PHYSIOLOGICAL EFFECTS OF WATER LEVEL FLUCTUATIONS ON THE SUBMERGED PLANT *POTAMOGETON CRISPUS*

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Abstract. Water level fluctuations in lakes are a fundamental feature of wetland hydrology, influencing the growth and development of wetland plants, species composition, and community succession. To study the effects of different water level fluctuations on the morphology and physiological characteristics of the submerged plant *Potamogeton crispus*. Experiments were conducted to investigate how varying intensities and durations of rising and falling water levels influence the growth and physiology of *Potamogeton crispus*. We analyzed the changes in the physiological indicators of the plant, such as antioxidant enzyme activity (peroxidase, superoxide dismutase, catalase), osmoregulatory substances (soluble sugars, soluble proteins), superoxide anion and malondialdehyde under different water-level conditions. The results showed that water level fluctuations lead to higher malondialdehyde and superoxide anion contents, which cause damage to the plant, while the plant responds to unfavorable environments by adjusting the activities of antioxidant enzymes as well as the content of osmoregulatory substances. The antioxidant system of *Potamogeton crispus* was limited by the duration and intensity of water level fluctuation. And in the later stages of the experiment, the scavenging capacity of reactive oxygen species in the plant was reduced and malondialdehyde content increased.
Keywords: *wetland plants, water level changes, abiotic stress, osmoregulatory substance, antioxidant enzyme*

Introduction

Disturbance events, while detrimental to individuals, can positively affect species diversity within communities by promoting diversity through moderate disturbances (Shea et al., 2004). In nature rivers and lakes are characterized by many disturbances that affect the survival of aquatic plants, and changes in water levels are one of them (Peintinger et al., 2007; Wilcox and Nichols, 2008).

Water level fluctuations (WLF) significantly influence the composition and diversity of wetland plants, altering vegetation types and spatial distribution patterns of wetland plant communities, and it is also an important factor in regulating wetland ecosystem processes and functions (Bai et al., 2021; Li, 2015; Rosenzweig et al., 2002). The response of plants to changes in water level is mainly expressed through their biomass and morphological indicators, such as plant height and leaf number, as well as physiological indicators, such as enzyme activities and photosynthetic pigment content (Li et al., 2018; Yang et al., 2014). It has been found that high amplitude WLF inhibits plant flowering and seed production, and appropriate water level fluctuations promote plant distribution and growth (Zhang et al., 2013). For example, scholars have studied the morphological and physiological characteristics of submerged plants under different WLF and found that the number of leaves and biomass of *Hydrilla verticillata* became less with the increase of the rate of water level rise, and the increase of the water depth led to the decrease of the number of stolons of *Vallisneria natans* (Gu et al., 2017; Wu et al., 2012). However, the increased frequency of water level fluctuations led to an increase in the biomass of the roots and foliage of *Alternanthera philoxeroides* (Zhang et al., 2015a). Changes in WLF have significant effects on morphological and physiological indicators of plants, but different species show different environmental adaptations to WLF.

As a dominant species of submerged plants in spring and winter, *Potamogeton crispus* is vital in ecological restoration projects (Wang et al., 2011). *P. crispus* belongs to the family of Ophiopogonaceae of perennial submerged herbaceous plants and grows in lakes, ponds, and other slow-flowing rivers, *P. crispus* is wildly competent, abundant, and easy to collect (Jia et al., 2021; Zhang et al., 2015b). *P. crispus* can extract nutrient salts from the water, promoting a rise in dissolved oxygen levels and improving water quality. Furthermore, the tightly packed clusters of *P. Crispus* effectively strain suspended particles from the water. And the roots of the plants play a crucial role in stabilizing the bottom sediment, resulting in a decreased amount of suspended matter (Wang et al., 2011; Zhang et al., 2015b). WLF significantly impacts the growth and reproduction of *P. crispus*. The plant will adjust its physiological and morphological characteristics to adapt to the changes. While previous research has focused on the ecological function, comprehensive utilization, and extracts of *P. crispus* (Kang et al., 2020; Ren et al., 2011), fewer studies have explored the effect of water level changes on this species. We conducted an indoor controlled experiment to explore the impact of rising and falling water levels on the physiology of *P. crispus* and provide a reference basis for restoring wetland plants. This is important for the conservation of wetland species diversity and the restoration of wetland ecosystems.

