuin and Shabala 2008). Thus, ROS concentration can be used as an important indicator to monitor the physiological state of plants and to quantify the plant response to the intensity of environmental stress (Asaeda et al. 2022). Superoxide anion (O_2^-) is a major reactive oxygen species, and its accumulation seriously damages plants through lipid peroxidation, protein degradation, breakage of DNA and cell death (Gill and Tuteja 2010). To cope with the increased ROS level, plants possess well-developed antioxidative systems which are composed of non-enzymic defense and enzymatic antioxidants to scavenge overproduced ROS (Mansoor et al. 2022), thereby avoiding deleterious effects. Superoxide dismutase (SOD),

catalase (CAT) and peroxidase (POD) are major components of the antioxidant protective enzyme system, which can reduce the toxic effect of ROS on cells (Bhaskaran and Panneerselvam 2013); therefore, they are often used as physiological biomarkers of crop stress resistance. The root is the first affected part of a plant directly faced with drought stress (Brunner et al. 2015) and the major organ for the uptake of water and nutrients (Kim et al. 2020). It is widely acknowledged that changes in root architecture and metabolism can influence aboveground characteristics, such as seed yield and photosynthesis (Cui et al. 2016). Therefore, root development and activity are inhibited when plants are grown in a water-deficit environment, which causes a series of depressive effects on the physiological functions of above-ground parts. In addition, root vigor is considered an essential physiological characteristic for measuring the growth of terrestrial plants, which can reflect the absorptive, synthetic, oxidative, and reducing capacities of the root system (Kajikawa et al. 2010). Therefore, a sufficient level of root vigor is crucial for plants to adapt to drought and to recover normal metabolism after the stress is relieved.

In the middle and lower reaches of the Yangtze River in China, *A. selengensis* is a herbaceous perennial plant of the *Compositae* family that is widely distributed in wetlands, marshes, wet meadows, and freshwater lake meadows (Zhang et al. 2018). *A. selengensis* has been used as wild vegetable and medicinal herb in China, and a variety of antioxidants and anticarcinogenic substances can be extracted from the plant (Zhang et al. 2015; Wang et al. 2016). Most of the current research on the effects of drought stress on plants has focused on crops (Voronin et al. 2019; Auler et al. 2021) and medicinal herbs (Yan et al. 2015). Other studies considered the physiological response of plants to re-watering after drought stress, suggesting that re-watering has a compensatory effect on the growth and physiological characteristics of plants (Liu et al. 2021). Most of these previous studies focused on arid plants distributed in arid and semi-arid regions. However, compared with arid plants, wetland plants are endangered by drought stress and also face the situation of rising water tables, and these stresses have magnified under the background of climate change and frequent extreme weather (Deng et al. 2022). When the water level in a wetland exceeds or is below the ecological amplitude

of wetland plants, it will lead to poor growth and possibly mortality (Luan et al. 2013; Yan et al. 2020). However, less attention has been paid to drought stress in wetland plants growing in wet areas over time, and no studies have been reported on the physiological characteristics of *A. selengensis* in response to drought stress and rehydration.

We here investigate the physiological response of *A. selengensis* to different drought levels and rewatering through simulation experiments to reveal the adaptation mechanism of *A. selengensis* to soil water content changes.

Materials and methods

Plant materials

A. selengensis seedlings were used as our primary experimental materials. On January 13, 2021, we collected thriving, homogeneous-sized wild *A.*

selengensis from Poyang Lake National Wetland Park, Jiangxi Province, China (Fig. 1). Poyang Lake is the largest freshwater lake in China with a natural connection to the Yangtze River. The lake is coupled to the river flow and stage, often experiencing dramatic water-level fluctuations and backflow, and these processes are being exacerbated by climate change and human activities. Thus, the plants in the wetland are subjected to intermittent droughts and floods. The collected seedlings were brought back to the laboratory and cut into small sections about 5 cm long, each section having one or two lateral buds. The stems were planted in plastic pots ($35 \times 26 \times 13$ cm^3) with the bottom part buried in the soil for about 2 cm, and 30 plants were planted in each pot. We precultured the *A. selengensis* seedlings for subsequent experimental treatments. The substrate soil used for preculture was extracted from Aixi Lake National Wetland Park, Nanchang City, Jiangxi Province, China. The basic properties of the soil are shown in Table 1.
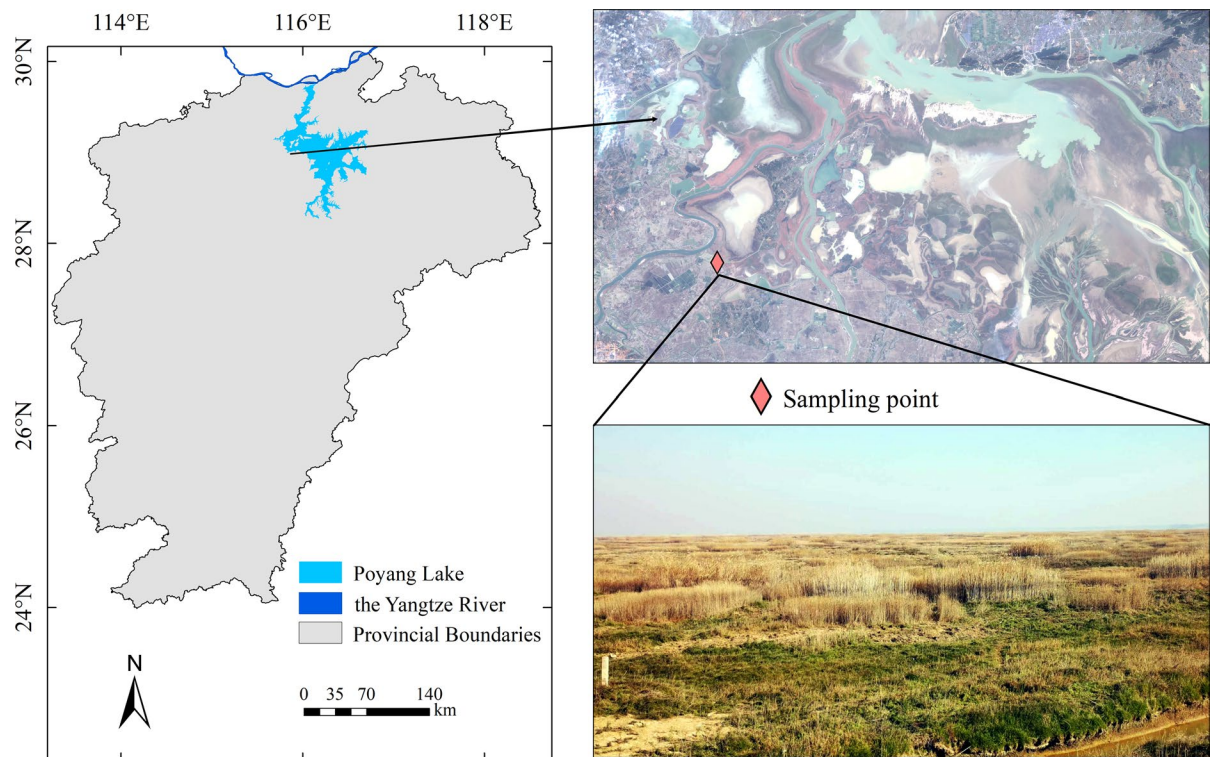
Fig. 1 Overview of the sampling area

