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Research Article

Responses of physiological activities and lateral root anatomical structure of *Cercis glabra* to waterlogging stress

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Abstract

Cercis glabra is a colour-leaf tree with excellent ornamental value, whereas its physiological and morphological responses to waterlogging stress are still unclear. A potted study was conducted to determine the effects of waterlogging stress on antioxidative enzymes (superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)), lipid peroxidation (in terms of malondialdehyde (MDA) content), relative electric conductivity, and osmotic substance (free proline) of leaves and aerenchyma, lignification, suberization and Casparian strip of lateral roots of *C. glabra*. The result showed that the SOD, POD, and CAT activity and free proline content of *C. glabra* were significantly increased by the different degrees of waterlogging stress compared with the non-waterlogged treatment at 8 and 12 days, and the MDA content and relative electric conductivity of *C. glabra* leaves were significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 16 days, and the degrees of change increased among treatments was ranked as total waterlogged > semi-waterlogged > shallow waterlogged. The lateral roots of *C. glabra* not only formed developed aerenchyma in the cortex but also formed suberization and Casparian strip in the endodermis under semi-waterlogged treatment at 16 days. These results implied that *C. glabra* had a certain tolerance to waterlogging stress, which was associated with the increasing antioxidant enzyme activity and osmotic adjustment substance content, and with the formation of aerenchyma, suberization and Casparian strip in the lateral root to adapt to the waterlogged environment.

Keywords: *Cercis glabra* Pamp; physiological anatomic structure; waterlogging stress

Introduction

Waterlogging, being the most important environmental stress, severely affects plant growth and development, and limited the performance of plants (Yu *et al.*, 2019). However, plants can acclimate to waterlogging stress through physiological and morphological responses (Naseer *et al.*, 2012; Di *et al.*, 2018). The generation of reactive oxygen species (ROS) is one of the earliest biochemical responses of eukaryotic cells to waterlogging stress (Jia *et al.*, 2019). The production of ROS in plants, known as the oxidative burst, is an early event of plant defense response to waterlogging stress and acts as a secondary massager to trigger subsequent defense reactions in plants (Guo, 2018). ROS, which includes oxygen ions, free radicals, and peroxides, form as a natural by-product of the normal metabolism of oxygen and has an important role in cell signalling (Lal *et al.*, 2019). However, during waterlogging stress, ROS levels increase dramatically resulting in

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oxidative damage to proteins, DNA and lipids (Liu, 2019; Škute *et al.*, 2019). Antioxidant enzymes are key players in ROS detoxification in plants under waterlogging stress (Duhan *et al.*, 2019; Salah *et al.*, 2019). Activities of antioxidant enzymes in plants under waterlogging stress are usually regarded as indicators of tolerance of genotypes against waterlogging stress (Qi *et al.*, 2019). The SOD, POD, and CAT activities increase, causing ROS scavenging under waterlogging stress (Faseela *et al.*, 2018; Peng *et al.*, 2018).

Leaves are an important organ of the plant to produce organic matter by photosynthesis (Lu *et al.,* 2019). Leaf growth is sensitive to waterlogging stress and may be inhibited by a slight reduction in the water potential of tissues (Jogawat *et al.*, 2019). Leaves will lose water under waterlogging stress, but plants can accumulate different types of organic solutes in the cytosol to lower osmotic potential thereby maintaining cell turgor under waterlogging stress (Tian *et al.*, 2019; Velasco *et al.*, 2019). The maintenance of leaf turgor may also be achieved by the way of osmotic adjustment in response to the accumulation of soluble sugar, proline, and other solutes in cytoplasm improving water uptake from waterlogging soil (Majumder *et al.*, 2019; Zeng *et al.*, 2019). In addition, the aerenchyma and Casparian strips will be formed in some plant roots to adapt to the waterlogged environment under waterlogging stress (Ejiri and Shiono, 2019; Shiono *et al.*, 2019).

Cercis glabra Pamp. of the Leguminosae family is a leguminous tree and is one of the species with excellent ornamental value (Roberts and Werner, 2016). *C. glabra* is tall and straight, tree crown resembles umbrella form, after flowering first, grow leaf, when flowering full tree is amaranth or pink, the flower-like violet butterfly, quite moving. *C. glabra* flowers in spring, heart-shaped glossy leaves in summer, reddish-brown fruit pods in autumn, and straight trunk in winter can be appreciated. Garden plants with high waterlogging resistance in waterlogged areas are of great significance. However, the literature does not provide the research about the influence of waterlogging stress on physiological of leaves and morphological of roots of *C. glabra*. The influence of waterlogging stress on SOD, POD, and CAT activities, and relative electric conductivity, MDA, and proline contents of leaves wad investigated in the present study. Moreover, we observed the anatomical structure of the lateral root. This study reveals the adaptive capacity and mechanism of *C. glabra* to waterlogging stress and provides a theoretical foundation for the promotion and application of *C. glabra*.

