

Article

Exogenous Absciscic Acid Enhances Waterlogging Tolerance in *Lindera megaphylla*

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Abstract

The waterlogging tolerance of *Lindera megaphylla*, an evergreen species valued for ecological restoration and its role in landscapes, remains unclear, hindering its broader use in riparian green spaces and rain gardens. This study systematically assessed its physiological responses to simulated waterlogging stress (control/CK, mild/W1, moderate/W2, and severe/W3) and exogenous abscisic acid (ABA) applications (0, 1, and 3 $\mu\text{mol/L}$). The results showed that severe waterlogging (28 d) drastically reduced seedling survival to 30%, inhibited growth, induced significant reactive oxygen species (ROS) accumulation and membrane damage (malondialdehyde (MDA) +118.59%, relative conductivity (REC) +85.54%), and decreased photosynthetic pigments (Chla -41.60% , Chlb -40.02% , Car -34.33%). Exogenous ABA (3 $\mu\text{mol/L}$) substantially alleviated stress, increasing survival by 60.61% and enhancing tolerance through three integrated processes: (1) enhancing antioxidant defense (superoxide dismutase (SOD) +10.63%, peroxidase (POD) +9.33%) and reducing ROS; (2) stabilizing osmotic regulation (lower soluble sugars, proteins, and proline and increased leaf water content by +7.89%); (3) preserving photosynthetic integrity, evidenced by restored chlorophyll levels and significantly improved photosystem II and I efficiency. This study is the first comprehensive demonstration that ABA enhances *L. megaphylla*'s waterlogging tolerance by coordinating antioxidant, osmotic, and photosynthetic responses.

Keywords: *L. megaphylla*; flooding stress; ABA; antioxidant defense; photosynthetic protection; osmotic adjustment



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1. Introduction

Lindera megaphylla is a subtropical evergreen broadleaf tree of the Lauraceae family, characterized by a deep rooting system and persistent foliage that contribute significantly to soil and water conservation. Its volatile emissions possess pronounced antimicrobial properties, helping to enhance surrounding air quality. Beyond its roles in ecological restoration and landscape design, *L. megaphylla* also shows substantial promise for pharmaceutical use [1–3]. Given its preference for moist habitats and its notable value in ecological remediation, *L. megaphylla* is a prime candidate for prioritization in landscape designs for riparian green spaces, rain gardens, and other environments susceptible to periodic or accidental flooding events, positioning it as a key species for ecological restoration in flood-prone areas. However, a critical bottleneck exists in current practice; although adapted to humid environments, the physiological mechanisms and adaptations that enable its tolerance to

waterlogging remain largely unknown, which considerably restricts its practical application in riparian ecosystems. Therefore, systematically elucidating the fundamental basis of *L. megaphylla*'s waterlogging tolerance (including its tolerance threshold and critical adaptive stages) and exploring effective mitigation strategies are essential for minimizing the risks associated with its use in flood-vulnerable zones and safeguarding its ecological and economic value.

Flooding stress severely impairs plant growth and development by altering morphological traits, disturbing physiological metabolism, and suppressing photosynthetic capacity [4]. In addition, waterlogging triggers a cascade of secondary stresses, including energy crisis caused by oxygen deprivation, cytoplasmic acidification, nutrient imbalance (especially N, P, and K leaching), and ethanolic fermentation that leads to cytotoxic acetaldehyde accumulation [5]. Previous studies have demonstrated that short-term hypoxic conditions trigger excessive ROS production, which promotes the lipid peroxidation of membranes, as indicated by increased MDA content, REC, and osmotic disequilibrium [6,7]. Meanwhile, under hypoxia, root elongation is suppressed, while morphological adaptations such as adventitious roots and aerenchyma are induced. Roots rapidly switch to glycolysis and alcoholic fermentation, leading to ATP depletion and a drop in cytosolic pH, which further reduces root hydraulic conductance and nutrient uptake [8]. Further, extended exposure to waterlogging causes stomatal closure, damages chloroplast ultrastructure, decreases chlorophyll content and photosynthetic enzyme activity, and suppresses photosystem performance and efficiency, eventually leading to photosynthetic collapse [9–11].

Absciscic acid (ABA) is a crucial signaling molecule that plays a pivotal role in plant stress responses by activating diverse protective pathways [12,13]. For example, exogenous ABA substantially alleviates water-stress-induced oxidative injury by suppressing ROS accumulation, decreasing MDA levels, and enhancing antioxidant enzyme activities, including SOD and POD [14,15]. Furthermore, ABA fine-tunes osmotic balance by modulating the accumulation of osmolytes such as proline, soluble sugars, and soluble proteins, thereby maintaining cellular water homeostasis under stress conditions [16,17]. Moreover, in terms of photosynthetic performance, ABA restricts the breakdown of photosynthetic pigments, preserves the structural and functional stability of PSII and PSI, and mitigates photoinhibition, resulting in sustained photosynthetic efficiency under adverse conditions [18,19]. Taken together, these findings underscore ABA's dual role as both a signaling molecule and a physiological safeguard that enhances stress tolerance, providing a valuable theoretical basis for developing stress-resilient plant cultivars. However, most existing research on ABA-regulated water stress responses has centered on drought tolerance [20,21], with flooding tolerance examined mainly in model species (e.g., tomato and *Arabidopsis*) and crops such as soybean, rice, and maize [22–24]. Specifically, ABA modulates waterlogging tolerance through conserved molecular mechanisms. For example, it activates antioxidant enzymes via ABA-responsive element binding factors (ABFs), suppressing ROS accumulation and membrane peroxidation [25,26]. It fine-tunes osmotic balance by inducing osmolyte biosynthesis (e.g., proline via P5CS, soluble sugars via invertases) to maintain cellular water potential [27,28]. It preserves photosynthetic function by stabilizing D1 protein turnover in PSII and protecting PSI electron transport chains from stress-induced photodamage [29]. In contrast, the waterlogging adaptation mechanisms of evergreen woody species like *L. megaphylla* remain largely unexplored, particularly with respect to the critical role of ABA in preserving photosystem II and photosystem I functionality.

Prior research on the stress tolerance of *L. megaphylla* has predominantly focused on its physiological responses to temperature variations and acid rain [30–32], while its waterlogging tolerance and associated adaptations remain largely unknown [33]. Specifically, the dynamic adjustments of photosynthetic characteristics, such as light response curves and

electron transport chain activity, as well as the ameliorative effects of exogenous growth regulators under flooding stress, have not been previously examined. To address this gap, we established a double-pot system to apply gradient waterlogging combined with exogenous ABA treatments, with the goals of (1) elucidating the physiological response patterns of *L. megaphylla* to waterlogging; (2) uncovering the mechanisms through which ABA mitigates flooding damage; (3) identifying the most effective ABA concentration for enhancing flood tolerance.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

The experimental materials comprised robust 1-year-old seedlings of *L. megaphylla*. These seedlings were initially cultivated in a substrate mixture of nutrient soil:vermiculite:perlite at a 3:1:1 ratio, under routine water and fertilizer management. After one year of growth, seedlings were transplanted individually into polyethylene pots (approximate substrate volume ≈ 1.6 L per pot). All plants were grown in an incubator (Kesheng, Ningbo, China) with a photoperiod of 12 h of light and 12 h of darkness, a light intensity of 10,000 lx, relative humidity ranging from 50% to 60%, and temperatures maintained at 25 °C during the day and 23 °C at night.

2.2. Experiment Design

Healthy *L. megaphylla* seedlings, exhibiting consistent growth (7–8 leaf age, plant height: 9.8 ± 0.8 cm; basal diameter: 4.1 ± 0.7 mm) and free from pests and diseases, were selected for a first experiment. As shown in Figure 1, a normal watering treatment (CK) was used as a control, while a double-pot method was employed to simulate a gradient flooding environment. The specific treatments included half-submerged soil in the flooding pot (simulation of mild or intermittent flooding stress, W1), fully saturated (submerged, W2), and soil flooded 5 cm above the surface (W3). During the waterlogging stress period, fertigation was completely suspended to avoid nutrient leaching and confounding effects of nutrient availability on the stress response. All plants, including those in the control group, received their last fertilization one week prior to the initiation of the stress treatment. Daily observations of water level changes were made, with timely replenishment of water. Water was changed every 7 d, with three repetitions for each treatment, involving 30 seedlings per repetition.

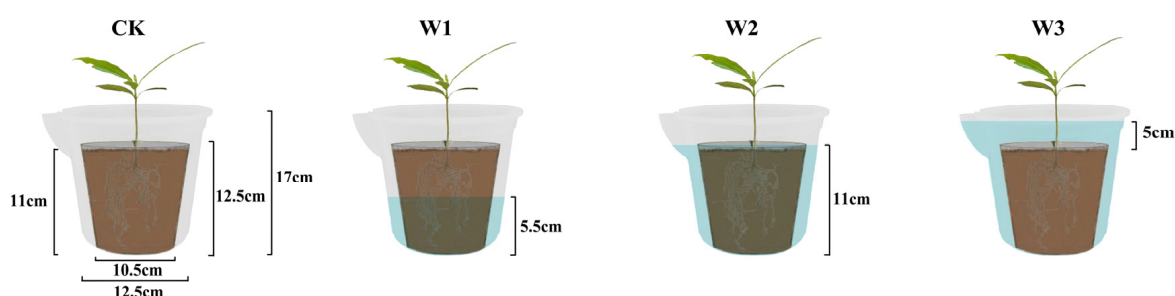


Figure 1. Simulation plot of waterlogging stress in *L. megaphylla* seedlings. Basin height is 17 cm, bottom diameter is 12.5 cm. Inner basin height is 12.5 cm, substrate mixture height is about 11 cm, bottom diameter is 10.5 cm. W1 means that half of the substrate mixture is flooded, with a water depth of 5.5 cm; W2 means the water level is at the soil surface, with a water depth of 11 cm; W3 means the water level is 5 cm above the soil surface.