Materials and methods

Experimental materials

The materials used in this study were clints collected from Poyang Lake National Wetland Park, Jiangxi Province, China (29°05′30″N, 115°55′39″E) on November 6th, 2021, with healthy and complete specimens selected for cultivation. The clint is planted in cylindrical (specifications: 16 cm high, 17 cm diameter at the top, and 13 cm diameter at the bottom) plastic test pots, with ten plants planted in each pot and a total of 60 banks, and the test pots are tied with a rope to facilitate the later picking up and putting down. And the substrate for cultivation was Poyang Lake wetland meadow swamp soil.

Experimental design

The experiment was conducted in the plant sunroom of the Key Laboratory of Poyang Lake Wetland Watershed Research of the Ministry of Education, Jiangxi

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Normal University, Jiangxi Province, China. The average air temperature during the test period was 17.2 ± 8°C, the average water temperature was 14.8 ± 5°C, the light during the test period was natural light, and the water used was tap water.

P. crispus through the clint propagation on November 6, 2021, to select the morphology is more consistent, the prolonged state of suitable plants, using a double set of pots method that is the plastic test pots into the upper aperture of 57 cm, the lower gap of 45 cm, the height of 60~150 cm of the glass barrel of the *P. crispus* seedlings for two weeks of pre-cultivation, the incubation of the period of the water level of 50 cm. The glass bucket had a 4 cm diameter hole located 10 cm from the bottom, sealed with a rubber stopper to adjust the water level. Six groups of three replicates were set up for each of the rising water level test groups and the falling ones. The water level change control test was conducted on November 6, 2021.

The initial water level of the rising group was 50 cm, and there were seven groups with treatment intensity of 0.0 cm/d (CK), 0.2 cm/d, 0.5 cm/d, 0.8 cm/d, 1.1 cm/d, 1.4 cm/d, and 1.7 cm/d. After 50 d, the water level of each group in the rising fluctuation group reached 60 cm, 75 cm, 90 cm, 105 cm, 120 cm, and 135 cm. The initial water level in the falling fluctuation group was 60 cm, 75 cm, 90 cm, 105 cm, 120 cm, and 135 cm, and the water level in each group decreased to 50 cm after 50 d. The water level of the groups after 50 days is shown in *Figure 1*. All the indexes were tested once on the 60th day.

The test lasted 60 days, and the physiological indicators of *P. crispus* were tested every 10 days, the water level was controlled at 8:00 a.m. Every day according to the designed intensity of water level changes to reach the set value.