Materials and Methods

Habitat condition

The study site was in the agronomy practice base of Yangtze University, Jingzhou City (30°21′N, 112°8′E) in Hubei Province, China. The environment has subtropical monsoon climate with mean rainfall of 1100-1300 mm. Annual mean temperature is 15.9-16.6 ℃, and annul sunshine duration is 1800-2000 h. Annual frost period is 242-263 days.

Plant materials and waterlogging stress

The same size of annual seedlings of *C. glabra* (plant height: 99.33±1.65 cm, stem diameter: 7.27±0.10 mm) from seed sowing was collected in December 2017 from Xingshan District, Hubei province, China. One seedling was cultivated per pot, in a total of 60 pots (20 cm in diameter and 16 cm in height) on 16 December 2017. Each pot was filled with the same amount of soil and humus (3:1) mixture (the total volume is 4.8L). Waterlogging stress treatment was initiated on 9 May 2018. The two-factor completely random design was laid in the experiment. Factor 1 included the degree of waterlogging (control, shallow waterlogged, semi-waterlogged and total waterlogged), which was 0, 4, 8 and 16cm from the bottom of the bucket, respectively. And Factor 2 included the time of waterlogging (0, 4, 8, 12 and 16 days). The control plants were grown under normal watering conditions. The depth of shallow waterlogging, semi-waterlogging and total waterlogging the change of water level was observed every day, and the water was filled to the corresponding waterlogged depth in time. Physiological parameters were measured in leaves of control and waterlogged treatment groups, and complete lateral roots of control and waterlogged treatment were preserved with FAA fixator at 0, 4, 8, 12 and

16 days of waterlogging (Jahromi *et al*., 2019). Four treatments and three biological replications were conducted.

Antioxidant enzyme activity assays

For extraction of antioxidant enzymes, 0.2 g of frozen leaves were homogenized with 5 ml of 50 mM buffer solution, which contained 0.07% of $NaH_2PO_4{\cdot}2H_2O$ and 1.6% $Na_2HPO_4{\cdot}12H_2O$, crushed with a mortar and pestle, and centrifuged at 10 000 × *g* for 20 min in a refrigerated centrifuge (Fiasconaro *et al*., 2019). The supernatant was collected in a bottle for the determination of enzymes activities, and MDA content. The SOD activity was determined according to the method of Giannopolitis and Ries with some modifications (Giannopolitis *et al*., 1977). A 3.0 ml reaction mixture contained 63 mM nitro-blue tetrazolium (NBT), 1.3 mM riboflavin, 13 mM methionine, 0.1 mM ethylene diamine tetraacetic acid (EDTA),50 mM phosphate buffer (pH 7.8), and 0.2 mL of enzyme extract. The test tubes containing the mixture were placed under light at 78 mmol photons s^{-1} m^{-2} for 10 min, and absorbance at 560 nm was recorded. A nonirradiated reaction mixture that did not develop color served as the control, and its absorbance was subtracted from A_{560} of the reaction solution. One unit of SOD activity was defined as the amount of enzyme required to cause 50% inhibition of the rate of NBT reduction at 560 nm. Activities of CAT and POD were measured using the method of Chance and Maehly (1955). For POD, the oxidation of guaiacol was measured by the increase in absorbance at 470 nm for 1 min. The 3 mL reaction mixture contained 20 mM guaiacol, 40 mM H_2O_2 and 0.2 ml enzyme extract, which initiated the reaction. For CAT, the decomposition of H_2O_2 was measured by the decline in absorbance at 240 nm for 1 min. The 3 mL reaction mixture contained 50 mM phosphate buffer (pH 7.0), 15 mM H_2O_2, and 0.2 ml enzyme extract, which initiated the reaction.

Determination of lipid peroxidation and relative electric conductivity

Lipid peroxidation was determined by estimating MDA (Esterbauer and Cheeseman, 1990). For measurement of MDA content, 2.5 mL of 20% trichloroacetic acid containing 0.5% thiobarbituric acid was added to a 2.5 mL aliquot of the supernatant. The mixture was heated at 100 °C for 30 min and then quickly cooled in an ice bath. After the tube was centrifuged at 10 000 × *g* for 10 min, the absorbance of the supernatant was read at 532 nm. The value for the nonspecific absorption at 600 nm was subtracted from the 532 nm reading. MDA content of the sample was calculated using the formula: $C\ (\mathrm{nmol/g}) = (6.45\ (A532 - A600) - 0.56\ A450) * 5/0.2$. The relative electric conductivity (REC) was measured and calculated as described by Leopold and Toenniessen (1984).