Table 1 Basic properties of soils

Soil index	Value
SOM	39 g.kg^{-1}
TN	1.8 g.kg^{-1}
pH	5.4
SWC	43.8%

SOM soil organic matter, *TN* total nitrogen, *SWC* soil saturated water content

Experimental design

The experiment was conducted in the plant sunlight culture room at the Key Laboratory of Poyang Lake Wetland and Watershed Research, Ministry of Education, Jiangxi Province, China, from March to June 2021. The test seedlings were exposed to four soil water contents during the drought treatment: Plants were watered to 85–90% of soil saturated water content (control group, CK), 60–65% of soil saturated water content (mild drought, MID), 45–50% of soil saturated water content (moderate drought, MD) and 30–35% of soil saturated water content (severe drought, SD). In the rehydration stage, all treatment groups were watered to 95–100% of soil saturated water content. Three pots of *A. selengensis* seedlings were placed in each test group, totaling 12 pots. Before the experiment, soil water content was measured using an HH2 soil moisture meter (Delta-T, UK) and controlled to the setting drought levels by adjusting the watering rate and natural evaporation. To maintain the soil water content at the set levels in all treatment groups during the experiment, it was measured daily at 17:00 with soil moisture meter, followed by quantitative water replenishment. The drought experiment began on March 23 and ended on June 1, 2021, for 70 days. All treatment groups were rehydrated to SWC after 70 days and rehydrated for 28 days. The overall duration of the experiment was 98 days. During the experiment, the culture room was naturally illuminated with an average air temperature of 26.1 ± 5.9 °C and average air humidity of $77.09 \pm 14.08\%$.

Analyzed parameters

Sampling

On days 0, 14, 28, 42, 56, and 70 after initiation of the drought treatment and days 14 and 28 after re-watering, we measured the physiological parameters of plants in each pot. On the sampling day, we chose all-green functional leaves except for the top three leaves that were used as samples, because this could reflect the function of plant leaves without affecting photosynthesis. The root of a part of the seedlings was excavated and washed to measure root vigor. Three samples were collected per potted plant ($n=3$), and all samples were immediately frozen.

Root vigor assay

The TTC method (Zhang et al. 2019) was used to measure the root vigor of plants. Dehydrogenases in plant roots reduce TTC and produce red, water-insoluble trithizone. Therefore, the amount of TTC reduction can indicate dehydrogenase activity and serve as an indicator of root vigor. We next weighed 200 mg of fresh root sample in a test tube, added 5 mL each of 0.4% TTC solution and 1/15 mM phosphate buffer solution (PBS) and soaked for 3 h. The reaction was then terminated by adding sulfuric acid. The root sample was taken, ground with ethyl acetate and fixed to 5 mL. The absorbance was measured by spectrophotometer at 485 nm (Jinghong Experimental Equipment Co., Ltd., Shanghai, China), and the amount of TTC reduction was obtained from the standard curve.

Determination of MDA and O_2^- content

MDA content was determined by the thiobarbituric acid (TBA) method (Dong et al. 2019). In total, 500 mg of fresh leaf samples was ground with 5% trichloroacetic acid (TCA), and the ground homogenate was centrifuged at 3000 r/min for 10 min. Two milliliters of upper supernatant was added with 2 mL of 0.67% TBA, mixed thoroughly, placed in a boiling water bath for 30 min, cooled rapidly and centrifuged again. The absorbance of the extracts was measured at 450 nm, 532 nm and 600 nm, respectively. The concentration of MDA in the extract can be used to determine MDA content in the sample using:

$$C\left(\mu\text{mol} \cdot L^{-1}\right) = 6.45\left(A_{532} - A_{600}\right) - 0.56A_{450}$$

where *C* represents the MDA concentration in the extract; A_{450}, A_{532} and A_{600} represent the absorbance values at 450 nm, 532 nm and 600 nm, respectively.

The O_2^- content was determined using the hydroxylamine oxidation method (Li et al. 2010). The fresh leaf tissue (200 mg) was ground in 5 mL of PBS (pH 7.8), and the homogenate was centrifuged at 3000 r/min for 10 min. After adding 0.5 mL of 50 mM PBS (pH 7.8) and 1 mL of 10 mM hydroxylamine hydrochloride to the supernatant (0.5 mL), the mixture was incubated at 25 °C for 1 h and then adding 1 mL of 17 mM sulfanilamide and 1 mL of 7 mM naphthylamine. After standing for 20 min at 25 ℃, the absorbance of the solution was measured at 530 nm. The O_2^- content was calculated using the nitrite radical (NO_2^-) standard curve.