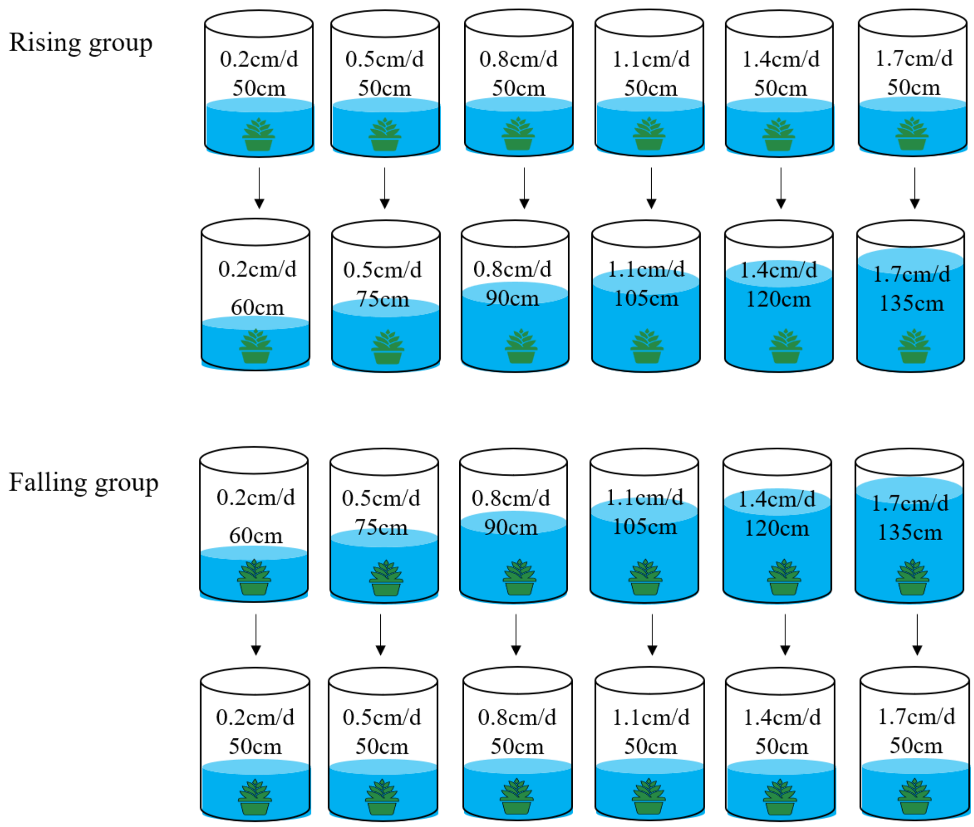

***Figure 1.** Schematic diagram of the test*

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Measurement of physiologic indicators

There were seven sampling times, including 0, 10, 20, 30, 40, 50, and 60 days after fluctuation treatment. We collected fresh leaves from three pots of the plants to obtain the average values.

Measurement of physiological indicators: peroxidase (POD) activity was determined by the guaiacol method; catalase (CAT) activity was determined by the UV absorption method; soluble protein (SP) content was determined by Coomassie brilliant blue G-250 method and The soluble sugar (SS) was determined by the anthrone colorimetric method; Malondialdehyde (MDA) content was determined by thiobarbituric acid method; The rate of superoxide anion (O_2^-) production was determined using the hydroxylamine oxidation method (Bradford, 1976; Wang, 2006.). Finally, the results of the measurements are then statistically analyzed.

Data analytics

Excel 2010 and Origin 2022 were used for data analysis and graphing. SPSS 27.0 was used to conduct one-way ANOVA for the data, and two-way ANOVA was performed by combining the two factors of water lever fluctuations and test time.

Results and analysis

Results of two-way ANOVA of water level, time, and their interactions on P. crispus

A two-way ANOVA analysis of the effects of different fluctuation intensities and test time in rising and falling water levels and their interaction on morphological and physiological indexes of *P. crispus* are shown in *Table 1*. In the rising fluctuation group, the water level change had a significant effect on plant height, and POD activity ($P < 0.001$). The test time considerably affected POD activity ($P < 0.001$). In the interaction between the fluctuations intensity and time, MDA content had a substantial effect at 0.05 levels. POD and CAT activity showed a considerable correlation ($P < 0.001$); the interaction of the two did not show an interaction effect on plant height. In the falling group, the falling water levels showed a significant effect on plant height, POD, and CAT activity ($P < 0.001$). And the test time showed a highly substantial correlation on leaf number, and CAT activity ($P < 0.001$). In their interaction, plant height, and POD activity had significant interaction ($P < 0.001$) with water level condition and time of the experiment.

Effects of water level fluctuations on the antioxidant system of P. crispus

Different WLF had significant effects on *P. crispus* POD activity (*Fig. 2*). In the rising group, showed a trend of rising, then falling, and rising again at days 50-60. There were two apparent peaks of POD activity value in the rising group, which appeared on day 10 in the group of 1.4 cm/d, with the most significant increase in the POD activity value of 477.38 μmol/(g·min), as well as in the 1.7 cm/d group at day 30, with the value of 399.38 μmol/(g·min). In the falling group, except for the CK group, the peak values of other groups appeared on day 10. With the increase in treatment intensity, the POD activity values generally showed an increasing trend, with the maximum value of 647.20 μmol/(g·min) increased by 528.06 μmol/(g·min) compared with the initial value. The POD activity values of the experimental groups with different treatment intensities at different periods showed a general trend of increasing and then decreasing.