Determination of free proline

Samples of 0.1 g of frozen leaves were ground in an ice-cold mortar and pestle containing potassium phosphate buffer (50 mM, pH7.5). The homogenates were centrifuged at 10000×g and 4 °C for 10 min. The supernatant was collected and stored at 4 °C for free proline determination. Proline concentrations in leaves were determined per the method of Li (2000). A mixture of 0.2 *g* fresh samples and 5 mL sulfosalicylic acid was homogenized and then centrifuged at 3 000 rpm for 10 min. The supernatant was mixed with 2 mL glacial acetic acid and 2 mL acidic ninhydrin, and resulting mixture was boiled at 100 °C for 25 min in water bath. After cooling, 4 mL of toluene were added to the liquid. Absorbance of extracts was evaluated at 520 nm.

Observation of root anatomy

Take the *Cercis glabra* root which was semi-waterlogged as the material (according to the data of physiological indexes, the results showed that *Cercis glabra* had the best adaptability to semi-waterlogged) the root hair zone (3 cm from root apex) was sectioned by freehand sectioning under an atomic microscope. Sections were stained with toluidine blue for aerenchyma, phloroglucinol-HCl for lignin, Sudan red 7B for suberin lamellae, and berberine hemisulfate and aniline blue for Casparian strips. Specimens were examined under brightfield and epifluorescence microscopy and photographed as described by Yang *et al.* (2014).

Statistical analysis

All data were analyzed with SAS 9.1 software, and Duncan's new complex range method was used to compare the significant differences. Least significant difference for multiple comparison tests was used to identify significant differences among all treatments at 0.05 level.

Results

Changes in SOD activity

The SOD activity of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 8, 12 and 16 days, and the degrees of SOD activity was increased among treatments was ranked as semi-waterlogged > total waterlogged > shallow waterlogged ($P < 0.05$) (Figure 1). The SOD activity was significantly increased by 65.2%, 85.3% and 91.1% under semi-waterlogged, by 55.1%, 59.1% and 51.7% under total waterlogged, by 16.7%, 43.7% and 44.9% under shallow waterlogged compared to the non-waterlogged seedling at 8, 12 and 16 days, respectively (Figure 1). SOD activity was decreased first and then increased under different degrees of waterlogging stress at 0-16 days.

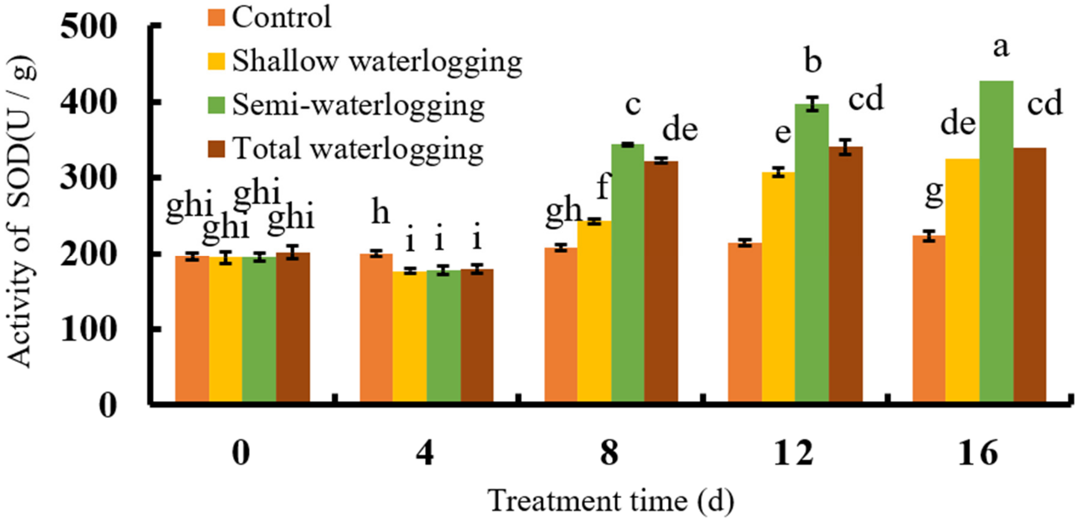

Figure 1. SOD activity in leaves of *Cercis glabra* under waterlogging stress

Data were shown as means ± SE. Different letters in the figure indicate significant differences between treatments ($P < 0.05$).