Determination of SOD activity

The 200 mg fresh leaf samples were ground with PBS (pH 7.8, contains 1% polyvinylpyrrolidone) and fixed to 5 mL and then centrifuged (4000 r/min) to obtain the supernatant. SOD activity was measured based on the inhibition of the reduction of nitrogen blue tetrazolium (NBT) by SOD under light conditions. The 50 mM PBS (pH 7.8), 130 mM methionine, 100 μM EDTA, 750 μM NBT and 20 μM riboflavin were added to 0.05 mL supernatant, and the mixture was reacted under light (4000 Lx) for 20 min, and then the absorbance was measured at 560 nm. One unit of SOD activity was defined as the amount of enzyme that inhibits 50% NBT photoreduction.

Determination of POD activity

The POD activity was measured by guaiacol method. Two hundred milligrams of fresh leaves was chopped, ground in a mortar with PBS (pH 5.5, contains 1% polyvinylpyrrolidone) and fixed at 5 mL to obtain homogenate, which was then centrifuged (3000 r/min) for 10 min to obtain the supernatant, then refrigerated and stored. The reaction system for the POD assay included 50 mM PBS (2.9 mL), 2% H_2O_2 (1 mL), 50 mM guaiacol (1 mL) and supernatant (0.1 mL). The mixture was held at 37 °C for 15 min, and then the reaction was terminated by adding 20% trichloroacetic acid (2 mL). The boiled enzyme supernatant was used as a control. The absorbance was measured at 470 nm after centrifugation and read once per minute for 4 min, and the change in absorbance of 0.01 per minute was used as one POD activity unit.

Determination of CAT activity

The UV absorption method was used to assay CAT activity. First, 200 mg of fresh leaves was ground and fixed with PBS (contains 1% polyvinylpyrrolidone) of pH 7.8 to obtain a homogenate, which was then centrifuged at 4000 r/min for 15 min, and the supernatant was the crude CAT extract. The extracts (0.2 mL), 0.2 M PBS (1.5 mL) and 0.1 M H_2O_2 (0.3 mL) were mixed, and then the absorbance was measured at 240 nm and read once per minute for four minutes. The amount of enzyme decreasing by 0.1 per minute of absorbance was used as one CAT activity unit. The determination of SOD, POD and CAT activity was based on the *Principles and Techniques of Plant Physiological and Biochemical Experiments* (Wang 2006).

Statistical analysis

At least three replicates were used in this study, and all data are presented as mean ± standard deviation (SD). Statistical analysis was performed using SPSS 26.0 (SPSS Inc., Chicago, IL, USA) software, and the effects of drought and rehydration on *A. selengensis* were analyzed by one-way variance analysis (ANOVA) using Duncan's multiple range tests ($p < 0.05$). Two-way variance analysis (two-way ANOVA) was used to analyze the treatment × time interaction with the physiology of *A. selengensis*. Pearson's correlations were calculated to measure the relation of the variables. All figures in this paper were produced by Origin 2021b.

Results

Effects of drought and re-watering on root vigor

Root vigor showed different behavior depending on the soil moisture (Fig. 2), and the effects of soil moisture, duration and their interactive effect on root vigor were highly significant as shown in Table 2 ($p < 0.001$). The trends of root vigor in different drought groups were consistent during the drought period. Root vigor in the drought groups increased rapidly with treatment time for days 0–28 days, and each group's root vigor was ranked as: SS > MD > MID > CK. For days 42–70, root

Fig. 2 Effects of different levels of drought and re-watering on root vigor. RW14: 14th day of re-watering, RW28: 28th day of re-watering, different capital letters stand for significant differences between different experimental times ($p < 0.05$), and different lowercase letters stand for significant differences between different drought groups ($p < 0.05$)
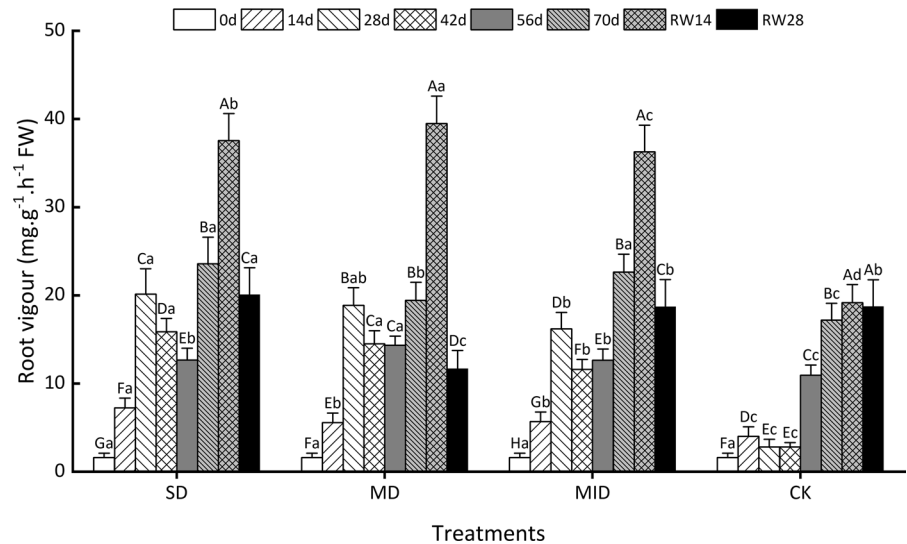
Table 2 Result (*F*-value) of two-way ANOVA of physiological indexes of *A. selengensis* under different soil moistures and treatment times