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Table 1. *Result of two-way analysis of variance (ANOVA) testing for main effects of water level rising/falling, time, and their interactions on P. crispus (F-value)*

Rising water level			
Type	**Water level fluctuations**	**Test time**	**Water level fluctuations × test time**
CAT	14.568**	869.729**	48.278***
POD	1054.703***	3642.408***	594.56***
MDA	303.538ns	3683.445**	269.361*
O_2^-	18.159**	810.879**	13.566**
SP	66.759**	414.849**	28.044**
SS	13.244**	28.649**	6.522**
Falling water level			
Type	**Water level fluctuations**	**Test time**	**Water level fluctuations × test time**
CAT	144.304***	1539.873***	108.187**
POD	296.301***	19136.494**	746.073***
MDA	113.716*	2307.114**	195.127*
O_2^-	7.508*	363.881**	8.681*
SP	27.201*	790.889*	12.016*
SS	6.358**	56.092**	6.157**

CAT, catalase; POD, peroxidase; MDA, malondialdehyde; O_2^-, superoxide anion; SP, Soluble protein; SS, Soluble sugar; The number in the table is F values, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$

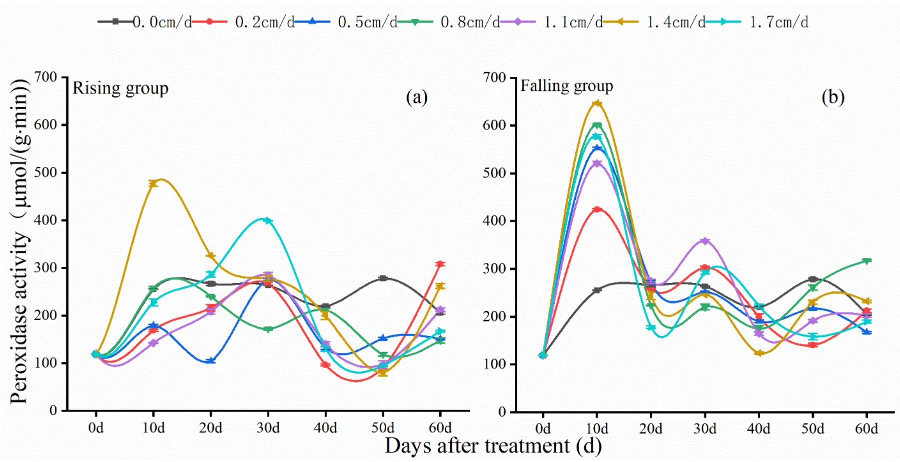

Figure 2. *Effect of rising and falling water level on POD activity of P. crispus. (a) Changes in POD activity in the rising group. (b) Changes in POD activity in the falling group (Test data are mean ± SD, n = 3)*

During the testing phase, it was observed that the CAT activity of plants was higher on day 0 than on day 60 (*Fig. 3*). On days 40-50, the values of CAT activity were low, and on days 50-60, there was an upward trend in both rising and falling groups. In the rising group, the difference in intensity between groups was more significant in the first 20 days, indicating that the CAT activity of the high-intensity group was higher than the

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low-intensity one, however, the difference decreased on days 20-60. In the falling group, the CAT activity of plants showed a trend of decreasing and then increasing with the enhancement of the intensity. The CAT activity of plants in both groups showed significant variation on days 30-40, with the maximum increases in rising and falling groups being 46.00 μmol/(g·min) (50 d~60 d, 0.5 cm/d) and 73.98 μmol/(g·min) (0 d~10 d, 1.7 cm/d), respectively.

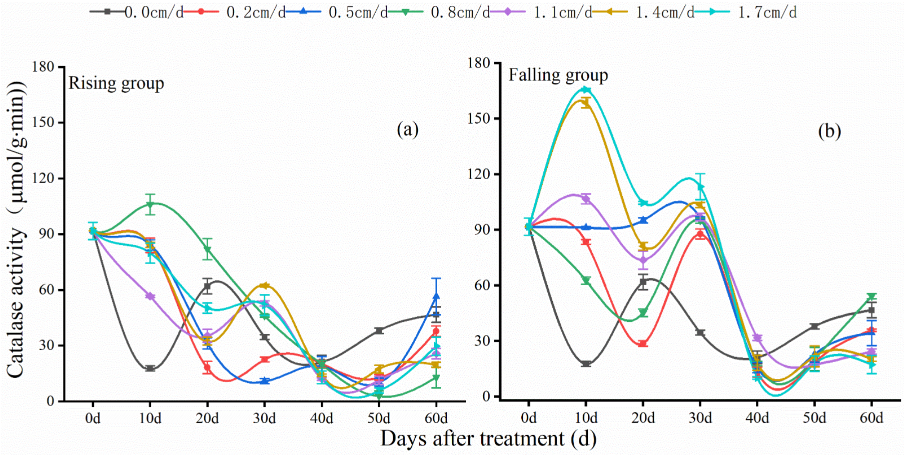

Figure 3. *Effect of rising and falling water level on CAT of P. crispus. (a) Changes in CAT content in the rising group. (b) Changes in CAT content in the falling group (Test data are mean ± SD, n = 3)*