Changes in POD activity

The POD activity of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 4, 8 and 12 days, and the degrees of POD activity was increased among treatments was ranked as semi-waterlogged > total waterlogged > shallow waterlogged ($P < 0.05$) (Figure 2). The POD activity was significantly increased by 66.7%, 127.3% and 212.1% under semi-waterlogged, by 25.4%, 47.9% and 105.6% under total waterlogged, by 9.5%, 15.8% and 54.1% under shallow waterlogged compared to the non-waterlogged seedling at 4, 8 and 12 days, respectively (Figure 2). The POD activity was increased first and then decreased under different degrees of waterlogging stress at 0-16days.

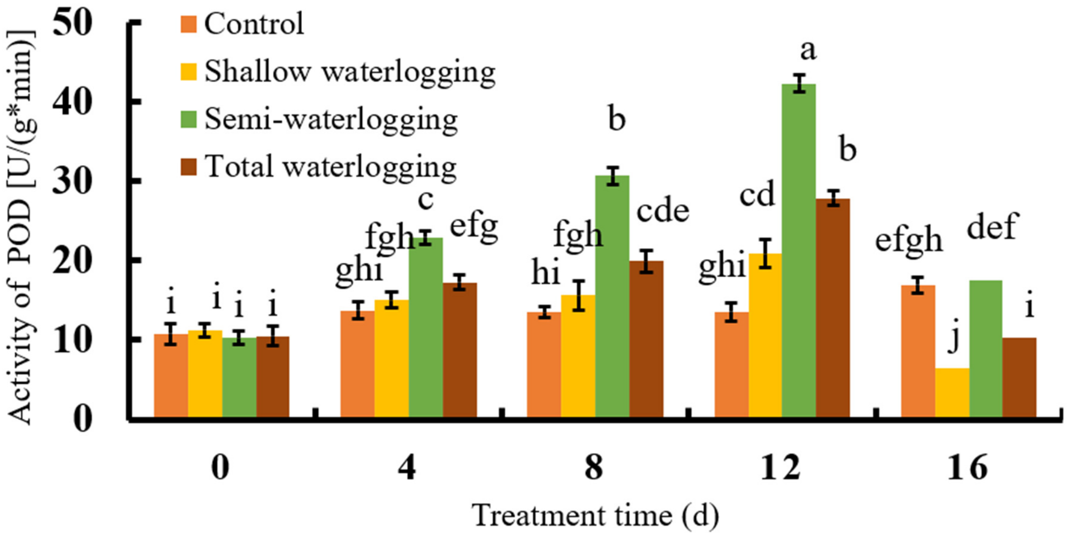

Figure 2. POD activity in leaves of *Cercis glabra* under waterlogging stress
Data were shown as means ± SE. Different letters in the figure indicate significant differences between treatments ($P < 0.05$).

Changes in CAT activity

The CAT activity of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 4, 8, 12 and 16 days, and the degrees of CAT activity was increased among treatments was ranked as semi-waterlogged > total waterlogged > shallow waterlogged ($P < 0.05$) (Figure 3). The CAT activity was significantly increased by 39.1%, 63.4%, 110.0% and 149.9% under semi-waterlogged, by 18.8%, 37.5%, 56.7% and 103.6% under total waterlogged, by 7.6%, 27.5%, 40.1% and 48.1% under shallow waterlogged compared to the non-waterlogged seedling at 4, 8, 12 and 16 days, respectively (Figure 3). The CAT activity was gradually increased under different degrees of waterlogging stress at 0-16 days.