For the second experiment aimed at alleviating the effects of waterlogging stress, robust and uniformly growing seedlings of *L. megaphylla* (plant height: 16.3 ± 0.8 cm; Basal stem diameter: 5.9 ± 0.7 mm) were selected. Based on the results obtained from

the waterlogging stress tests and observations of plant morphology and physiological indicators, severe waterlogging conditions (W3) were chosen for this ABA (Solarbio, Beijing, China) relief experiment. Three concentrations of the hormone were established, 0 $\mu\text{mol/L}$ (A0), 1 $\mu\text{mol/L}$ (A1), and 3 $\mu\text{mol/L}$ (A3), with plants under normal watering conditions serving as the control group (CK) (Table 1). Following the method of Salvatierra et al. [34], ABA was applied via root drenching. A defined volume of the ABA solution (200 mL per pot) was slowly and evenly poured onto the soil surface around the base of each plant. The initial drench was applied 3 h prior to the initiation of waterlogging stress, followed by subsequent applications at 7-day intervals throughout the stress period.

Table 1. Design of experimental treatments for *L. megaphylla* seedlings. “+” Waterlogging stress, “−” no waterlogging stress.

Groups	ABA Concentration ($\mu\text{mol/L}$)	Waterlogging Stress
CK	0	−
A0	0	+
A1	1	+
A3	3	+

For both experiments, mixed sampling was conducted at 0 d, 7 d, 14 d, 21 d, 28 d, and 7 days after recovery (R7d). The sampling site was the second layer of mature leaves from the bottom of the plant. After collection, the leaves were immediately rinsed with distilled water, blotted dry, flash-frozen in liquid nitrogen, and then stored in an ultra-low-temperature freezer (Midea, Hefei, China) for subsequent physiological parameter determination. Chlorophyll fluorescence parameters were directly measured at the same leaf positions of the plants.

2.3. Determination of Morphological Indicators

Following the methodology outlined by Sha et al. [35], the analysis and photographic documentation of the plants were conducted based on their morphology and color. The height and diameter of the seedlings were measured using a measuring tape and vernier caliper at intervals of 0 d, 7 d, 14 d, 21 d, 28 d, and R7d, allowing for a comprehensive recording of the seedlings' growth status.

Plant height: Under water stress, the height of the plants was measured every 7 d using a measuring tape (H0, H1), with the net growth in height calculated as $\Delta H = H1 - H0$.

Basal stem diameter: Under water stress, the diameter was measured every 7 d using a vernier caliper (GD0, GD1), with the net growth in diameter calculated as $\Delta GD = GD1 - GD0$.

2.4. Determination of Physiological Indicators

Grind the frozen samples into fine powder. For each analysis, weigh a specific mass of the powder and homogenize it in a designated volume of extraction buffer. All measurements were conducted with three independent biological replicates for each treatment, with each replicate consisting of a pooled sample from multiple seedlings.

The relative water content (RWC), relative conductivity (REC), superoxide dismutase (SOD) activity, peroxidase (POD) activity, soluble sugar (SS) content, and free proline (Pro) content were measured following the methods of Feng et al. [36]. The content of malondialdehyde (MDA) was determined using the thiobarbituric acid method [37]; the content of soluble protein (SP) was measured using the Coomassie Brilliant Blue method [38]; and the Chl content was determined following the methods of Bello et al. [39]. O_2^- staining was performed using the Nitro blue tetrazolium (NBT, Biotopped, Beijing,

China) staining method as described by Grellet Bournonville and Díaz-Ricci [40]; the rate of O_2^- generation was measured using a kit (Solarbio, Beijing, China); H_2O_2 staining was carried out using the diaminobenzidine (DAB, Biotopped, Beijing, China) staining method as described by Daudi et al. [41]; and the H_2O_2 content was determined using a kit (Nanjing Jiancheng, Nanjing, China).

2.5. Determination of Chlorophyll Fluorescence Parameters

Following the methodologies established by Liu [42] and Strasser et al. [43], the leaves were initially secured with a leaf clip for a dark adaptation period of 30 min. Subsequently, the rapid chlorophyll fluorescence induction kinetics (O-J-I-P) curve of the leaves was measured using an M-PEA multifunctional plant efficiency analyzer (Hansatech, Pentney, UK). Relevant chlorophyll fluorescence parameters were subsequently calculated using the JIP measurement (JIP-test) method [44].

2.6. Correlation Analysis of Physiological Parameters

To quantify the degree of association among morphological, physiological, and photosynthetic traits under waterlogging stress, Pearson's correlation coefficients were calculated for all 26 variables measured after 28 d of stress. The analyzed parameters included growth (ΔH , ΔGD), water status (RWC), membrane integrity (REC, MDA), oxidative stress (O_2^- , H_2O_2), antioxidant enzymes (SOD, POD), osmolytes (SS, SP, Pro), and photosynthetic indices (Chla, Chlb, Car, Chla+b, Fv/Fm, Fv/Fo, ABS/CSo, DIO/CSo, TRo/CSo, ETo/CSo, ϕRo , δRo , REo/CSo, PI_{total}). Prior to analysis, normality and homoscedasticity were verified using the Shapiro–Wilk and Levene tests, respectively. Correlation matrices were generated with SPSS 22.0, and the significance levels were set at $p < 0.05$ and $p < 0.01$. The resulting correlation coefficients were visualized as a heatmap using OriginPro 2022, where positive correlations are shown in green and negative correlations in blue.

2.7. Data Statistics and Analysis

All data are expressed as the mean $\pm$ standard deviation of three biological replicates. Statistical analysis were performed using SPSS 22.0 (IBM Research, New York, NY, USA) and GraphPad Prism 10 (Version 10.1.2, GraphPad Software, San Diego, CA, USA). Graphs were created using OriginPro 2022 (Version 2022b, OriginLab Corporation, Northampton, MA, USA).

For the first experiment (gradient waterlogging stress: CK, W1, W2, W3), data were analyzed by one-way or two-way analysis of variance (ANOVA), with treatment and time as factors, followed by the Least Significant Difference (LSD) post hoc test for multiple comparisons. Significance was set at $p < 0.05$. Lowercase letters indicate significant differences between different treatments at the same time point, while uppercase letters indicate significant differences across different time points for the same treatment.

For the second experiment (ABA amelioration under severe waterlogging: A0, A1, A3, with CK as a reference), the dose–response effects of exogenous ABA concentration (0, 1, and 3 $\mu\text{mol/L}$) on all physiological parameters were analyzed using regression analysis. Simple linear or nonlinear regression models were fitted using GraphPad Prism to quantify the relationship between ABA concentration (the independent variable) and each measured parameter (the dependent variable). The significance of the regression model (F-test), the coefficient of determination (R^2), and the significance of the model parameters (t -test) were evaluated. A probability level of $p < 0.05$ was considered statistically significant.

3. Results

3.1. The Effects of Waterlogging Stress on the Growth, Survival, and Water Homeostasis of *L. megaphylla* Seedlings

Flooding stress significantly restricted the morphological development and growth of *L. megaphylla* seedlings (Figure 2A). After 28 d, seedlings under the mild flooding group (W1) maintained 100% survival, exhibiting only slightly lower leaf yellowing (Table 2). In contrast, moderate (W2) and severe (W3) flooding reduced survival to 91.7% and 30%, respectively, and induced symptoms including leaf browning, apical wilting, and complete mortality. Growth inhibition was positively correlated with flood intensity. W3 completely suppressed height (ΔH) and basal diameter (ΔGD) growth (100% inhibition), significantly exceeding the reductions observed under W1 (33.33% decrease in ΔH ; 14.27% decrease in ΔGD) and W2 (94.44% decrease in ΔH ; 85.73% decrease in ΔGD) (Figure 2B,C). Following R7d, ΔH returned to 66.67% and 2.39% of CK levels in W1 and W2 seedlings, respectively, while ΔGD recovered to 78.57% and 7.16% of CK. By contrast, the W3 group showed no recovery, indicating irreversible root damage. RWC dynamics further demonstrated the impact of flood severity. During stress, the RWC in W1 remained comparable to CK, while that in W3 declined by 16.22% after 28 d and remained 25.85% below CK even after recovery, signifying a permanent loss of water retention capacity under severe flooding. Conversely, W2's RWC rebounded to 92.71% of that of CK, indicating retained osmotic regulation capacity under moderate flooding stress (Figure 2D).

Table 2. Survival rate of *L. megaphylla* seedlings under gradient waterlogging stress.

Treatment	Time	0 d	7 d	14 d	21 d	28 d	R7d	Survival Rate
CK		-	-	-	-	-	-	100%
W1		-	-	-	-	c	c+	100%
W2		-	a	a, b	a, b+, c	a+, b++, c+	a++, b++, c+, d	91.7%
W3		-	a, b	a, b+	a+, b++, c, d	a++, b++, c+, d	a++, b++, c++, d+, e	30%

Note: “-” represents normal growth; “a” represents new leaves drooping or scorching; “b” represents leaves withering or drooping; “c” represents lower leaves turning yellow; “d” represents leaf abscission; “e” represents plant death; “+” represents the degree of severity, “++” indicates a more pronounced effect than “+”.

3.2. The Effects of Waterlogging Stress on Membrane Damage, Oxidative Stress, and Osmotic Regulation in the Leaves of *L. megaphylla*

Waterlogging stress significantly compromised membrane integrity in the leaves of *L. megaphylla*, triggering oxidative damage and osmotic imbalances (Figure 3). Both MDA and REC increased progressively with greater flooding severity and duration (Figure 3A,B). After 28d, MDA and REC in the W3 group were 118.59% and 85.54% higher than in the control, reflecting extensive membrane damage. Following R7d, W1 and W2 showed partial restoration, with MDA declining by 40.44% and 24.38%, and REC decreasing by 19.49% and 4.13%, respectively, while W3 sustained significant injury. Waterlogging stress also led to pronounced ROS accumulation. Histochemical staining with NBT and DAB, supported by quantitative measurements, indicated that O_2^- production and H_2O_2 content rose proportionally with stress intensity (Figure 3C,D,G,H). After R7d, ROS accumulation was markedly reduced in W1 and W2, whereas the H_2O_2 levels remained elevated in W3, indicating a disruption of redox homeostasis. Further analysis revealed that SOD activity continuously increased over the stress duration, while POD followed a biphasic pattern of an initial rise, subsequent decline, and later recovery, with these fluctuations most pronounced in W3 (increasing by 88.81–113.79% at later stages). After R7d, enzyme activities in W1 and W2 tended to recover, while those in W3 remained significantly suppressed,

indicating that sustained severe waterlogging diminished the antioxidant repair capacity. Meanwhile, the contents of SS, SP and Pro increased by 148.21%, 36.02%, and 130.55%, respectively, relative to the control, with particularly significant accumulations of SS and Pro. Upon recovery, the osmolyte levels in groups W1 and W2 declined substantially, while those in group W3 remained high (Figure 3I–K), reflecting a persistent impairment of osmotic regulation.