Effects of water level fluctuations on the degree of cytoplasmic oxidation in P. crispus

The changes in MDA content were different for different intensity fluctuations (*Fig. 4*). In the rising group, the MDA content generally showed a trend of increasing and decreasing with the change of intensity simultaneously on days 0-50. On day 20, the groups of 0.2 cm/d, 0.8 cm/d, 1.4 cm/d, and 1.7 cm/d showed prominent peaks, of which the maximum was in the power of 0.2 cm/d group, and the content was 27.38 μmol/g. Compared to the other groups, the MDA content of 0.5 cm/d and 1.1 cm/d groups did not have a significant change throughout the test period, and there was no pronounced peak. In the group with falling water levels, the MDA content of plants generally showed a higher trend on days 0-30 than on days 30-60. The MDA content of the plants peaked at day 20 in the 1.7 cm/d group. The overall change of MDA content in the falling group was smaller than in the rising group. The general evolution of *P. crispus*'s MDA content under the two conditions was the same on days 0-50, showing an upward and then downward trend.

The changes in O_2^- content was similar in the rising and falling groups throughout the test period (*Fig. 5*). Overall, they both showed an increase followed by a decrease, and then both showed a small peak on day 30. The overall highest values were found on day 10, and the values on day 30 were lower than those on day 10. Except for the CK group, on day 10, the rising water level groups showed that the higher the intensity of fluctuation, the higher the value of their O_2^- content, with the highest being in the 1.4 cm/d and 1.7 cm/d groups, and the lowest being in the 0.2 cm/d and 0.5 cm/d groups, which means that as the intensity of fluctuation increased, so did their O_2^- content. In contrast, in the declining water level, the higher the fluctuation intensity the

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lower the O_2^- content of the group, the highest is 0.2 cm/d and 0.5 cm/d group, the value of O_2^- content decreases with the increase of fluctuation intensity. Whereas, the group with the intensity of 0.0 cm/d, which is also known as the CK group, had the highest value of O_2^- content in both ascending and descending water levels at day 10.

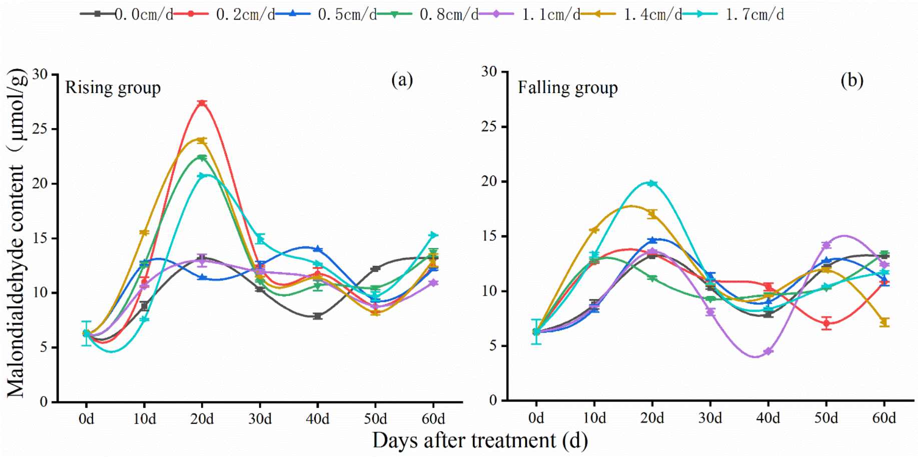

Figure 4. *Effect of rising and falling water level on MDA of P. crispus. (a) Changes in MDA content in the rising group. (b) Changes in MDA content in the falling group (Test data are mean ± SD, n = 3)*