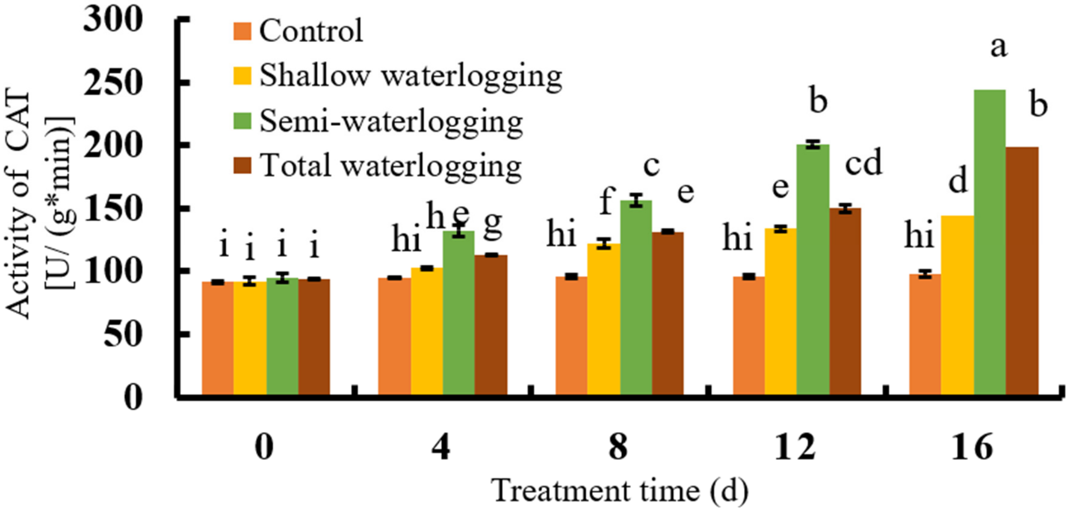

Figure 3. CAT activity in leaves of *Cercis glabra* under waterlogging stress
Data were shown as means ± SE. Different letters in the figure indicate significant differences between treatments ($P < 0.05$).

Changes in lipid peroxidation

The MDA content of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 8, 12 and 16 days, and the degrees of MDA content was increased among treatments was ranked as total waterlogged > semi-waterlogged > shallow waterlogged ($P < 0.05$) (Figure 4). The MDA content was significantly increased by 52.4%, 83.7% and 78.8% under total waterlogged, by 23.3%, 51.0% and 61.4% under semi-waterlogged, by 13.5%, 27.8% and 39.9% under shallow waterlogged compared to the non-waterlogged treatment at 8, 12 and 16 days, respectively (Figure 4). The MDA content was gradually increased under different degrees of waterlogging stress at 0-16 days.

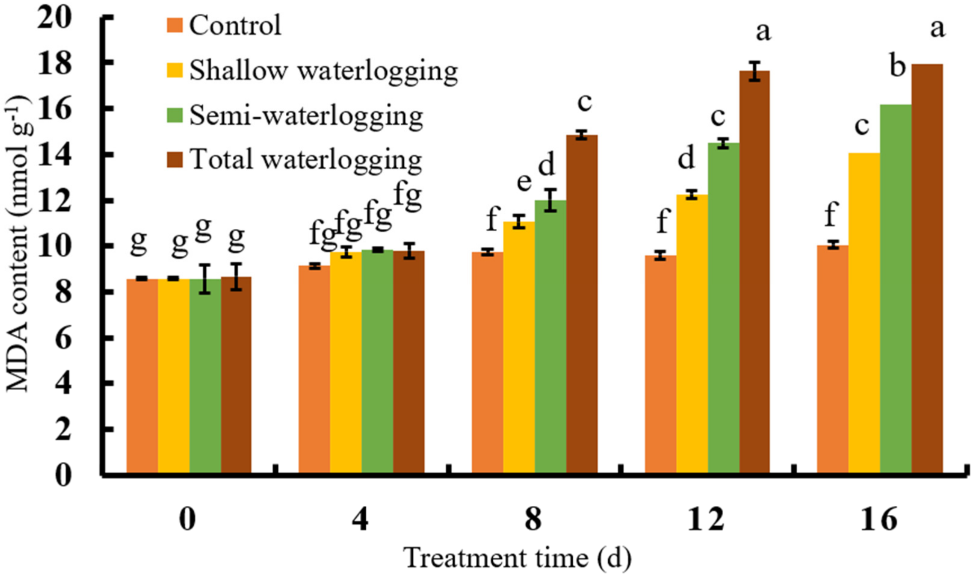

Figure 4. Leaf malondialdehyde (MDA) content in *Cercis glabra* under waterlogging stress
Different letters in the figure indicate significant ($P < 0.05$) differences between treatments.

Changes in relative electric conductivity

The relative electric conductivity of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 16 days, and the degrees of relative electric conductivity was increased among treatments was ranked as total waterlogged > semi-waterlogged > shallow waterlogged ($P < 0.05$) (Figure 5). The relative electric conductivity was significantly increased by 40.7% under total waterlogged, by 33.3% under semi-waterlogged, by 16.8% under shallow waterlogged compared to the non-waterlogged seedling at 16 days, respectively (Figure 5). The relative electric conductivity was gradually increased under different degrees of waterlogging stress at 0-16 days.

Changes in free proline content

The free proline content of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 12 and 16 days, and the degrees of free proline content was increased among treatments was ranked as semi-waterlogged > total waterlogged > shallow waterlogged ($P < 0.05$) (Figure 6). The free proline content was significantly increased by 43.7 and 29.9 times under semi-waterlogged, by 26.4 and 18.2 times under total waterlogged, by 12.4 and 0.8 times under shallow waterlogged compared to the non-waterlogged seedling at 12 and 16 days, respectively (Figure 6). The free proline content was increased first and then decreased under different degrees of waterlogging stress at 0-16 days.