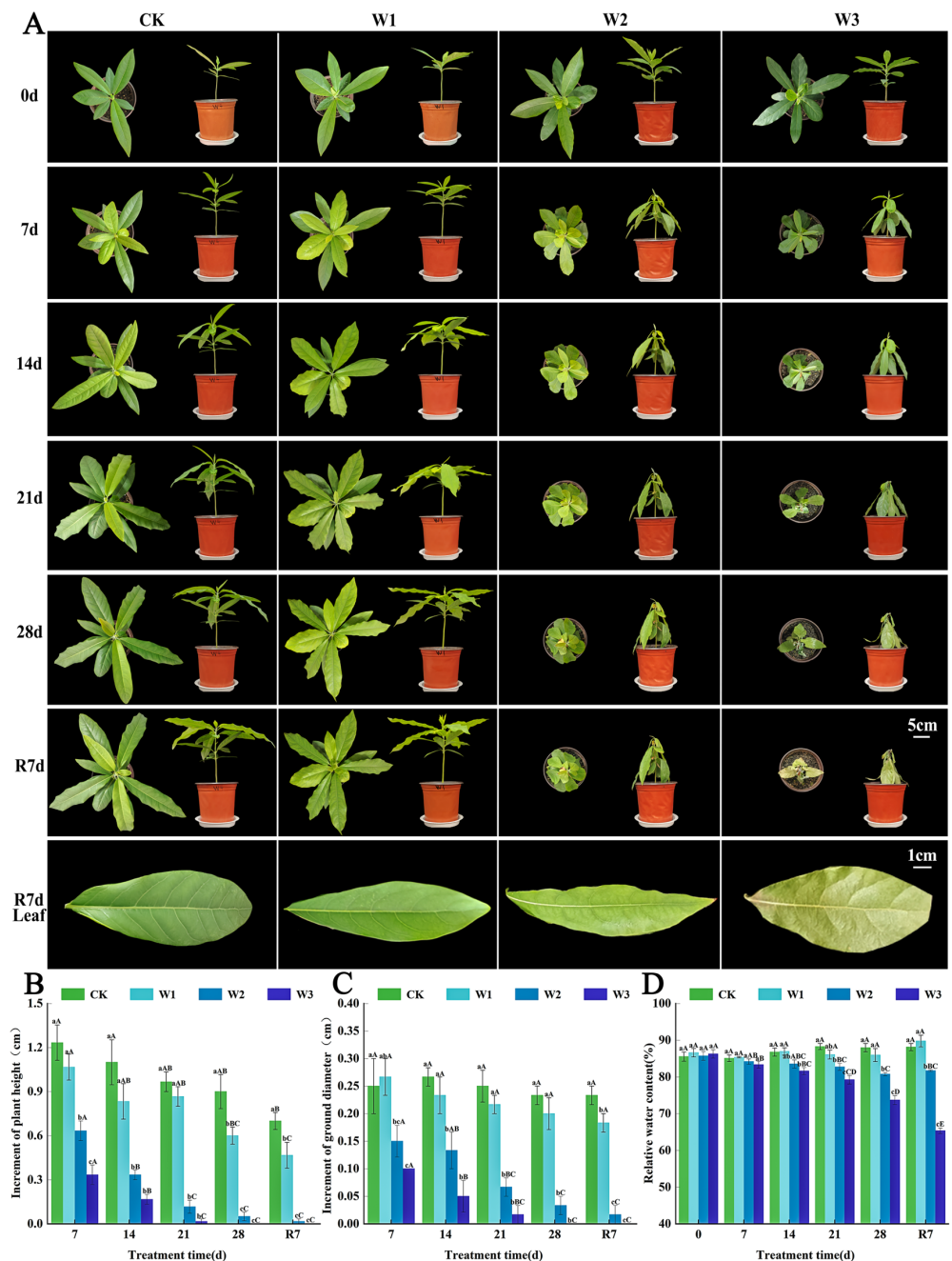


Figure 2. Effects of flooding stress on the morphology, growth, and water homeostasis of *L. megaphylla* seedlings. (A) Comparison of phenotypes after 28 d of different flooding stress treatments and R7d (7 days after recovery). (B) Impact of flooding stress on the height, basal diameter (C) growth, and REC (D) content of *L. megaphylla* leaves. CK denotes the control treatment; W1–W3 represent mild, moderate, and severe flooding stress, respectively. Lowercase letters indicate significant differences between different treatments at the same time point ($p < 0.05$), while uppercase letters indicate significant differences at different time points for the same treatment ($p < 0.05$). Data represent the mean and standard deviation of three biological replicates.

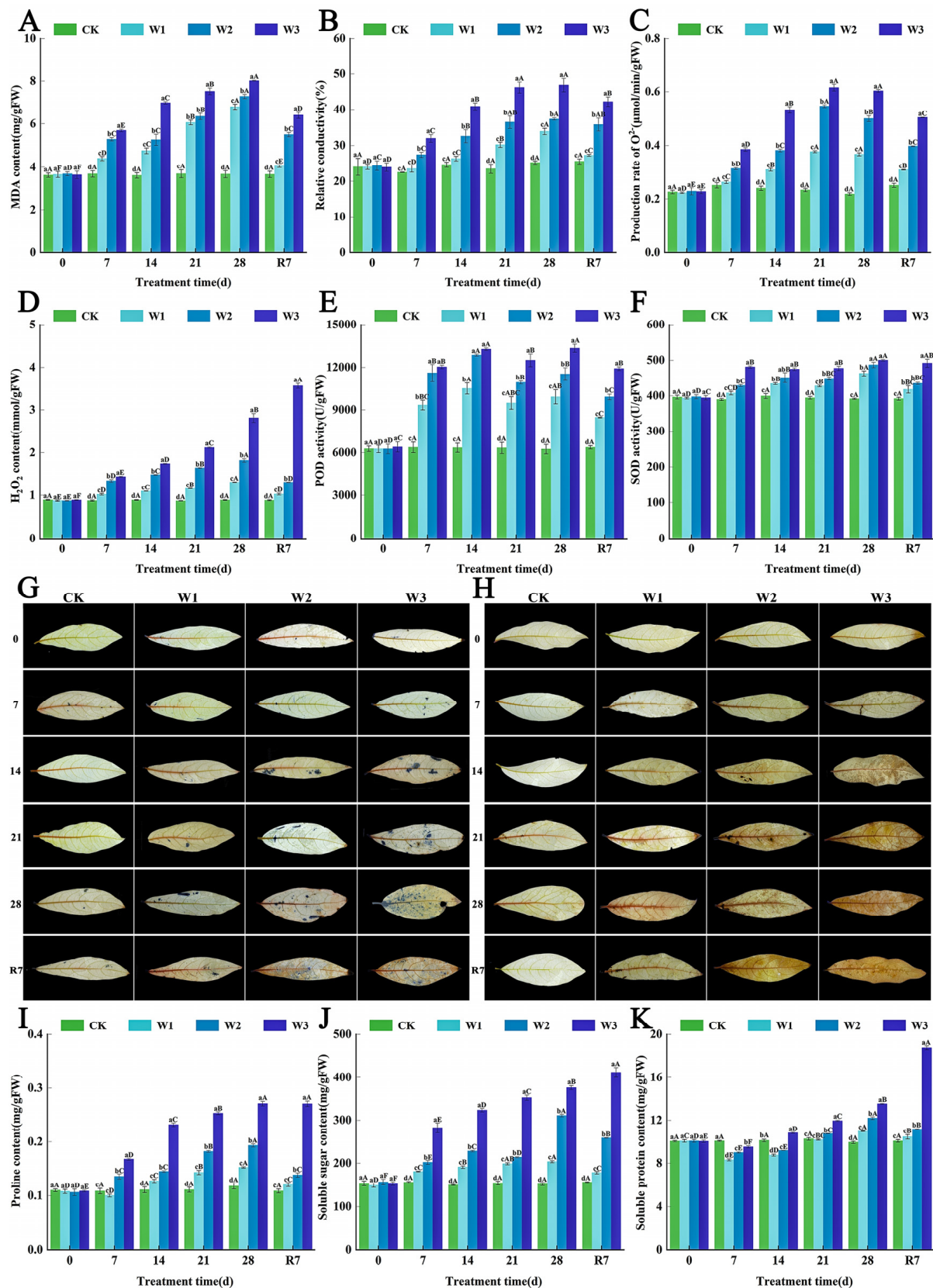


Figure 3. Effects of waterlogging stress on membrane damage, oxidative stress, and osmotic regulation in *L. megaphylla* seedlings. The impact of different levels of waterlogging stress on the MDA content (A),

REC (**B**), O_2^- production rate (**C**), H_2O_2 content (**D**), POD activity (**E**), and SOD activity (**F**) in *L. megaphylla* leaves; (**G**) NBT staining; (**H**) DAB staining; (**I–K**) effects of different levels of waterlogging stress on soluble sugars, soluble proteins, and proline content in *L. megaphylla* leaves. CK represents the control treatment. W1–W3 represent light, moderate, and severe waterlogging stress, respectively. Lowercase letters indicate significant differences between different treatments at the same time point ($p < 0.05$), while uppercase letters indicate significant differences at different time points for the same treatment ($p < 0.05$). Data are presented as the mean and standard deviation of three biological replicates.

In summary, under mild to moderate waterlogging, *L. megaphylla* is able to sustain physiological homeostasis through the coordinated activation of its antioxidant defenses and osmotic adjustment. In contrast, prolonged severe stress induces irreversible damage to the membrane system, disrupts redox balance, and impairs osmotic regulation capacity.