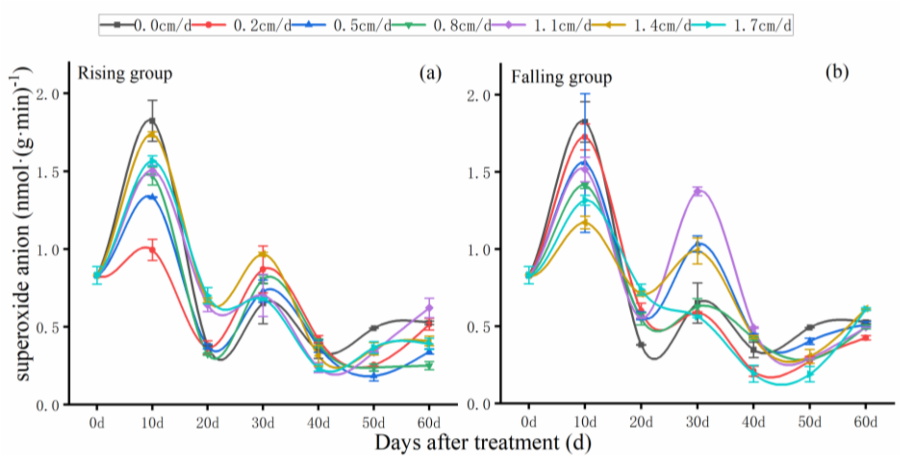

Figure 5. *Effect of rising and falling water level on O_2^- of P. crispus. (a) Changes in O_2^- content in the rising group. (b) Changes in O_2^- content in the falling group (Test data are mean ± SD, n = 3)*

Effects of water level fluctuations on osmoregulatory substances in P. crispus

The effects of different intensities of rising and falling water levels on the SP of *P. crispus* were different (*Fig. 6*). In the rising test, the difference in SP content between different treatments was significant on days 20-30, minor on day 60, and the content on days10-30 of the test was higher than at other times, except the group of 0.5 cm/d. The SP content of *P. crispus* in the different periods generally showed a rising trend with the enhancement of the intensities, and there was no obvious peak value. In the falling water levels group, the overall change was small, and the general trend showed a first

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rise and then decline; the more obvious peak appeared at day 30 when the treatment intensity was 1.7 cm/d group, and the highest value was 89.15 mg/g. In the same period, the content of plant-SP increased overall with the enhancement of the fluctuation intensity. The overall variation in the falling group was less than that in the rising group, and the SP content increased in both variations compared to the initial value.

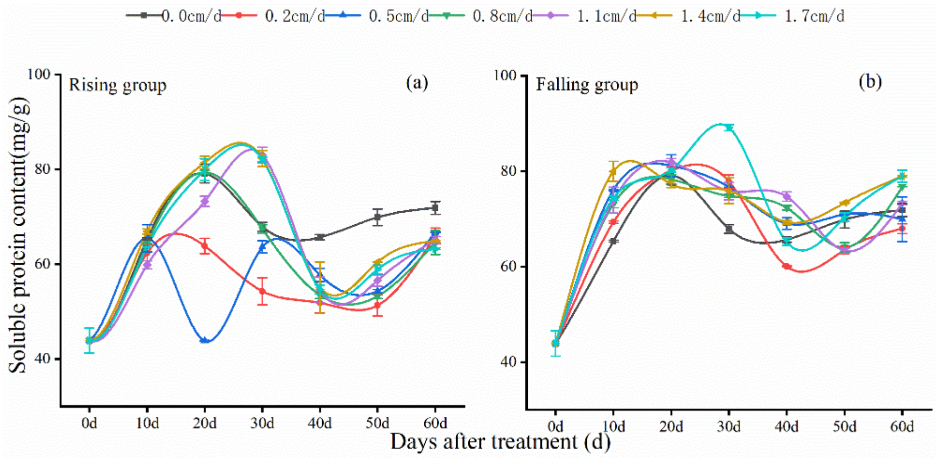

Figure 6. *Effect of rising and falling water levels on the soluble protein content of P. crispus. (a) Changes in soluble protein content in the rising group. (b) Changes in soluble protein content in the falling group (Test data are mean ± SD, n = 3)*

The SS content of plants in the rising and falling group showed overall fluctuating changes (*Fig. 7*). In the rising group, the content of SS showed an increasing trend, the 0.2 cm/d intensity group had the lowest SS content, while the group of 0.5 cm/d to 1.1 cm/d had the highest. At day 60, the 0.8 cm/d group reached a 3.11 mg/g peak. The SS content increased in all groups on day 60. In the falling test, the SS content increased initially, decreased in the middle, and increased again towards the end of the test. The 1.4 cm/d group had the highest SS content, with 4.64 mg/g on day 10. The SS content of each group was lower on days 20-40. The content of the high-intensity group (1.7 cm/d) under both treatment conditions was relatively low compared to other groups.