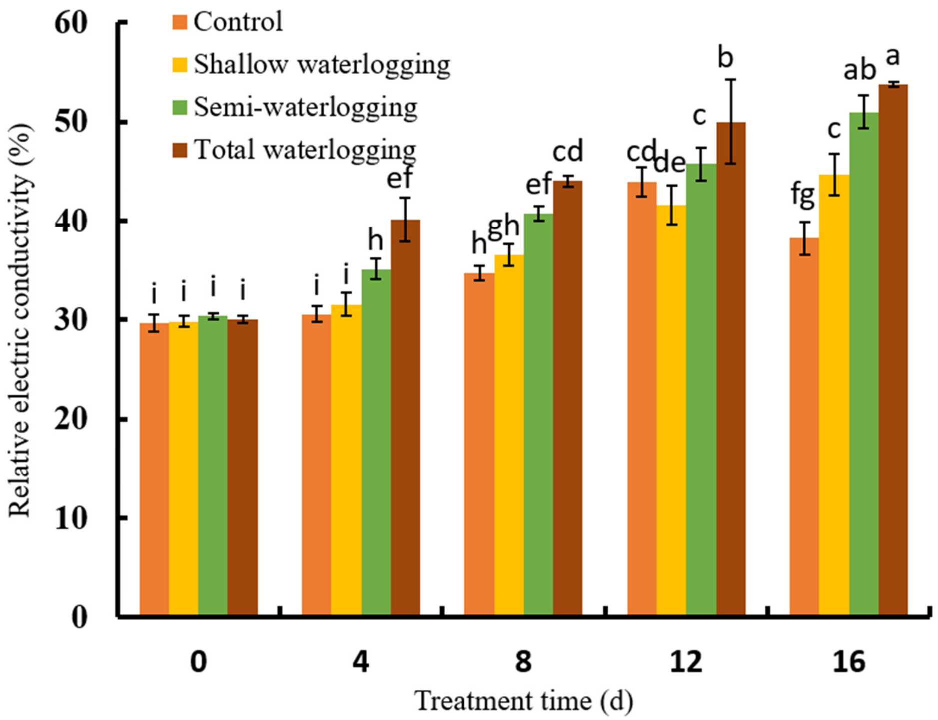

Figure 5. Relative electric conductivity of *Cercis glabra* leaves under waterlogging stress

Data were shown as means ± SE. Different letters in the figure indicate significant differences between treatments ($P < 0.05$).

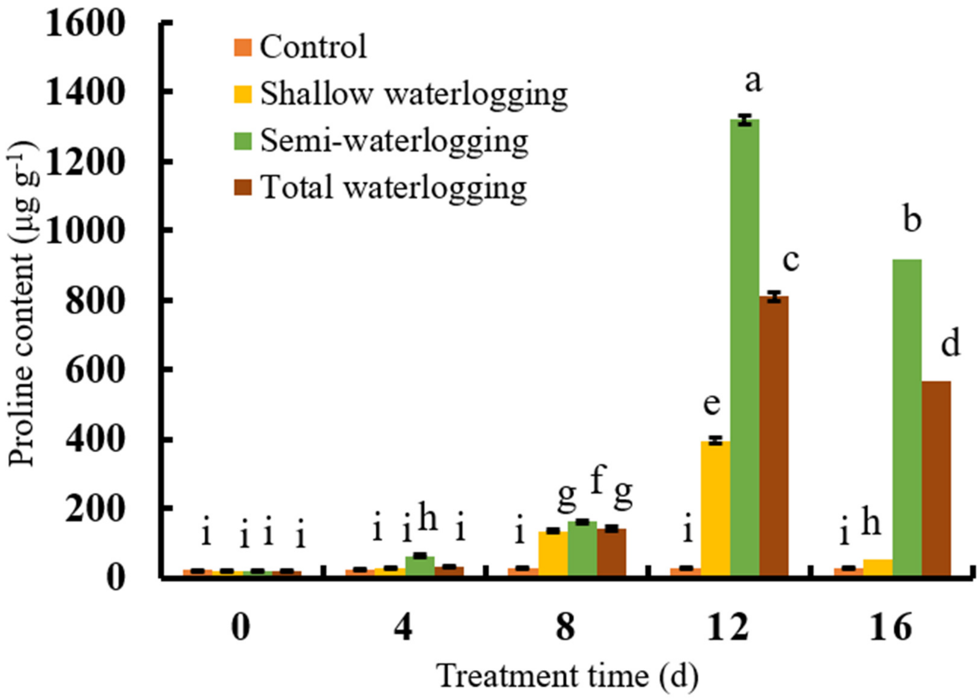

Figure 6. Proline content in leaves of *Cercis glabra* under waterlogging stress

Data were shown as means ± SE. Different letters in the figure indicate significant differences between treatments ($P < 0.05$).