3.3. The Effects of Waterlogging Stress on Photosynthetic Pigment Metabolism and Photosystem Function in the Leaves of *L. megaphylla*

Waterlogging stress significantly inhibited the synthesis of photosynthetic pigments in *L. megaphylla* leaves (Figure 4A–D). Chlorophyll a (Chla), chlorophyll b (Chlb), carotenoids (Car), and total chlorophyll (Chla+b) decreased progressively as waterlogging severity and duration increased, with the most pronounced reductions observed in the W3 group after 28 d, where Chla, Chlb, and Car were reduced by 41.60%, 40.02%, and 34.33%, respectively, relative to the control. Following R7d, the pigment levels in the W1 and W2 groups showed partial restoration, with Chla+b recovering by 3.25% and 6.82%, respectively. In contrast, the pigment levels in the W3 group continued to decline, suggesting that sustained severe waterlogging inflicted irreversible damage.

Waterlogging stress reduced the photosystem performance of *L. megaphylla*, and PSI activity was significantly inhibited (Figure 4E–H). Severe stress markedly reduced the light energy transfer efficiency at the PSI acceptor side, with ϕRo and PI_{total} declining by 67.86% and 88.15%, respectively, compared to CK, and also diminished the PSII–PSI coordination index (REo/CSO) by 60.14%. After R7d, ϕRo and PI_{total} in the W1/W2 groups recovered to 86.51% and 95.29%, and 61.84% and 35.58% of the control. In contrast, the W3 group failed to recover, indicating that the PSI electron transport chain had sustained irreversible damage.

Additionally, the performance of PSII was highly sensitive to waterlogging stress (Figure 4). Examination of the OJIP curve revealed that after 28 d of stress, the fluorescence intensity at the P-step in the W3 group reached its lowest level, characterized by a pronounced rise in the O–J phase and a significant decrease in the I–P phase (Figure 5A–E). Chlorophyll fluorescence imaging confirmed that the Fv/Fm ratio in the W3 group was 28.70% lower than the control group (CK), with no significant recovery following restoration (Figure 5F,G). An analysis of JIP-test parameters further indicated that severe stress reduced the potential activity of PSII (Fv/Fo) and the quantum yield of electron transport (ETo/CSO) by 61.37% and 69.28%, respectively, while dissipated energy per unit area (DIO/CSO) increased by 231.15% (Figure 5H–L). After R7d, Fv/Fo in the W1 and W2 groups increased by 21.06% and 16.66%, whereas that in the W3 group remained significantly lower than the CK, indicating an irreversible impairment of PSII repair capacity.

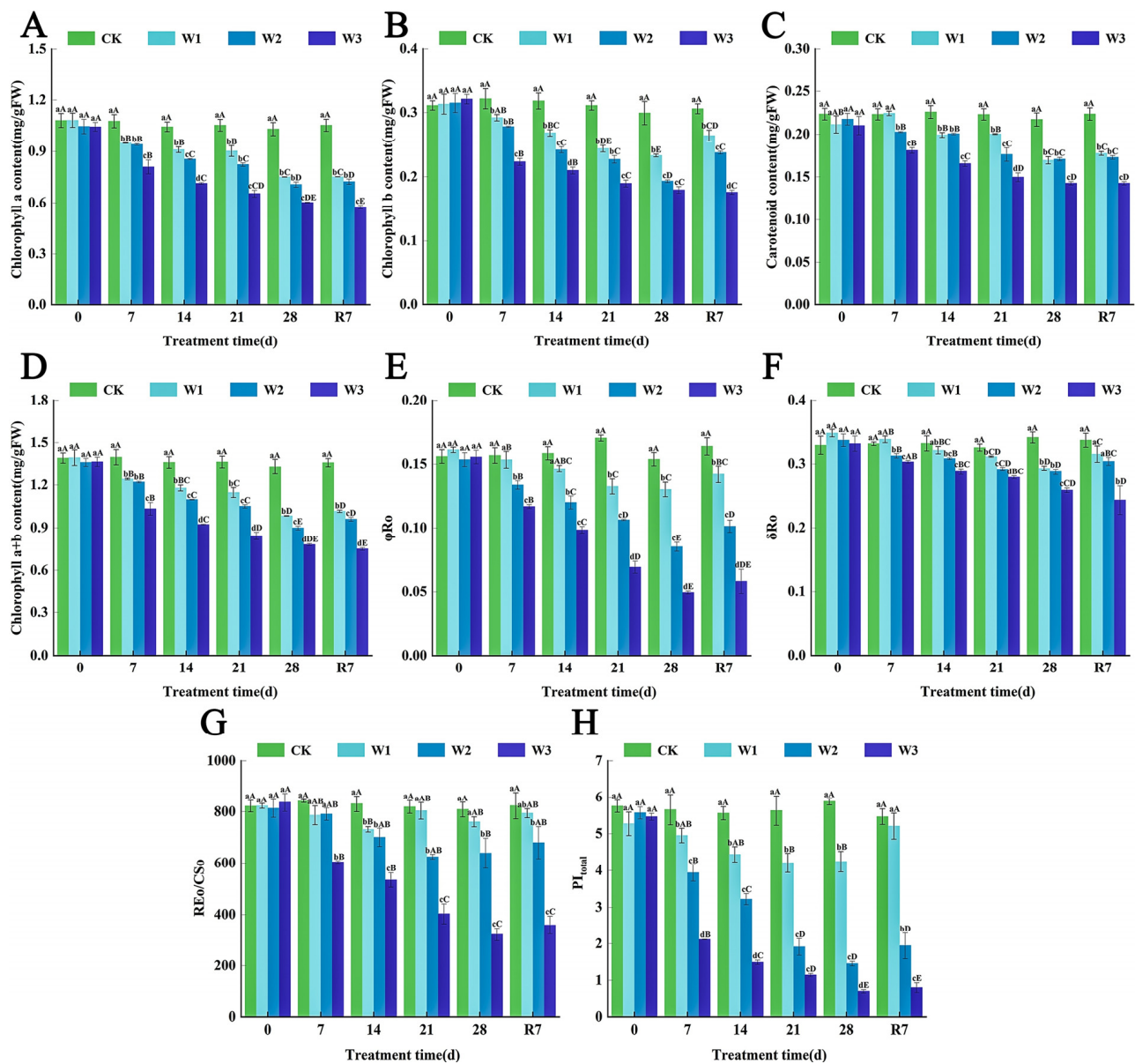


Figure 4. Effects of flooding stress on the photosynthetic pigment content and PSI functionality of *L. megaphylla* seedlings. (A) Chl a content; (B) Chl b content; (C) Car content; (D) total chlorophyll (Chl a+b) content; (E) end energy transfer efficiency of PSI (ϕRo); (F) electron transfer efficiency of PSI (δRo); (G) coordination between PSII and PSI (RE_o/CS_o); (H) overall electron transfer activity (PI_{total}). CK represents the control treatment. W1–W3 represent light, moderate, and severe flooding stress, respectively. Lowercase letters indicate significant differences between different treatments at the same time point ($p < 0.05$), while uppercase letters indicate significant differences between different time points for the same treatment ($p < 0.05$). Data represent the mean and standard deviation of three biological replicates.