Discussion

WLF is the key factor that limits plant growth and development. In this study, we tested the effects of WLF of different intensities on plants. Plants produce excessive amounts of reactive oxygen species (ROS) when in a stressful environment, while oxygen free radicals (such as O_2^-) cause peroxidation of membrane lipids to produce MDA, which is the final breakdown product of membrane lipid oxidation. Excess accumulation of MDA leads to changes in the structure and function of cell membranes. Its content can represent the degree of damage to the cell membrane caused by ROS (Huang et al., 2023; Liu et al., 2021b; Zhao et al., 2012). At the same time, as essential protective enzymes for plants, POD and CAT will increase self-enzymatic activity to prevent excess ROS from harming the plants (Zhan et al., 2010). Then POD works with CAT to eliminate the excess H_2O_2 produced by the stress environment and keep it at a low level (Chen et al., 1998; Hu et al., 2011).

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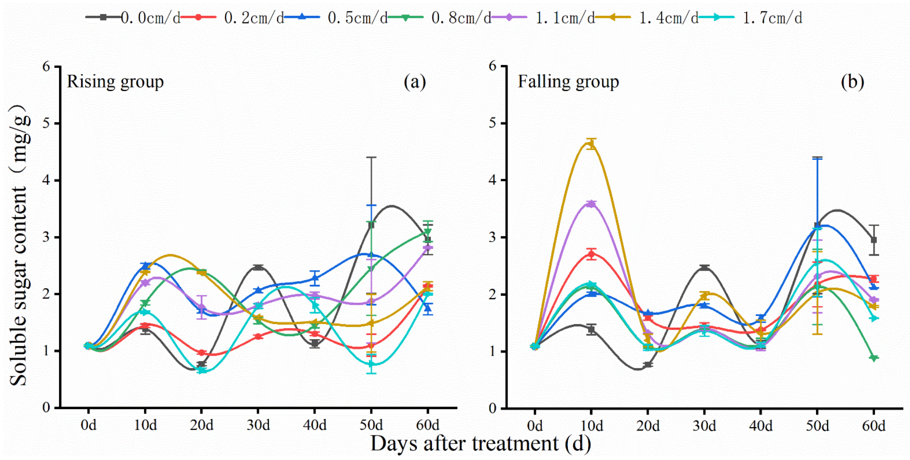

Figure 7. *Effect of rising and falling water levels on the soluble sugar content of P. crispus. (a) Changes in soluble sugar content in the rising group. (b) Changes in soluble sugar content in the falling group (Test data are mean ± SD, n = 3)*

We found that during the first 20 days of the experiment, the plants were subjected to environmental stress and the plant's MDA and O_2^- content increased. Accordingly, its content of antioxidant enzymes and osmotic regulators also rose. WLF influences the light required for plant photosynthesis by varying the magnitude and frequency of rising and falling changes (Wang et al., 2016).

The CAT and POD activities of plants in the experiment were all at a higher value on days 0-20, which was similar to the results of the study on the growth and physiological effects of water level changes on *Artemisia selengensi*, which means that when plants are initially stressed by WLF, several enzymes in the body will be elevated to work together to avoid a large accumulation of ROS (Li et al., 2022; Zhan et al., 2010)

On days 40-60, both conditions were unfavorable to plant growth due to the high water level in the rising group, which caused the plants to be unable to absorb enough light, as well as the low water level in the falling group, which resulted in too much light, leading to the plants being under stress again, and the concentration of O_2^- in the plants was elevated. And due to the accumulation of oxygen free radicals such as O_2^- which had a toxic effect on the plants, the MDA content of the plants was also elevated and the membrane lipid peroxidation was enhanced (Li et al., 2001).

POD activities in plants reached higher values on day 10, in comparison, CAT activity got higher values on day 0, indicating that CAT activity was more sensitive to WLF. This was similar to the results of Zhan Jiahong, who investigated the changes of several enzymes in *Panicum repens* under flooding stress (Zhan et al., 2010). POD activity in plants tends to rise on days 50-60 of the experiment, and some scholars believe that this is the duality of the role of POD. POD can act as a scavenger of hydrogen peroxide in the early stages of adversity and senescence to protect or as a participant in the generation of ROS in the later stages of trouble and senescence to trigger membrane lipid peroxidation to cause injury (Hu et al., 2011; Zhang and Kirkham, 1994).