Test indicators	Soil moisture	Time	Soil moisture × Time
Root vigor	598.037***	1280.926***	69.753***
MDA	28.932***	164.346***	4.071***
O_2^-	36.765***	196.171***	31.774***
SOD	28.684***	33.560***	38.020***
POD	125.868***	469.869***	55.783***
CAT	690.081***	1256.967***	35.338***

*$p < 0.05$

**$p < 0.01$

***$p < 0.001$

vigor decreased and then increased and reached a maximum at 70 days, and root vigor in the drought groups was significantly higher than that of the CK group ($p < 0.001$). After 14 days of re-watering, the root vigor increased in all treatments as compared to 70 days, and the SD, MD, MID, and CK groups increased by 14.00, 20.06, 13.65, and 1.97 mg. g^{-1}.h^{-1}, respectively, with significant differences ($p < 0.001$). After 28 days of rehydration, root vigor decreased in all groups, and the root vigor in drought groups was significantly different than pre-rehydration ($p < 0.01$). The root vigor under SD was significantly higher than that of the CK group ($p < 0.001$), the MD group was significantly lower than that of the CK group ($p < 0.001$), and the MID

group was not significantly different from the CK group.

Effects of drought and re-watering on MDA content

The MDA content of drought groups increased for days 0–28, decreasing for days 28–42 and increasing again for days 42–70, while the MDA content of the CK group was relatively stable in 0–56 days (Fig. 3). During the drought period, the MDA content in the SD, MD and MID groups was generally significantly higher than that of the CK group ($p < 0.05$). Longer drought treatment time increased the difference in MDA content between drought groups, and that of the SD group was significantly higher than that of other treatment groups at 70 days ($p < 0.05$). The change of MDA content was influenced by the drought degree, but drought duration also affected it significantly ($p < 0.001$; Table 2). After 14 days of re-watering, each group showed different changes, and MDA content increased in the MD, MID and CK groups, while it decreased in the SD group. The MDA content of the CK group was significantly higher than those of drought groups, and the SD group was significantly lower than the MD group and the MID group ($p < 0.001$), while those of MD and MID were closer and the difference was not significant. After 28 days of rehydration, the MDA content of each group decreased, and that of drought groups was even significantly lower ($p < 0.05$) than pre-rehydration. The content of MDA in the SD, MD and MID groups was

Fig. 3 Effects of different levels of drought and re-watering on MDA content. RW14: 14th day of re-watering, RW28: 28th day of re-watering, different capital letters stand for significant differences between different experimental times ($p < 0.05$), and different lowercase letters stand for significant differences between different drought groups ($p < 0.05$)
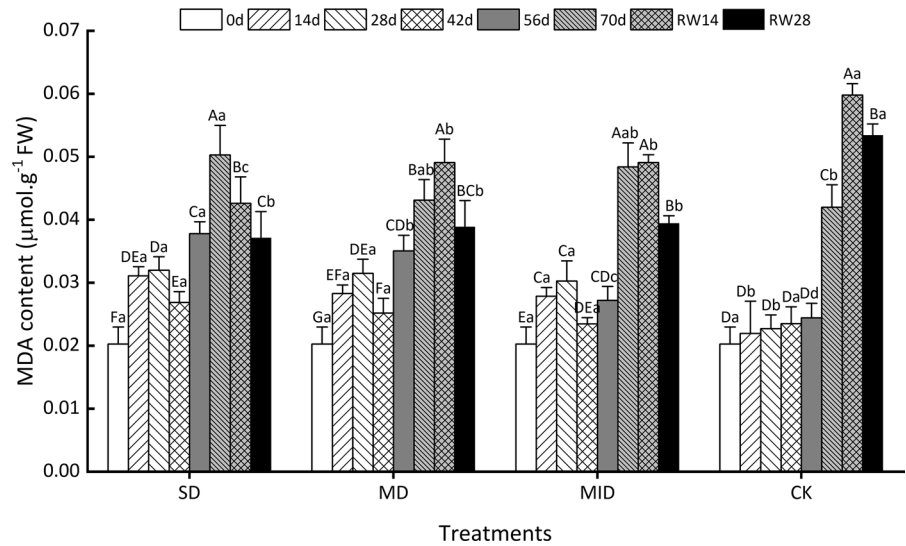
closer and did not show significant differences. However, they were significantly lower than the CK group ($p < 0.001$).

Effects of drought and re-watering on O_2^- content

During the drought period, the O_2^- content fluctuated significantly among drought groups, which first increased and then decreased (Fig. 4). For days 0–28 days of drought treatment, the O_2^- content was not significantly different among the SD, MD and MID groups, and was generally higher than that of the CK group ($p < 0.001$). For days 42–70, the O_2^- content

in drought groups was gradually lower than that of the CK group, and the O_2^- content was lower with deeper drought. As shown in Table 2, the O_2^- content was significantly ($p < 0.001$) affected by the drought level and treatment duration; thus, it varied with drought time and level. After re-watering, the O_2^- content increased in all groups and the difference was highly significant ($p < 0.001$) compared to 70 days. The O_2^- content of each group was ranked as MD > MID > SD > CK, and there was a highly significant difference between these groups ($p < 0.001$). After 28 days of rehydration, the O_2^- content in all groups decreased, and that of the MD group and MID group was significantly