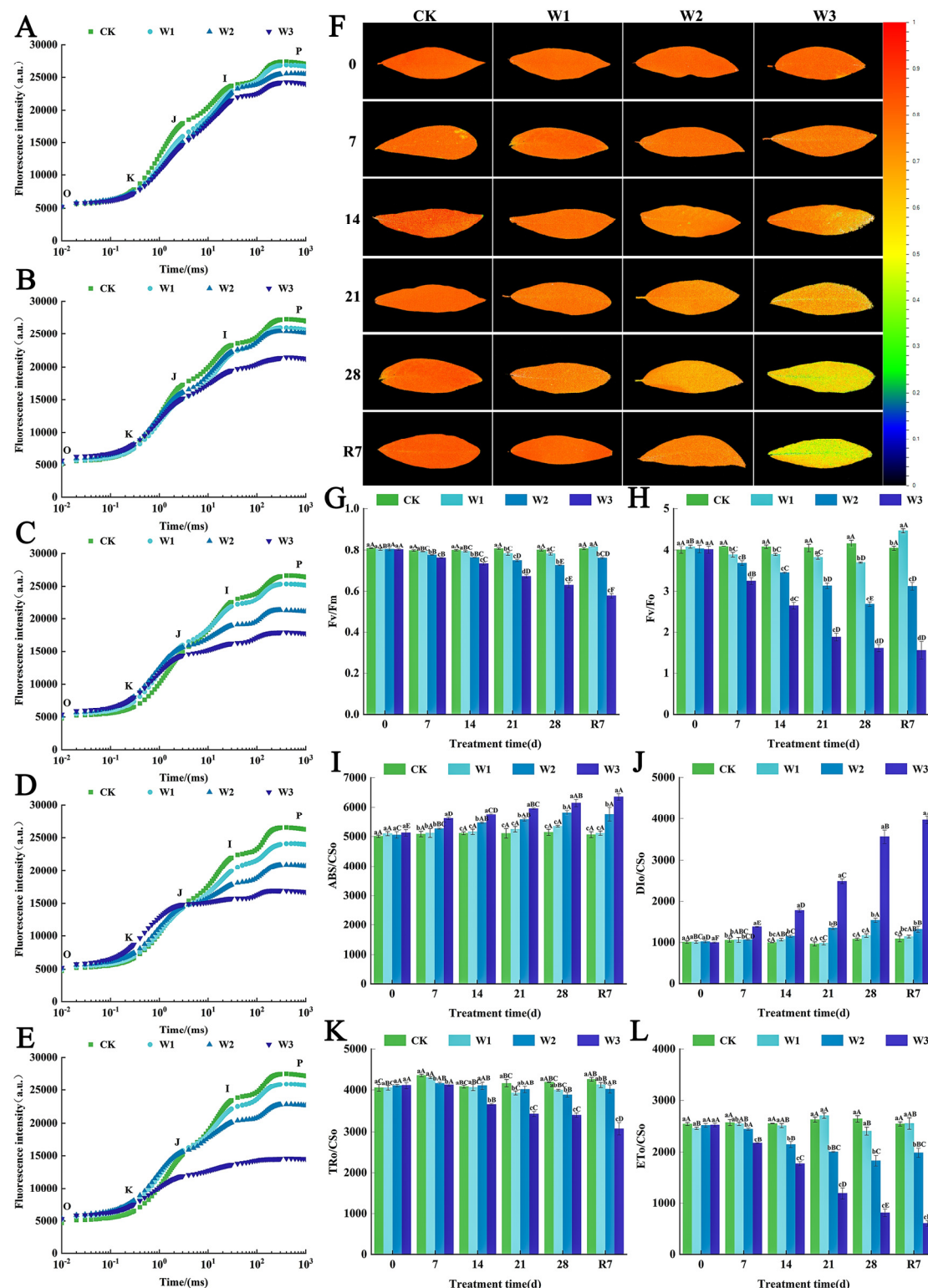


Figure 5. Effects of flooding stress on the PSII functionality of *L. megaphylla* seedlings. (A–E) OJIP curves of chlorophyll fluorescence kinetics in *L. megaphylla* leaves under varying degrees of flooding stress at 7 d, 14 d, 21 d, 28 d, and R7d. (F) Changes in chlorophyll fluorescence imaging of *L. megaphylla* leaves under different flooding stress levels; (G) Fv/Fm; (H) Fv/Fo; (I) ABS/CS₀; (J) DIO/CS₀; (K) TRo/CS₀; (L) ETo/CS₀. CK represents the control treatment. W1–W3 correspond to mild, moderate, and severe flooding stress, respectively. Lowercase letters indicate significant differences between treatments at the same time point ($p < 0.05$), while uppercase letters denote significant differences at different time points for the same treatment ($p < 0.05$). Data represent the mean and standard deviation of three biological replicates.

3.4. Comprehensive Effects of Waterlogging Stress on Physiological and Biochemical Indicators of *L. megaphylla* Seedlings

After 28 d of waterlogging, multiple physiological parameters showed significant correlations (Figure 6). In terms of osmotic balance regulation, RWC was negatively correlated with REC ($r = -0.78, p < 0.01$), indicating that increased membrane permeability led to greater water loss and higher REC. Meanwhile, SS and SP showed significant positive correlations with Pro ($r = 0.94$ and $0.73, p < 0.01$), suggesting a cooperative role in sustaining osmotic homeostasis under waterlogging. The antioxidant enzymes SOD and POD were highly synchronized ($r = 0.88, p < 0.01$), effectively mitigating ROS accumulation. In terms of photosynthetic efficiency, the Fv/Fm of photosystem II was tightly linked to Fv/Fo ($r = 0.94, p < 0.01$), indicating a consistent reflection of PSII photochemical activity. Furthermore, ABS/CSo was positively correlated with DIo/CSo ($r = 0.83, p < 0.01$), pointing to the coordinated regulation of light energy absorption and dissipation under flooding stress.

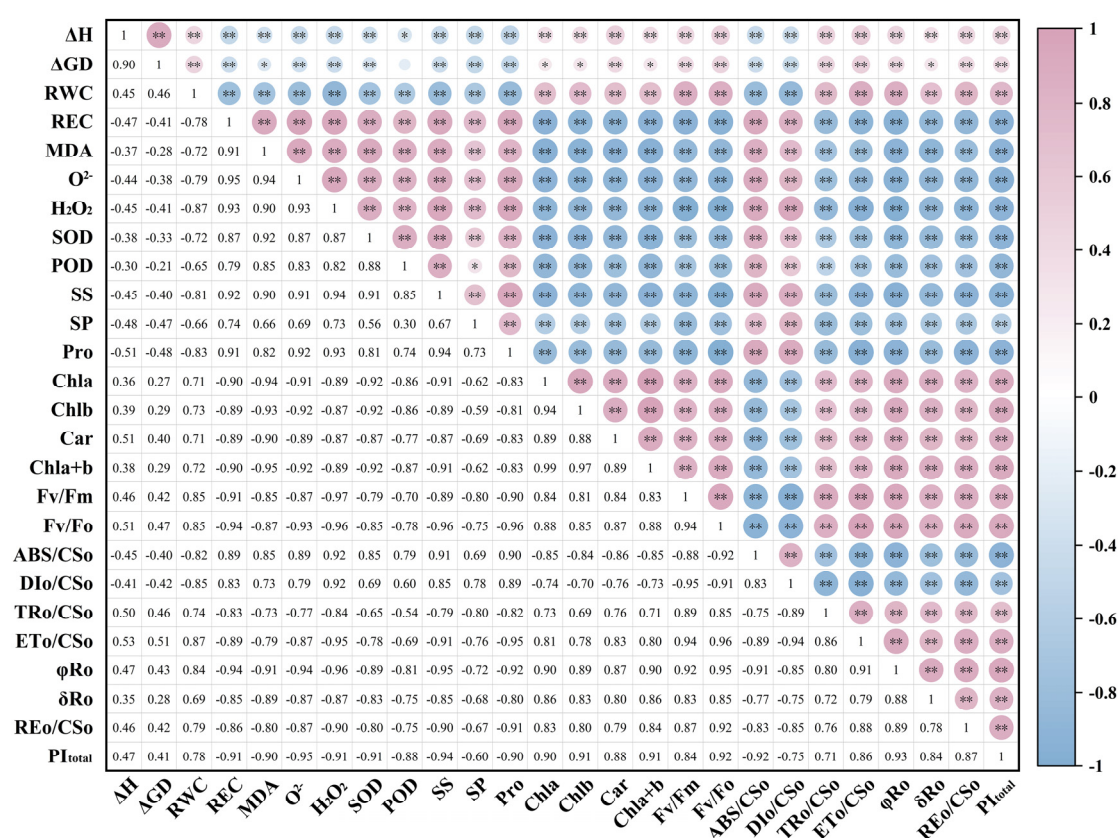


Figure 6. Correlation analysis of physiological parameters of *L. megaphylla* seedlings under gradient waterlogging stress for 28 d. Green indicates a positive correlation (+1.0 to 0), while blue indicates a negative correlation (0 to −1.0). ΔH: height growth rate; ΔGD: diameter growth increment; RWC: relative water content; REC: relative conductivity; MDA: malondialdehyde; O_2^- : rate of superoxide radical production; H_2O_2 : hydrogen peroxide content; SOD: superoxide dismutase activity; POD: peroxidase activity; SS: soluble sugar content; SP: soluble protein content; Pro: proline content; Chla: chlorophyll a content; Chlb: chlorophyll b content; Car: carotenoid content; Chla+b: total chlorophyll content; Fv/Fm: maximum photochemical efficiency; Fv/Fo: potential photochemical efficiency; ABS/CSo: light energy absorbed per unit area; DIo/CSo: light energy dissipated per unit area; TRo/CSo: light energy captured per unit area; ETto/CSo: quantum yield of electron transfer per unit area; ϕRo : energy transfer efficiency at the PSI terminal; δRo : PSI electron transfer efficiency; REo/CSo: coordination between PSII and PSI; PI_{total} : overall activity of electron transfer. * Significant at $p < 0.05$. ** Highly significant at $p < 0.01$.

3.5. Exogenous ABA Alleviates Growth Inhibition and Water Imbalance

The exogenous application of 3 $\mu\text{mol/L}$ ABA significantly increased the flood tolerance of *L. megaphylla* seedlings (Figure 7A). As shown in Table 3, the survival rate of the A3 group reached 53%, which was 60.61% higher than that of the A0 group (33%). Throughout the stress period, the A3 group sustained significantly greater growth, with $\Delta\text{H}/\Delta\text{GD}$ exceeding the A0 group by 0.07 cm (Figure 7B,C). After R7d, the height recovery in the A3 group reached 49.93%, whereas the A0 group suffered nearly complete mortality. Additionally, the leaf RWC in the A0 group decreased by 15.32% relative to CK after 28 d of flooding, while the reduction in the A3 group was only 8.64%, corresponding to a 7.89% improvement over the A0 group. After R7d, the RWC in the A3 group rebounded to 88.74% of CK, which was substantially higher than that of the A0 group, remaining 25% lower than CK (Figure 7D). Overall, these findings suggest that 3 $\mu\text{mol/L}$ ABA mitigates waterlogging-induced dehydration damage by maintaining osmotic homeostasis and enhancing water uptake capacity.

Table 3. The effect of different concentrations of ABA on the survival rate of *L. megaphylla* seedlings under waterlogging stress.

Treatment \ Time	0 d	7 d	14 d	21 d	28 d	R7d	Survival Rate
CK	-	-	-	-	-	-	100%
A0	-	a	a+, b, c	a++, b+, c++	a++, b++, c++, d, e	a++, b++, c++, d+, e+	33%
A1	-	a, b	a+, b+	a+, b++, c+	a++, b++, c+	a++, b++, c++, d	43%
A3	-	-	a, b+	a+, b++, c	a+, b++, c+	a++, b++, c+	53%

Note: “-” represents normal growth; “a” represents new leaves drooping or scorching; “b” represents leaves withering or drooping; “c” represents lower leaves turning yellow; “d” represents leaf abscission; “e” represents plant death; “+” represents the degree of severity, “++” indicates a more pronounced effect than “+”.

3.6. Regulation of Membrane Damage and Oxidative Stress by Exogenous ABA

Exogenous ABA markedly mitigated membrane injury, with the A3 group showing the most pronounced improvement, decreasing REC and MDA levels by 21.59% and 17.95%, respectively, compared to the A0 group. After R7d, the reductions in REC and MDA in the A3 group were 1.36- and 1.69-fold greater than those in the A0 group, but still significantly higher than the CK, indicating that severe stress-induced membrane damage was not fully reversible (Figure 8A,B). Similarly, the A3 group exhibited lower rates of O_2^- and H_2O_2 accumulation, reduced by 30.56% and 25.76%, respectively, indicating the effective suppression of ROS production (Figure 8C,D). Concurrently, ABA significantly stimulated the antioxidant enzyme system (Figure 8E,F), with SOD and POD activities in the A3 group increasing by 10.63% and 9.33%, respectively, relative to the A0 group. Histochemical analyses with NBT and DAB staining further confirmed that ROS accumulation was effectively curtailed under ABA treatment (Figure 8G,H). After R7d, the ROS levels in the A3 group remained higher than those in CK ($p < 0.01$), indicating that ABA cannot fully reverse oxidative damage but helps maintain cellular homeostasis through sustained activation of antioxidant defenses. Moreover, ABA treatment significantly restricted excessive osmolyte accumulation, with the A3 group showing significant decreases in SS, SP, and Pro contents by 6.74%, 9.09%, and 36.25%, respectively, compared with A0 (Figure 8I–K). After R7d, the Pro levels in A3 group further declined to 1.2 times that of CK ($p < 0.05$), indicating that ABA alleviates osmotic stress by regulating proline metabolism, thus preserving cell turgor and normal physiological function.