Changes in anatomical structure of lateral roots

The formation of aerenchyma, suberization, and Casparian strip in the lateral roots of *Cercis glabra* were promoted by waterlogging stress (Figure 7). The lignification was not observed in the cortex in the root hair area of lateral roots in *Cercis glabra* compared with the day 0 of semi-waterlogged treatment at 16 days under semi-waterlogged treatment, but not only developed aerenchyma was formed in the cortex but also suberization and Casparian strip were formed in the endoderm in the lateral roots. The aerenchyma of *Cercis glabra* lateral root gradually expanded at 8-16 days.

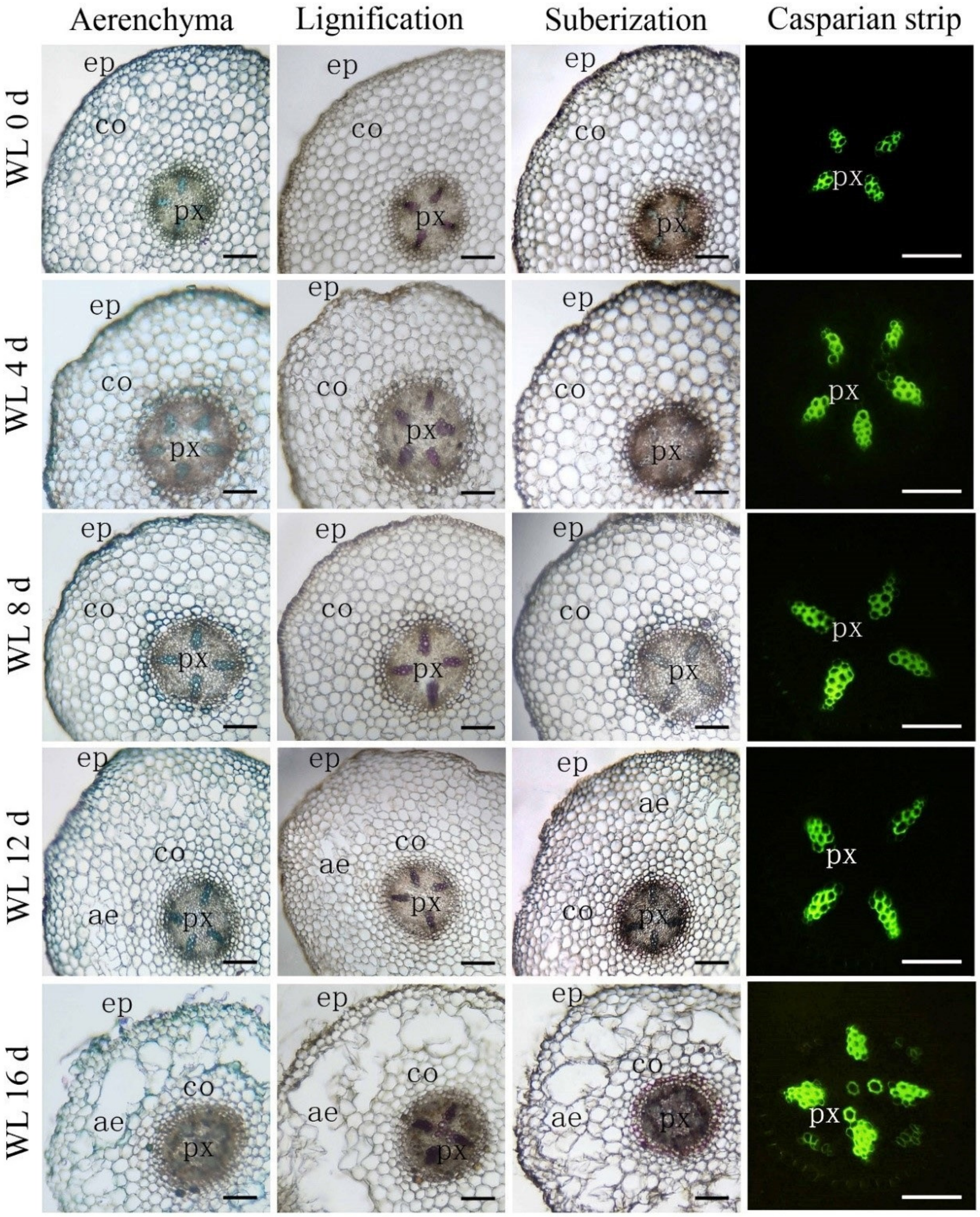

Figure 7. Effect of semi-waterlogged on anatomical structure of lateral root (3cm from root apex) of *Cercis glabra*

WL: Waterlogging, Ep: epidermis, Ae: aerenchyma, Co: cortex, Px: primary xylem. Ruler =50 μm.