Fig. 4 Effects of different levels of drought and re-watering on O_2^- content. RW14: 14th day of re-watering, RW28: 28th day of re-watering, different capital letters stand for significant differences between different experimental times ($p < 0.05$), and different lowercase letters stand for significant differences between different drought groups ($p < 0.05$)
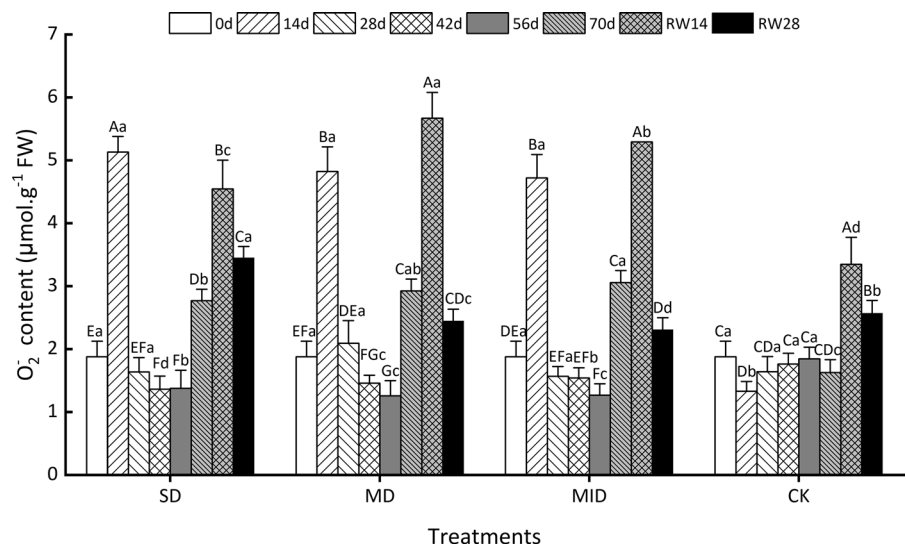
lower ($p < 0.05$) than pre-rehydration. In this case, the O_2^- content differed significantly among the different treatment groups, which were higher in the SD group and lower in the MD and MID groups compared to the CK group. In general, the O_2^- content trend was consistent with MDA under drought and rehydration.

Effects of drought and re-watering on antioxidative enzyme activity

SOD activity was significantly ($p < 0.001$) influenced by drought level, treatment time and their interaction effects (Table 2). The SOD activity was significantly higher during days 0–28 (Fig. 5a), and the SOD activity in drought groups was higher than that of the CK group at 28 days ($p < 0.01$). At 42 days, the SOD activity in the MID group was lower than that of other groups (Table 3A), and that of the SD group and MD group was significantly different from the CK group ($p < 0.001$). At 70 days, the SOD activity of the MID group reached the maximum value followed by SD, MD and CK, respectively, exhibiting significant differences among treatments ($p < 0.001$).

After re-watering, the SOD activity significantly decreased in all treatments compared to that of 70 days ($p < 0.001$). The comparison between groups revealed that the SOD activity of the MD group was significantly higher than that of the CK group at 14 days after rehydration ($p < 0.001$), while that of the SD group and the MID group was statistically similar to the CK group. The SOD activity of the SD group and MID group changed slightly from 14 to 28 days after re-watering, and that of drought groups was significantly higher than that of the CK group ($p < 0.05$).

POD activity was also significantly ($p < 0.001$) influenced by the drought level, treatment time and their interaction effects (Table 2). The POD activity of all groups showed an increase followed by a decrease during the drought treatment stage (Fig. 5b). For days 0–28, the POD activities of all drought groups were significantly lower than that of the CK group ($p < 0.001$) (Table 3B). For days 42 to 56, the POD activity of the MD and MID groups was significantly higher than that of the CK group, while that of the SD group was lower ($p < 0.001$). At 70 days, the maximum POD activity was found
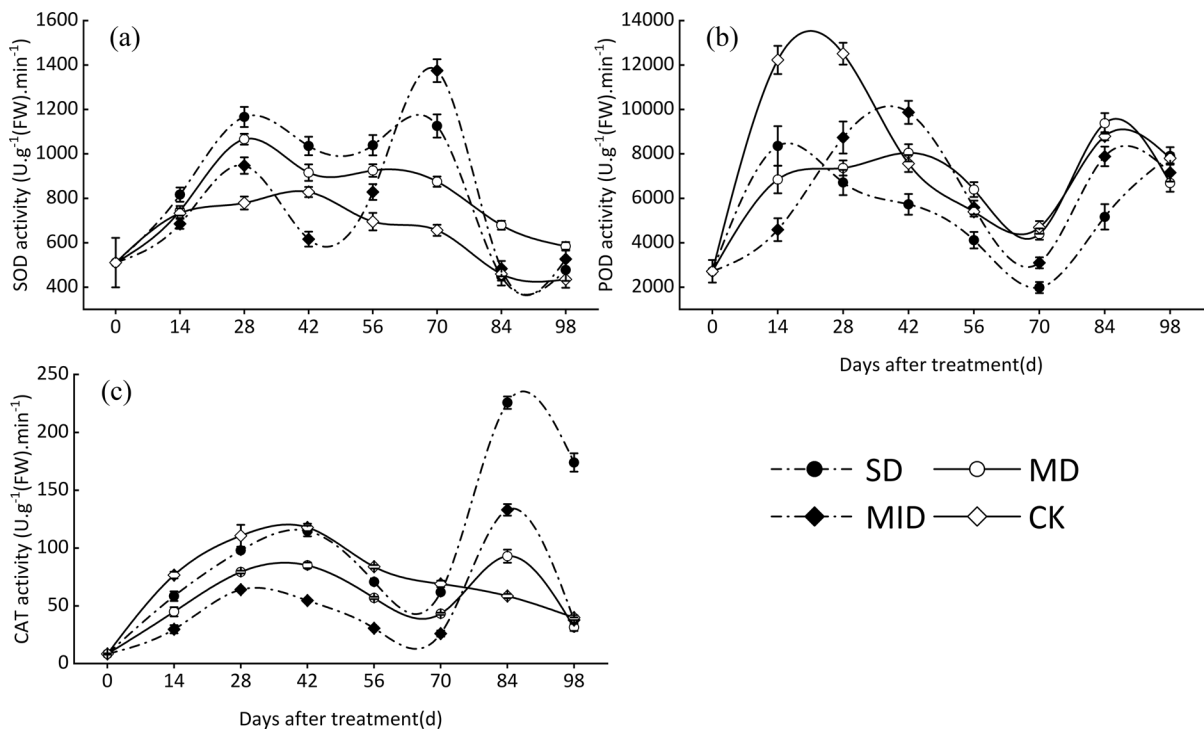
Fig. 5 Effects of different levels of drought and re-watering on antioxidant enzyme activity. 0–70 d for drought treatment and 70–98 d for re-watering treatment. **a** SOD activity, **b** POD activity, **c** CAT activity

Table 3 Antioxidative enzyme activity in *A. selengensis* leaf during drought stress and re-watering process.