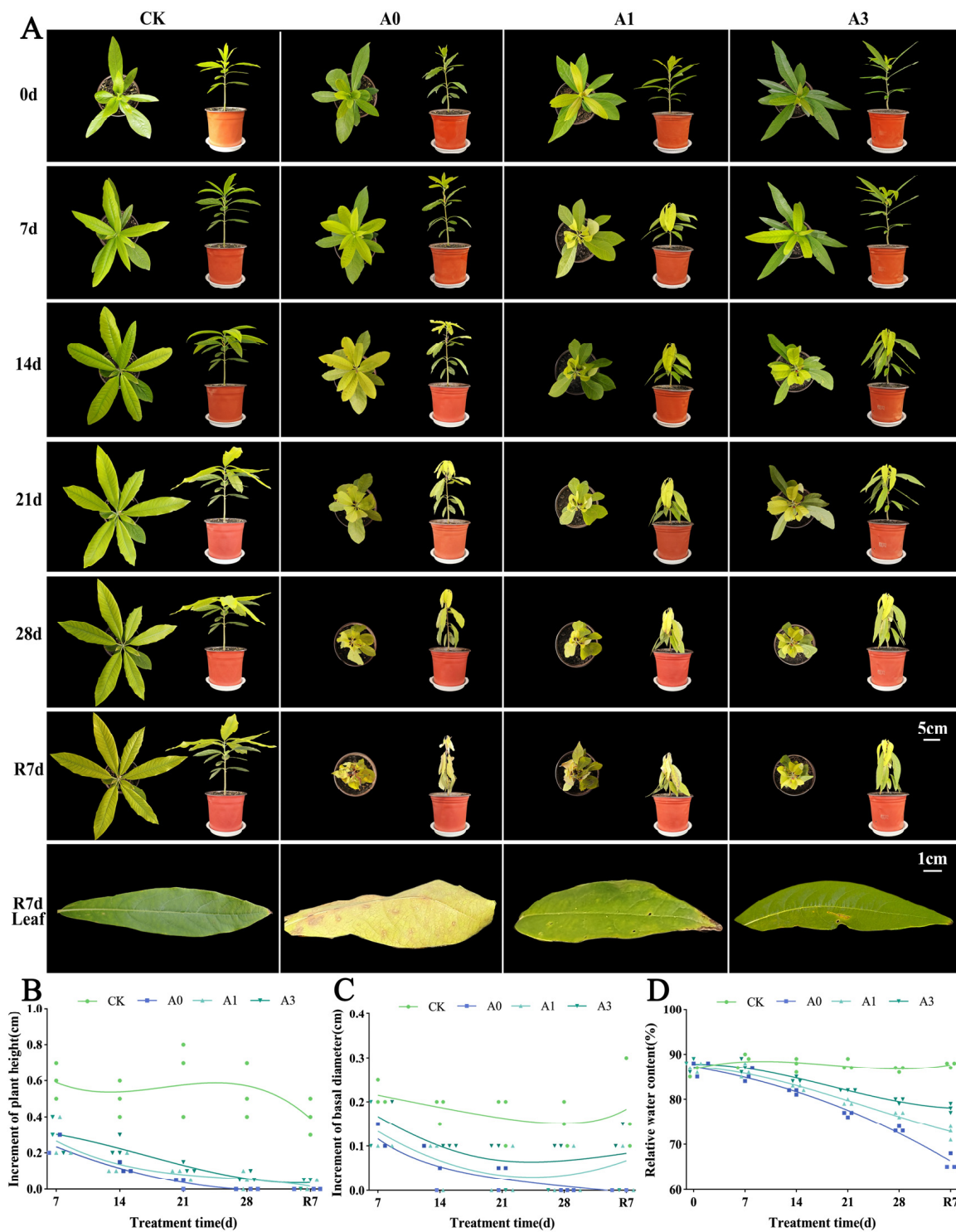


Figure 7. The alleviating effects of exogenous ABA at different concentrations on the morphology and water homeostasis of *L. megaphylla* seedlings. (A) Comparison of phenotypes of *L. megaphylla* seedlings under different waterlogging stress treatments for 28 d and R7d (7 days after recovery). The effect of different concentrations of exogenous ABA on the net growth of plant height (B), basal diameter (C), and REC (D) of *L. megaphylla* under waterlogging stress. A0: 0 $\mu\text{mol/L}$, A1: 1 $\mu\text{mol/L}$, A3: 3 $\mu\text{mol/L}$. Lowercase letters indicate significant differences between different treatments at the same time point ($p < 0.05$), while uppercase letters indicate significant differences at different time points for the same treatment ($p < 0.05$). Data represent the mean and standard deviation of three biological replicates.

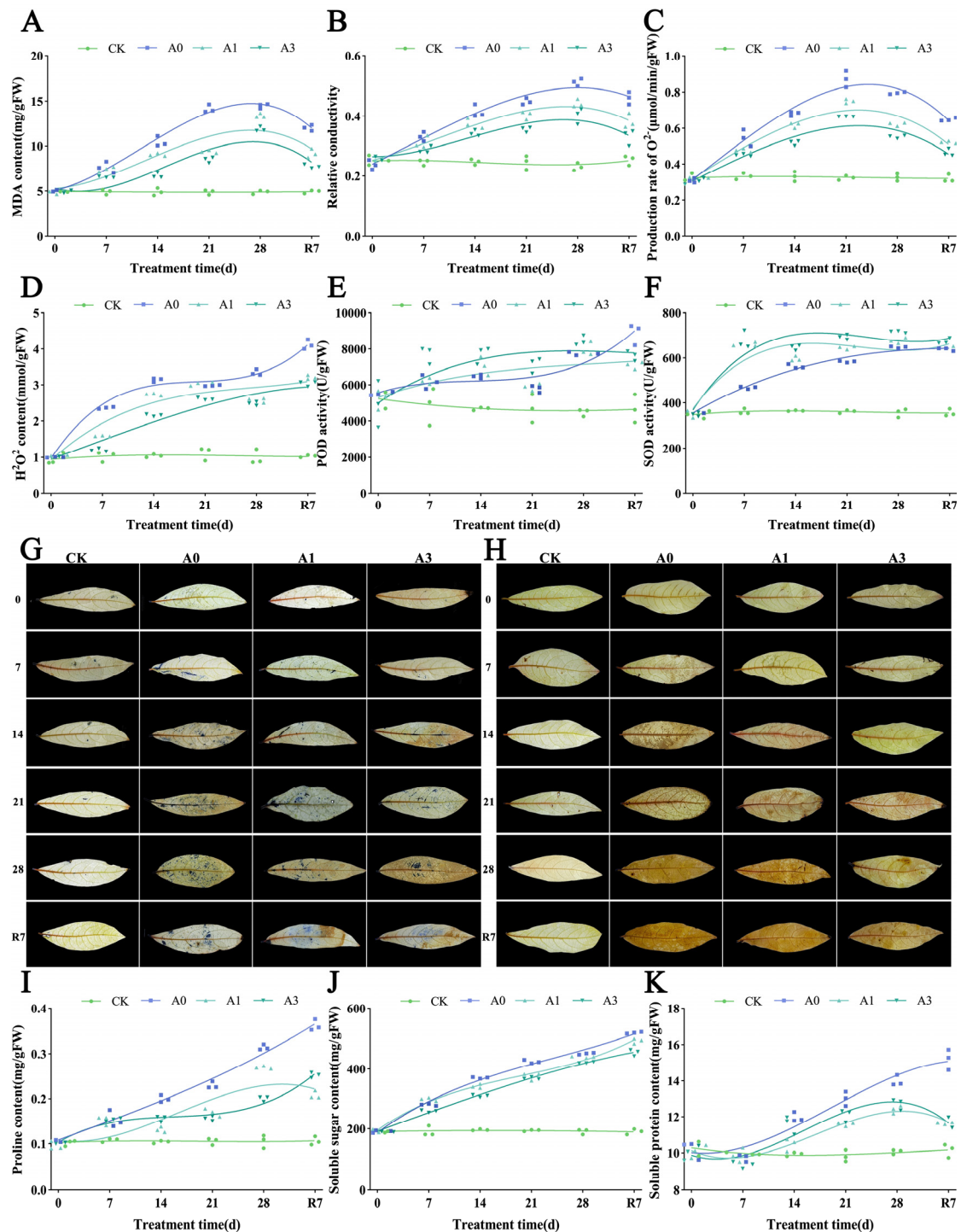


Figure 8. Effects of different concentrations of exogenous ABA on membrane damage and oxidative stress relief in *L. megaphylla* seedlings. The impact of different concentrations of exogenous ABA on MDA content (A), REC (B), O_2^- production rate (C), H_2O_2 content (D), POD activity (E), and SOD activity (F) in the leaves of *L. megaphylla* under flooding stress; (G) NBT staining; (H) DAB staining; (I–K) effects of different concentrations of exogenous ABA on SS, SP, and Pro content in the leaves of *L. megaphylla* under flooding stress. A0: 0 $\mu\text{mol}/\text{L}$, A1: 1 $\mu\text{mol}/\text{L}$, A3: 3 $\mu\text{mol}/\text{L}$. The lines represent the nonlinear regression fitting curves of the data in groups A0, A1, and A3 (coefficient of determination $R^2 > 0.75$, significance $p < 0.05$), while group CK is presented as the non-treated reference group.