Discussion

The content of ROS in plants generally was increased under the stress of waterlogging, but some plants will remove excessive ROS by increasing the activity of SOD, POD and CAT, such as *Triticum aestivum* L. (Škute *et al.*, 2019) and *Zea mays* L. (Salah *et al.*, 2019). In this experiment, the SOD, POD, and CAT activity of *Cercis glabra* was significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 8 and 12 days. It showed that *Cercis glabra* could resist waterlogging stress by improving antioxidant capacity as same as *Triticum aestivum* L. (Škute *et al.*, 2019) and *Zea mays* L. (Salah *et al.*, 2019). And the degrees of SOD, POD, and CAT activity increased among treatments was ranked as semi-waterlogged > shallow waterlogged > total waterlogged. The stress degree of shallow waterlogged is low, and the induction ability of antioxidant enzymes activity is weak. The stress degree of total waterlogged is too high, which destroys some antioxidant enzymes and makes the increasing degree of antioxidant enzymes low. The stress degree of semi-waterlogged is moderate, and the induction ability of antioxidant enzymes activity is the best. The SOD activity was decreased first and then increased, the POD activity was increased first and then decreased, the CAT activity was gradually increased under different degrees of waterlogging stress at 0–16 days. It is different from *Zea mays* L. (Tian *et al.*, 2019), may be caused by different test materials and methods. MDA content and relative electric conductivity of leaves are important indicators of plant injury degree (Liu, 2019). In this experiment, the MDA content and relative electric conductivity of *Cercis glabra* were significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 12 and 16 days, and the degrees of them were increased among treatments was ranked as total waterlogged > semi-waterlogged > shallow waterlogged. It indicates that the damage degree of *Cercis glabra* increases with the deepening of waterlogging. This occurs as a result of the higher the stress degree is, the higher the ROS content is. And the antioxidant enzyme cannot completely remove too much ROS, resulting in the higher the injury degree of plants. which is the same as *Cinnamomum camphora* L. (Liu, 2019).

Some plants also resist waterlogging stress by accumulating osmotic adjustment substances (Jogawat, 2019). Free proline is one of the most effective osmotics. In this experiment, the free proline content of *Cercis glabra* is significantly increased under the different degrees of waterlogging stress compared to the non-waterlogged treatment at 12 and 16 days, and the degrees of free proline content were increased among treatments was ranked as semi-waterlogged > shallow waterlogged > total waterlogged. It indicates that *Cercis glabra* can resist waterlogging stress by accumulating free proline, which is the same as *Zea mays* L. (Tian *et al.*, 2019) and *Phaseolus vulgaris* L. (Velasco *et al.*, 2019). The free proline content is increased first and then decreased under different degrees of waterlogging stress at 0-16 days. Maybe *Cercis glabra* first accumulated proline and then accumulated other osmotic adjustment substances to resist waterlogging stress.

Some plants can also adapt to waterlogging by forming aerenchyma and Casparian strip (Ejiri and Shiono, 2019; Shiono *et al.*, 2019). Aerenchyma can not only provide oxygen to plant roots in waterlogged environment, but also transport up harmful compounds such as ethanol. The Casparian strip is a barrier for the radial transport of water and ions in roots, preventing the radial oxygen loss (Naseer *et al.*, 2012). In this experiment, the lateral roots not only formed developed aerenchyma in the cortex but also formed suberization and Casparian strip in the endodermis under semi-waterlogged treatment at 16 days. It indicates that *Cercis glabra* can adapt to the waterlogging environment by the formation of aerenchyma, suberization and Casparian strip in the lateral root. In addition, it is worth noting that lateral root endodermis no lignification, only the suberization and Casparian strip, which is different from *Arabidopsis thaliana* (Naseer *et al.*, 2012), maybe because the lignification of endodermis to a lesser degree, colors of secondary metabolites in endodermis are darker which covers red of lignification.

Conclusions

To sum up, *Cercis glabra* has a certain tolerance to waterlogging stress, which is to resist waterlogging stress by increasing antioxidant enzyme activity and osmotic adjustment substance content on the one hand, and to adapt to the waterlogging environment by the formation of aerenchyma, suberization and Casparian strip in the lateral root on the other hand.

Authors' Contributions

Conceptualization: JL and YYL; Data curation: JL; Formal analysis: JL; Funding acquisition Investigation: JL; Methodology: JL; Project administration: YYL; Resources: YYL; Software: JL; Supervision: JL; Validation: JL; Visualization: JL; Writing-original draft: JL; Writing-review and editing: JL and YYL. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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