Time	SD	MD	MID	CK
(A) SOD				
0 d	510.58 ± 111.40^{Ca}	510.58 ± 111.40^{Da}	510.58 ± 111.40^{Ea}	510.58 ± 111.40^{Da}
14 d	816.49 ± 31.85^{Ba}	743.92 ± 21.81^{Cb}	685.06 ± 22.36^{Dd}	733.03 ± 21.77^{BCc}
28 d	1166.32 ± 45.40^{Aa}	1065.99 ± 24.21^{Aa}	947.19 ± 37.00^{Bb}	779.06 ± 29.18^{ABc}
42 d	1035.32 ± 41.65^{Aa}	915.61 ± 37.00^{Bb}	616.15 ± 33.57^{Dc}	828.26 ± 22.59^{Ab}
56 d	1038.79 ± 45.65^{Aa}	925.19 ± 28.21^{Bb}	828.39 ± 35.37^{Cb}	695.13 ± 39.50^{Cc}
70 d	1125.74 ± 52.25^{Ab}	875.00 ± 22.99^{Bc}	1374.94 ± 51.45^{Aa}	656.08 ± 25.02^{Cd}
RW14d	448.28 ± 40.57^{Cc}	678.86 ± 20.00^{Ca}	483.08 ± 34.69^{Eb}	459.27 ± 29.50^{Dbc}
RW28d	477.46 ± 49.21^{Cc}	583.93 ± 19.12^{Da}	526.42 ± 42.14^{Eb}	435.36 ± 38.31^{Dd}
(B) POD				
0 d	2714.90 ± 509.75^{Ea}	2714.90 ± 509.75^{Fa}	2714.90 ± 509.75^{Ga}	2714.90 ± 509.75^{Fa}
14 d	8358.35 ± 889.52^{Ab}	6845.90 ± 619.00^{CDc}	4586.41 ± 513.25^{Fd}	$12,231.28 \pm 637.25^{Aa}$
28 d	6713.53 ± 568.79^{Bd}	7364.48 ± 338.54^{Cc}	8737.00 ± 720.14^{Bb}	$12,512.41 \pm 491.19^{Aa}$
42 d	5728.94 ± 467.26^{BCc}	8046.72 ± 385.88^{Bb}	9870.34 ± 522.54^{Aa}	7564.62 ± 382.17^{Cb}
56 d	4113.69 ± 369.66^{Dd}	6394.27 ± 332.33^{Da}	5584.43 ± 311.06^{Eb}	5392.64 ± 217.13^{Dc}
70 d	1982.45 ± 249.86^{Ed}	4390.11 ± 255.08^{Eb}	3096.53 ± 250.00^{Gc}	4687.78 ± 286.82^{Ea}
RW14d	5164.71 ± 570.04^{CDd}	9374.80 ± 463.29^{Aa}	7884.80 ± 440.20^{Cc}	8790.83 ± 180.37^{Bb}
RW28d	7906.08 ± 392.34^{Aa}	6683.83 ± 391.13^{Dc}	7156.54 ± 402.12^{Db}	7804.71 ± 232.32^{Ca}
(C) CAT				
0 d	8.29 ± 0.52^{Ga}	8.29 ± 0.52^{Ga}	8.29 ± 0.52^{Fa}	8.29 ± 0.52^{Fa}
14 d	58.40 ± 4.15^{Fb}	44.84 ± 3.99^{Ec}	29.68 ± 3.48^{Ed}	76.58 ± 2.88^{BCa}
28 d	97.93 ± 1.51^{Db}	$79.28 \pm .1.20^{Cc}$	64.01 ± 1.49^{Bd}	110.66 ± 9.45^{Aa}
42 d	114.76 ± 4.63^{Ca}	84.99 ± 2.52^{Bb}	54.57 ± 0.47^{Cc}	117.84 ± 3.21^{Aa}
56 d	70.79 ± 1.57^{Eb}	56.83 ± 1.04^{Dc}	30.60 ± 1.60^{Ed}	83.81 ± 1.584^{Ba}
70 d	61.88 ± 1.57^{EFb}	43.12 ± 0.99^{Ec}	25.96 ± 2.57^{Ed}	68.98 ± 2.86^{Ca}
RW14d	225.84 ± 5.39^{Aa}	92.96 ± 5.69^{Ac}	133.06 ± 5.05^{Ab}	58.47 ± 1.83^{Dd}
RW28d	174.04 ± 7.90^{Ba}	31.29 ± 3.09^{Fb}	37.65 ± 2.24^{Db}	39.76 ± 2.14^{Eb}

Values are given as mean ± SD of three replicates. Different capital letters stand for significant differences between different experimental times ($p < 0.05$), and different lowercase letters stand for significant differences between different drought groups ($p < 0.05$)

RW14: 14th day of re-watering, RW28: 28th day of re-watering

(A) SOD activity

(B) POD activity

(C) CAT activity

in the CK treatment followed by MD, MID and SD, respectively, with significant differences seen among treatments at the $p = 0.01$ level. After 14 days of re-watering, POD activity significantly increased as compared with 70 d ($p < 0.001$), and the difference between groups was significant ($p < 0.001$). After 28 days of rehydration, the POD activity of the SD group continued to increase, while other groups gradually decreased. The POD activity of the MD group and MID group was significantly lower than that of the CK group ($p < 0.001$), but the POD activity of SD group was recovered to the control level.