3.7. The Synergistic Protective Mechanism of Exogenous ABA on the Photosynthetic System

Under severe waterlogging stress (W3), the pigment content in the A0 group significantly degraded (Figure 9A–D). In contrast, exogenous ABA application (3 $\mu\text{mol/L}$) significantly curtailed pigment degradation, resulting in 20.72%, 22.22%, 18.56%, and 21.12% higher contents of Chla, Chlb, Car, and total Chla+b, respectively, compared with the A0 group. After R7d, the Chla+b content in A3 rebounded to 72.61% of CK, while that in the A0 group remained significantly lower than CK. These results indicate that ABA mitigates waterlogging-induced photosystem impairment by preserving photosynthetic pigments.

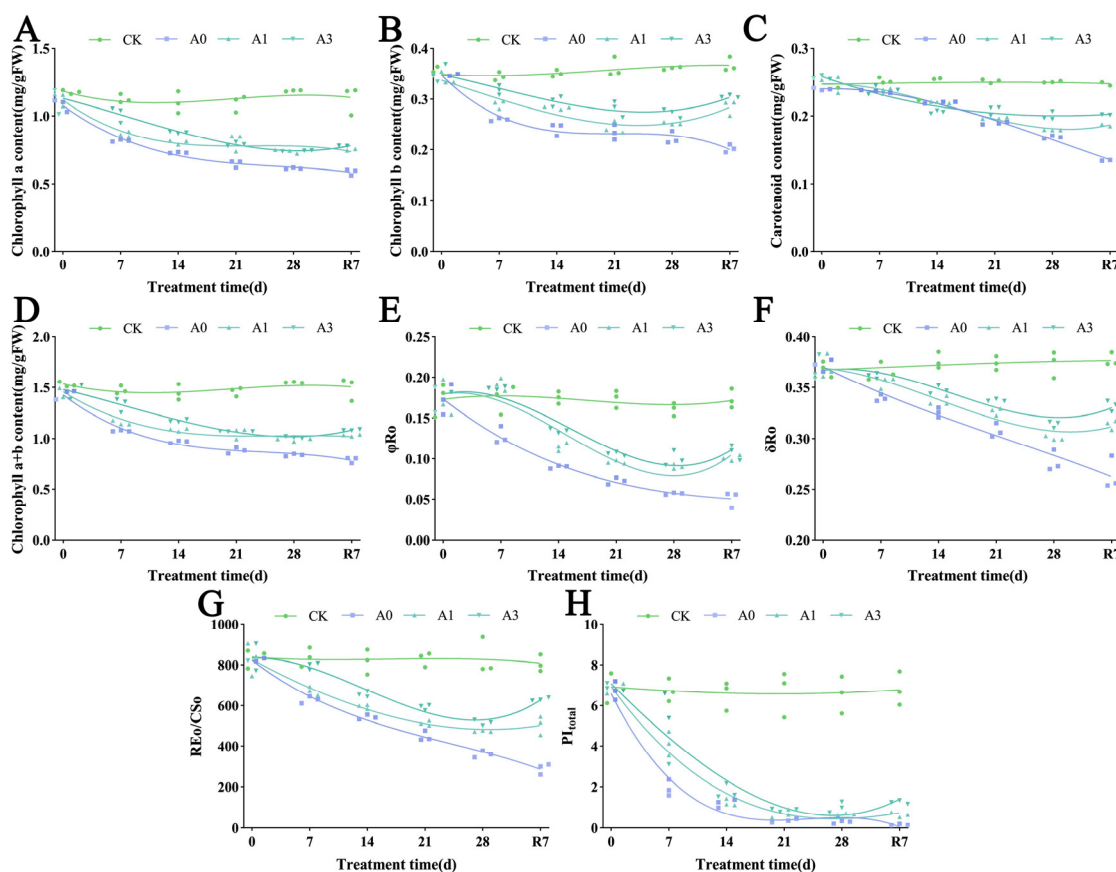


Figure 9. Effects of exogenous ABA at different concentrations on the photosynthetic pigments and PSI function in *L. megaphylla* seedlings. Content of Chla (A), Chlb (B), and Car (C); (D) Chla+b; (E) ϕRo of PSI; (F) δRo of PSI; (G) REo/CSO ; (H) PI_{total} . A0: 0 $\mu\text{mol/L}$, A1: 1 $\mu\text{mol/L}$, A3: 3 $\mu\text{mol/L}$. The lines represent the nonlinear regression fitting curves of the data in groups A0, A1, and A3 (coefficient of determination $R^2 > 0.75$, significance $p < 0.05$), while group CK is presented as the non-treated reference group.

PSI was severely inhibited under waterlogging stress (Figure 9E–H), as indicated by ϕRo , PI_{total} , and REo/CSO declining by 64.53%, 95.86%, and 56.84% in A0. The A3 group significantly alleviated the aforementioned damage, with ϕRo and PI_{total} increasing by 75.31% and 270.26%, respectively, compared to the A0 group. After R7d, the REo/CSO and PI_{total} in the A3 group had increased by 118.19% and 782.64%, respectively, compared to A0. Nevertheless, the PSI parameters in all groups remained markedly lower than in CK ($p < 0.01$), indicating that while ABA partially preserved PSI functionality by protecting the electron transport chain, it could not fully counteract long-term waterlogging injury.

Likewise, PSII displayed high sensitivity to waterlogging stress (Figure 10). Relative to the control, Fv/Fm and Fv/Fo in the A0 group declined markedly, whereas ABS/CSO and DIO/CSO increased significantly (Figure 10G–K). In contrast, the A3 group exhibited

improvements in F_v/F_m and F_v/F_o of 21.28% and 96.13%, respectively, while ABS/CS_o and DIo/CS_o reduced by 15.07% and 23.26% compared to A0. Chlorophyll fluorescence imaging and OJIP curve analysis further substantiated that, after R7d, the ET_o/CS_o in the A0 group continued to decrease by 25.31% compared to 28 d of stress, whereas the ET_o/CS_o in the A3 group increased by 20.02% (Figure 10A–F,L). However, the PSII parameters across all treatments remained substantially lower than the control, suggesting that prolonged waterlogging damage was not fully reversible.

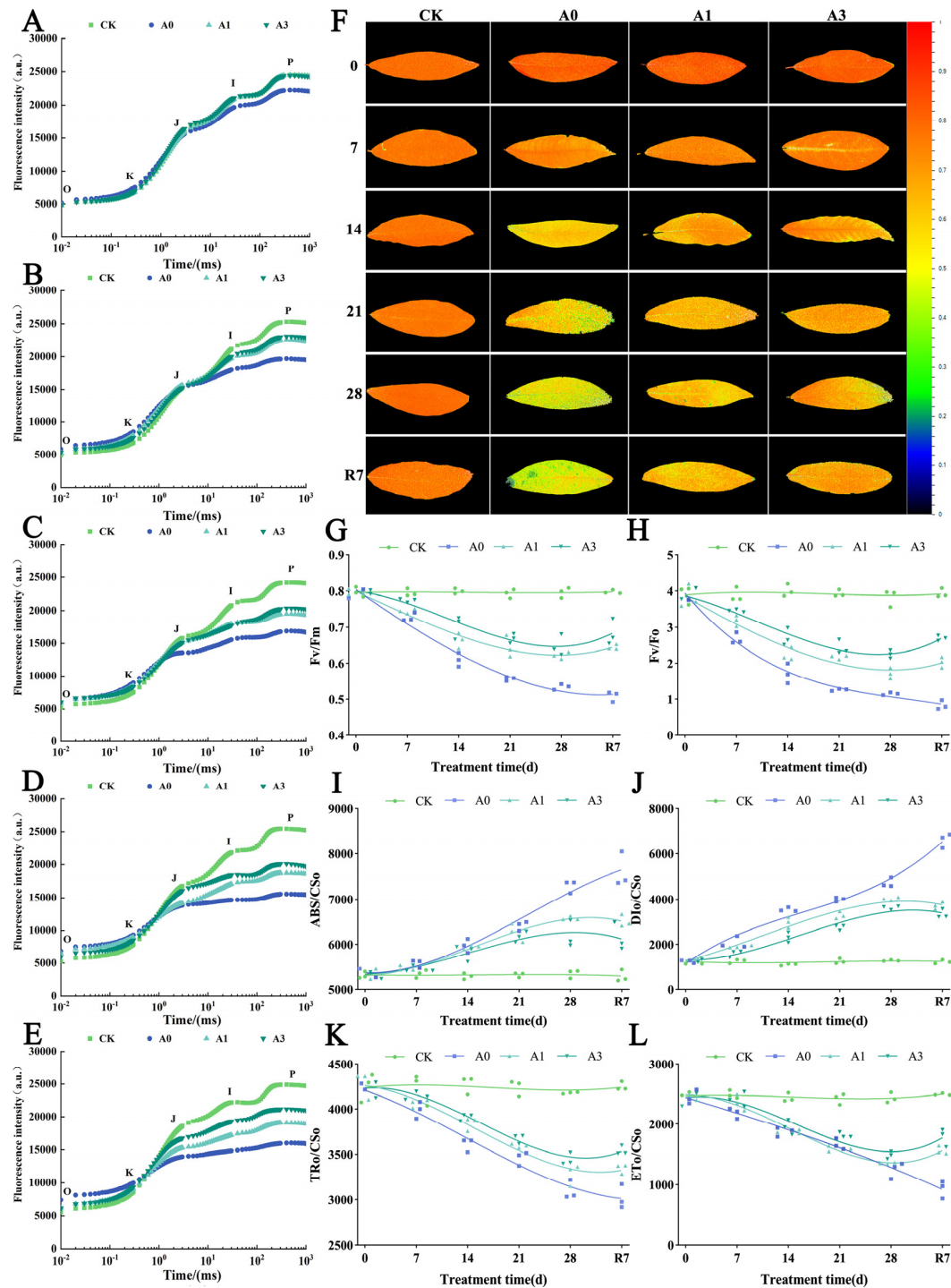


Figure 10. Effects of exogenous ABA at different concentrations on the PSII function of *L. megaphylla* seedlings under alleviation. (A–E) OJIP curves of *L. megaphylla* leaves treated with different concentrations

of ABA under flooding stress for 7 d, 14 d, 21 d, 28 d, and R7d (7 days after recovery). (F) Changes in chlorophyll fluorescence imaging of *L. megaphylla* leaves under flooding stress with different concentrations of ABA. (G) Fv/Fm; (H) Fv/Fo; (I) ABS/CSo; (J) DIO/CSo; (K) TRo/CSo; (L) ETo/CSo. A0: 0 $\mu\text{mol/L}$, A1: 1 $\mu\text{mol/L}$, A3: 3 $\mu\text{mol/L}$. The lines represent the nonlinear regression fitting curves of the data in groups A0, A1, and A3 (coefficient of determination $R^2 > 0.75$, significance $p < 0.05$), while group CK is presented as the non-treated reference group.