On days 10-20 of the experiment, the POD and CAT activities in the plant showed a decreasing trend, while the MDA content showed an increasing trend at this time. The two changes were opposite, which can be explained by the fact that the increase in

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MDA content inhibits the antioxidant enzyme activities of the plant (Ge et al., 2005). However, MDA, POD, and CAT content increased on days 50-60. It has been shown that if the activity of the cellular protective enzymes of submerged plants showed an increasing trend and the MDA content also increased significantly, the cellular protective enzymes did not play a role in completely removing the ROS (Zhang et al., 2021).

As intracellular protective substances, the content of osmoregulatory substances is positively correlated with plant resistance, and SS in plants reduces cellular water potential and maintains osmotic potential balance (Lin et al., 2019; Liu et al., 2021a; Zhao et al., 2017); The synthesis of SP is enhanced under adversity stress, and in cooperation with other osmoregulatory substances in plant to increase the resistance to adversity through osmotic interactions (Liu et al., 2021b). Increased levels of both can be considered as an adaptive mechanism to stress in plants (Liu et al., 2016). It has been shown that flooding stress can promote the accumulation of SP in plants for a certain period. Still, the different species' accumulation trend is not the same (Zhang et al., 2011). Wei et al. showed that WLF can affect SP content in plants, causing it to increase for a certain period to adapt to the stressful environment, after which it returns to its normal level (Wei, 2015). In the experiment, the content of SP in the 1.1 cm/d~1.7 cm/d test group of the rising water level was generally higher than that of the other intensity groups. The range of SP in the falling water level group generally showed an upward trend with the enhancement of fluctuations in intensity. This indicates that high-intensity WLF stimulated *P. crispus* to enhance the osmoregulatory substances in the body to form protection. In the rising water level group, the SP of the plants showed a decreasing trend in the later part of the experiment, which could be attributed to the increased stress on the plants caused by the rising water level in the last part of the experiment, which led to a decrease in the SP of the *P. crispus* leaves. In the rising and falling experiment, the plants in the group with fluctuations on days 0-20 had significantly higher SS levels than the CK group, which was attributed to the increase in the SS content of *P. crispus* at the beginning of the investigation in response to the stressful environment of WLF, and it was consistent with the studies on the adaptability of *Carex cinerascens* to different water level (Yao et al., 2020). It has been found that the higher the SS content in a plant, the greater the plant's tolerance to waterlogging (Zhang et al., 2019); the SS content of *P. crispus* in the rising group with high-intensity fluctuations tended to increase in the later part of the test, suggesting that high-intensity WLF might improve the flooding tolerance of plants for a certain time.

Conclusion

WLF can cause plants to accumulate excessive amounts of O_2^- and MDA, leading to enhanced membrane lipid peroxidation and damage. In response to the stressful environment, the plant's protective mechanisms are also improved, such as the increase in the activity of antioxidant enzymes and the increase in the content of osmoregulatory substances. Therefore, in the first 20 days of the experiment, we can see that the content of all indicators shows an increasing trend. On days 20-40, the plants were slightly adapted to the stress environment, so the content of MDA and O_2^- began to decline, but the content of MDA was still relatively high, indicating that the fluctuation of water level had been creating a stress environment for the plants. The content of soluble proteins was always high in the falling water level group, indicating that the falling

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water level fluctuation was more likely to imbalance the osmotic potential of the plant cells, and in order to avoid the osmotic potential loss of balance caused the death of the cells due to lack of water, so the plants kept accumulating soluble proteins to minimize the damage caused by the adversity to the plants. The antioxidant system capacity of the plant was affected by time and environment in the late stage of the experiment. The activities of the two enzymes in *P. crispus* were maintained at a low level, which weakened the scavenging capacity of ROS in the plant and made the MDA content show a tendency to increase, resulting in serious peroxidation of cellular plasma in *P. crispus*.

In summary, in the case of WLF, *P. crispus* can adapt to stress by controlling the osmotic substances and antioxidant enzyme systems to maintain the stability of the membrane structure and intra- and extracellular water under environmental stress, to ensure its normal growth activities.

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Conflict of interest. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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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