The activity of CAT was similar to SOD and POD activities, being significantly ($p < 0.001$) influenced by the drought level, treatment time and their inter-action effects (Table 2). Similar to POD, the CAT activity showed an increase followed by a decrease during the drought treatment (Fig. 5c). During this period, the CAT activity of the drought groups was always lower than that of the CK group. In general, the stronger the drought level, the higher the CAT activity. At 70 days, the order of the CAT activity in the different groups was: CK > SD > MD > MID, and the drought groups differed significantly ($p < 0.01$) from the CK group (Table 3C). After 14 days of re-watering, CAT activity increased significantly in the drought groups, which was significantly different from that of 70 days ($p < 0.001$), and CAT activity in the SD group showed the largest growth. The CAT activity of drought groups was significantly higher than that of the CK group ($p < 0.01$) at this time. After 28 days of rehydration, the CAT activity of each group gradually decreased. The CAT activity of the SD group was significantly higher than that of the CK group ($p < 0.001$), while the MD and MID groups recovered to the control level.

Correlation analysis of physiological parameters of
A. selengensis leaves

The correlations between root vigor, MDA, O_2^-,
SOD, POD and CAT were next analyzed in more
detail (Table 4). MDA and SOD showed a signifi-
cant positive correlation with root vigor ($p < 0.01$).
The responses of MDA, SOD and root vigor to water
changes were consistent. MDA was positively cor-
related with SOD, and their relationship was statis-
tically significant ($p < 0.01$). In addition, there is a
strong relationship between antioxidant enzymes,
SOD is positively correlated with CAT ($p < 0.05$),
and POD is positively correlated with CAT ($p < 0.01$).
It is thus highly suggested that multiple antioxidant
enzymes in plants during drought stress work together
to eliminate cell damage caused by ROS.

Discussion

Drought is a key factor limiting plant growth and
development. Root vigor has been proven to be a
reliable and sensitive indicator for assessing drought
resistance (Lan et al. 2022) and reflects root meta-
bolic activity (Liu et al. 2015). Previous studies have
found that drought stress greatly inhibits the root
growth and vigor, such as the root vigor of the aquatic
plants *Arundo donax var. versicolor* and *Typha ori-
entalis* decreases with the increase of groundwater
depth (Chen et al. 2021a, b; Huang et al. 2021). How-
ever, we demonstrated here that different levels of
drought can increase the root vigor of *A. selengensis,*
similar to terrestrial plants. For example, studies com-
paring oxidative damage and antioxidant responses of
two cotton cultivars found that drought-resistant cot-
ton showed increased root length and vigor for bet-
ter productivity under water-deficit conditions (Zhang
et al. 2014). Increased root vigor in potatoes can also

accelerate phosphorus acquisition and thus increases
yield (White et al. 2018). It has been suggested that
drought-tolerant plant species promote aboveground
biomass accumulation by maintaining higher root
vigor under drought conditions, which is a physiolog-
ical mechanism for their higher drought tolerance (Li
et al. 2020). Similarly, *A. selengensis* seedlings may
transport more photosynthetic products to the roots
under drought conditions, enhancing the roots in
up-taking soil nutrients and water by increasing root
vigor. In addition, *A. selengensis* adapts to soil water
deficit by increasing root vigor and also shows a com-
pensatory effect after re-watering, which increases
with the drought degree and duration (Li et al. 2021).

Cell membranes are one of the main targets of
environmental pressure. Lipids are important mem-
brane components that contribute to membrane
integrity and keep cell compartmentalization during
drought stress (Gigon et al. 2004). MDA is the end
product of membrane lipid peroxidation in plants and
represents the degree of damage to cell membranes
by ROS. Here, we found that the MDA content under
drought treatment was higher than that of the CK
group. It indicates that peroxidative damage occurred
in the cell membrane of *A. selengensis*, which led to
an accumulation of an excess level of MDA in cell
tissues. In addition, the MDA content of the drought
groups was substantially reduced at 42 days, indicat-
ing that *A. selengensis* can adapt to drought after suf-
ficient time, and changes in MDA under drought con-
ditions are generally considered to be related to the
drought tolerance and antioxidant system activity of
the plants (Shao et al. 2007). However, the regulatory
capacity of antioxidant system was clearly limited,
as evidenced by the re-increase of MDA content at
the later stages of drought. The observation of MDA
after re-watering is coherent with studies of wheat
seedlings, in which MDA content first increased and
then decreased (Maevskaya and Nikolaeva 2013). In

Table 4 Correlation coefficients between different parameters (*r*) in *A. selengensis* under drought stress

	Root vigor	MDA	O_2^-	SOD	POD	CAT
Root vigor	1	0.818**	−0.077	0.804**	−0.124	0.272
MDA		1	0.222	0.699**	−0.309	0.055
O_2^-			1	0.011	−0.122	−0.269
SOD				1	0.042	0.436*
POD					1	0.609**
CAT						1

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

those results, the initial elevation in MDA content is clearly related to the activation of oxidative processes, but plant metabolism normalizes with the extension of rehydration time and so MDA content begins to decrease. Interestingly, the MDA content of control group in our study increased at a later part of the experiment. A possible explanation for this could be that saturated soil moisture is not optimal for the survival of *A. selengensis*, which can be verified by inhibited root vigor and elevated O_2^-.

Plants produce reactive oxygen species such as O_2^- and H_2O_2 when subjected to stress. ROS are well known to cause lipid peroxidation and oxidative damage, which leads to the disruption of metabolic functions and loss of cellular integrity at their accumulation sites (Foyer et al. 1997). Previous work found increased O_2^- content in *Chrysanthemum* under drought stress (Sun et al. 2013), and similar changes were observed in *A. selengensis*. Additionally, we observed that the O_2^- content of *A. selengensis* gradually decreased with the duration of drought. These results suggest that water deficit leads to excessive accumulation of ROS, with serious negative effects for plants. This is consistent with studies on tea trees, purslane and other species (Hrishikesh et al. 2008; Jin et al. 2015). However, contrary results showed that *A. selengensis* can effectively scavenge ROS within a limited range by way of antioxidant enzymes, etc. This scavenging capacity is not limitless, however, and the antioxidant system of *A. selengensis* can be damaged by persistent drought so that O_2^- content is increased again in the later stages of drought. After 14 days of rehydration, O_2^- production and scavenging had not yet reached balance. It is thought that the increase in O_2^- content may be attributed to two reasons (Hura et al. 2015): One is the cumulative and lagged response of plant physiology to soil drought; the other is the negative effect of excessively rapid rehydration on plants under drought stress. The disruptive effects of rapid rehydration are expressed in the intensification of physiological processes associated with ROS production. It is suggested that the key reason for the over-production of ROS after rehydration could be the electron leakage due to the overloading of the electron transport chain (ETC) in PSI and PSII (Edreva 2005), leading to the reduction of molecular oxygen to superoxide radicals. Rapid rehydration may have further activated the

peroxidation process (Maevskaya and Nikolaeva 2013). After 28 days of rehydration, with the exception of the SD group, the O_2^- content in drought groups was significantly lower than the control level. One possibility is that the plant's antioxidant enzyme systems under severe drought were so seriously disrupted that they required a longer time than our study allowed to return to normal levels, or were unable to recover at all.

Drought disturbs the balance of ROS metabolism in plants. When the concentration of ROS is excessive, the balance of membrane lipid peroxidation and cellular material exchange is also disrupted, leading to a range of physiological and metabolic disorders (Gill and Tuteja 2010). To combat these illnesses, plants have evolved protective enzymes over long evolutionary period. The collaboration (or compensation) between antioxidant enzymes is a decisive factor in the capacity of the antioxidant (Blokhina et al. 2003), and they can eliminate ROS such as O_2^- and H_2O_2 as well as reduce the damage they cause to plants (Smirnoff 1993). Here, SOD and O_2^- were significantly positively correlated, both showing a bimodal trend, while POD and CAT increased and then decreased during the drought treatment. The POD and CAT activity reached a maximum in the middle of drought period, and the O_2^- and MDA content decreased during this period (Figs. 3, 4). The results indicate that the SOD is effective in scavenging O_2^- and protecting cells from peroxidative damage. Since SOD decomposes O_2^- to H_2O_2, which is then converted to H_2O by POD and CAT (Blokhina et al. 2003), the increases in POD and CAT may be due to elevated H_2O concentration. The physiological mechanism of drought tolerance in *A. selengensis* is similar to that of the sand plants *Agriophyllum squarrosum* and *Setaria viridis*, in that the accumulated ROS stimulates the antioxidant enzyme protection system to continuously increase the enzyme activity, thus maintaining the ROS balance (Chen et al. 2021a, b), showing a strongly ROS control and scavenging ability. However, the antioxidant enzyme system of *A. selengensis* may have been damaged with the longer drought time, leading to a decrease in enzyme activity and a rise in ROS. During the drought period, the POD and CAT activities of the CK group were quite elevated, indicating that too much soil moisture can be detrimental to *A. selengensis* and leads to an increase in antioxidant enzyme activity.

After rehydration, the SOD activities were significantly reduced, but these of drought groups were still slightly higher than that of the CK group, indicating that SOD activities were not fully recovered. The POD and CAT activities increased substantially at 14 days of rehydration, and a key reason for the inability of POD and CAT to recover may be that the O_2^- content was still increasing (Upadhyaya and Panda 2004) and recovered slowly during subsequent rehydration, which also matched the persistently high MDA and O_2^- content after rehydration (Figs. 3, 4). Other studies have also suggested that the lack of recovery of antioxidant enzymes after rehydration may be related to the fact that plant physiological metabolism has not improved immediately, meaning that there is a lag in plant response to soil moisture (Hura et al. 2015). Alternatively, their antioxidant enzyme systems may be disrupted and take longer than our research period allowed to restore to normal levels (Chen et al. 2021a, b). As expected, both POD and CAT activities gradually decreased after 28 days of rehydration, and these of all groups recovered to that of the CK group, except for CAT under severe drought. The synergistic changes in O_2^- content and antioxidant enzyme activities suggest that the antioxidant enzyme system also responds to water stress and then scavenges ROS to protect cells from excessive oxidative damage.

Conclusion

The physiological response of plants to environmental stresses was often more sensitive than changes in morphological features. Here, we observed that different drought levels contributed to improved root vigor. The changes in O_2^- and MDA content were consistent, indicating that drought induced an excessive accumulation of O_2^- and caused peroxidative damage to plant cells. Antioxidant enzymes had a major regulatory effect on O_2^-, particularly SOD activity, which was positively correlated with O_2^- content. The rehydration compensated root vigor, membrane lipid peroxidation and antioxidant enzyme activity in *A. selengensis*. However, it is remarkable that long-term soil saturation moisture also produced oxidative stress on *A. selengensis*, which was expressed by the progressively higher MDA and O_2^- contents as well as inhibited root vigor in the control group. Thus, *A.*

selengensis was unsuitable for high water conditions and even highly drought tolerant, although it is a wetland plant. The physiological indicators monitored in this study have the potential to predict the distribution of *A. selengensis* under the context of climate change.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval The work described here has not been published previously and was not considered for publication elsewhere before a decision was made by the journal. There is no conflict of interest in the submission of this manuscript, and the manuscript is approved by all the authors for publication.

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