4. Discussion

This study elucidates, for the first time, that exogenous ABA enhances the flood tolerance of *L. megaphylla* through multidimensional physiological regulation. Furthermore, it reveals the unique role of ABA in the coordinated repair of the photosynthetic system.

4.1. ABA Alleviates Waterlogging Damage by Maintaining Morphology and Water Homeostasis

Morphological traits are the most direct indicator of plant damage and serve as fundamental criteria for assessing adaptation to waterlogging stress [5,7,45,46]. By examining these traits under stress, it is possible to visually evaluate plant growth and developmental status and to assess the mitigating effects of exogenous substances on this stress [47]. Waterlogging stress typically induces leaf yellowing, drooping, wilting, growth stagnation, and a sharp decline in survival rate (as low as 30% survival) in *L. megaphylla* seedlings, consistent with the typical stress strategy in plants of sacrificing expendable tissues to protect core metabolism [48]. In this study, treatment with 3 $\mu\text{mol/L}$ ABA increased the survival rate to 53% (60.61% improvement relative to the untreated group) and significantly maintained seedling height and diameter growth, in contrast to the pronounced growth inhibition observed in the untreated group. These experimental results are consistent with those of Zhao et al. [49], who reported that exogenous ABA significantly improves the survival and tolerance of various plants under waterlogging stress across different concentrations. RWC reflects the moisture status and water retention capacity of plant tissues and is an important indicator for evaluating stress-induced damage [50]. In this study, ABA effectively enhanced the leaf RWC of *L. megaphylla* seedlings under waterlogging, which may be attributed to the dual regulatory mechanism of ABA. The first mechanism involves promoting water uptake by inducing the expression of PIP aquaporin genes. Previous studies have demonstrated that exogenous ABA markedly upregulates the expression of multiple PIP genes in wild-type *Arabidopsis thaliana* [51] and rice [52], thereby improving the hydraulic conductivity of root cells. Similarly, Li et al. [53] showed that, under salt stress, elevated endogenous ABA in maize significantly enhances the expression of several PIP genes, consequently increasing root hydraulic conductivity and water uptake. The second mechanism involves reducing water loss through stomatal closure, a well-documented response in plants. Numerous studies have demonstrated that ABA, a key stress-signaling hormone, regulates stomatal closure by activating the ABA signaling network, thereby modulating ion fluxes in guard cells and ultimately decreasing water loss [54,55]. Notably, the effectiveness of ABA in improving RWC decreases as stress intensity increases, indicating a threshold effect in its water retention capacity. For instance, ABA alleviated water loss in *L. megaphylla* seedlings under flooding stress; after R7d, although the RWC continued to decline in the A0, A1, and A3 groups, the decrease was relatively modest in A1 and A3 (5.06% and 2.01%, respectively), whereas the A0 group exhibited a significant decrease of 10.66%. This suggests that the water retention capacity conferred by ABA is constrained by the severity and duration of stress. Overall, these findings are consistent with previous reports that ABA enhances the relative water content in various plant species, including rose, melon seedlings, tobacco, maize, and soybean [56,57].

4.2. ABA Mitigates Oxidative Damage Through an Antioxidant–Membrane Protection Network

When plants are exposed to stressful environments, the balance between ROS accumulation and scavenging is disrupted, resulting in damage to biological membranes and their associated functions. MDA, a primary product of lipid peroxidation within cell membranes, and REC, an indicator of plasma membrane permeability, are critical parameters for evaluating the extent of membrane injury in plants [58,59]. This study demonstrated that exogenous ABA application reduced the production rate of O_2^- and reduced the H_2O_2 content in *L. megaphylla* leaves by 30.56% and 25.76%, respectively, thereby mitigating waterlogging-induced oxidative damage. Consistent with these findings, research by Jiang et al. [60] showed that exogenous ABA significantly decreases MDA and H_2O_2 levels in maize leaves under drought stress while enhancing antioxidant enzyme activities, suggesting that ABA plays a key role in ROS scavenging and the antioxidant defense system. Furthermore, ABA activated the SOD and POD enzyme systems, with activities increasing by 10.63% and 9.33%, respectively. The activity of endogenous protective enzymes, including SOD and POD, is crucial for eliminating free radicals, maintaining cellular redox homeostasis, and improving stress tolerance in plants [61–63]. In maize, exogenous ABA application can enhance SOD and POD activities, thereby alleviating drought-induced stress effects [64]. Similarly, applying exogenous ABA significantly increased the SOD and POD activities in adzuki bean leaves under flooding, effectively mitigating waterlogging damage [65], which is consistent with our findings. Compared with herbaceous species such as rice, *L. megaphylla* showed greater recovery of membrane integrity under ABA treatment, with MDA content decreasing by 17.95%. This may be attributed to its robust membrane repair capacity associated with its woody characteristics [66,67]. However, indices of membrane damage during the recovery period remained higher than those of the control, suggesting that severe stress induces irreversible damage to the membrane structure. This is consistent with observations made by Shi et al. [68], who reported anatomical and ultrastructural changes in the leaves of *Phoebe* seedlings under flooding stress.

4.3. ABA Maintains Cellular Homeostasis Through a Differential Osmotic Regulation Strategy

SS, SP, and Pro serve as crucial osmotic regulators in plants, playing a critical role in sustaining vital physiological processes and nutrient availability. Under adverse conditions, plants enhance osmotic synthesis to lower cellular osmotic potential and mitigate stress-induced damage [69,70]. This study presents a dynamic analysis of osmotic regulators in the leaves of *L. megaphylla* seedlings, demonstrating that ABA induces a unique “reverse regulation” of Pro metabolism, leading to a 36.25% decrease in Pro content. This finding contrasts with the typical Pro accumulation in most plant species under stress [71]. A previous study by Lee et al. [72] showed that ABA promotes Pro synthesis in rapeseed, thereby enhancing its stress tolerance. This distinctive pattern may reflect Pro’s dual role in osmotic protection and signal transduction in *L. megaphylla*. Indeed, Pro is known to fulfill diverse physiological and biochemical functions under adverse conditions and is considered a major regulatory factor in stress adaptation [73,74]. In contrast, ABA exerted a more moderate effect on SS and SP, resulting in reductions of 6.74% and 9.09%, respectively. This more tempered regulation prevents excessive consumption of carbon and nitrogen resources while maintaining osmotic homeostasis. Moreover, studies have indicated that SP can complement and enhance osmotic adjustment via protective enzymes or signaling components under specific conditions [75]. Similarly, energy deficiency under waterlogging conditions impedes phloem transport of SS from leaf tissues to roots, thereby leading to its accumulation [76]. This multi-tiered regulatory pattern, characterized by rapid Pro turnover and the long-term fine-tuning of SS/SP, may represent a key adaptive strategy that enables evergreen woody species to adapt to flooding stress.

4.4. ABA Enhances Light Energy Utilization Efficiency by Synergistically Protecting the Photosynthetic Apparatus

Chlorophyll fluorescence parameters in plant leaves can rapidly, sensitively, and non-destructively reflect light capture, absorption, dissipation, and electron transfer processes in PSII and PSI. These parameters serve as critical indicators for evaluating photosynthetic capacity and the extent of stress-induced damage [77–79]. This study first reveals that ABA confers photosystem-specific protective effects on the photosynthetic apparatus of *L. megaphylla*. In PSII, ABA predominantly sustains D1 protein turnover and PsbO complex stability, thereby alleviating damage to the photosynthetic electron transport chain, improving electron transfer capacity [80], and increasing Fv/Fm by 21.28%. In PSI, ABA preserves thylakoid membrane structure, mitigates electron transfer blockage at the PSI acceptor side, and reduces the decline in light energy utilization efficiency [81,82], resulting in a 270.26% increase in PI_{total} . Notably, ABA markedly enhances PSII–PSI coordination, as indicated by a 43.63% rise in REo/CSO. This synergistic protective effect has not been previously reported and may represent a unique photoprotective mechanism in evergreen woody species. Although the photosynthetic parameters after recovery remained lower than those of the control group, the Chla+b content in the ABA treatment group rebounded to 72.61%, suggesting that ABA delays photosystem collapse by preserving a balance between pigment synthesis and degradation. Chlorophyll is the primary pigment involved in photosynthesis, serving as a crucial mediator of light energy capture and electron transfer [83,84]. Pospíšilová et al. [85] reported that applying ABA to micropropagated tobacco seedlings after their transfer ex vitro significantly increased chlorophyll (a + b) and β -carotene contents compared with the control group. Similarly, Wang et al. [86] demonstrated that spraying ABA on hybrid roses subjected to high-temperature stress markedly elevated chlorophyll content in rose leaves. These findings highlight the critical role of ABA in regulating chlorophyll synthesis and degradation.

This study has certain limitations. Firstly, the absence of direct monitoring of rhizospheric dissolved oxygen (DO) prevents precise quantification of hypoxic stress intensity across different waterlogging treatments. Secondly, investigation of the glutathione–ascorbate (AsA-GSH) cycle would substantially deepen our understanding of the redox regulatory network. Future research employing comprehensive integration of these approaches will be crucial for establishing definitive links between environmental oxygen dynamics, complete redox systems, and physiological flooding tolerance mechanisms in *Lindera megaphylla*.

5. Conclusions

This study demonstrates that *L. megaphylla* seedlings exhibit a certain degree of flood tolerance, enduring mild and moderate flooding for up to one month. Correlation analysis identified five reliable physiological and biochemical indicators for assessing flood stress status: REC, MDA, Pro, Fv/Fm, and Chla+b. Exogenous ABA treatment significantly enhances flood tolerance through a coordinated mechanism that enhances SOD/POD antioxidant activity to reduce ROS (O_2^- , H_2O_2) accumulation, promotes osmotic regulators (Pro, SS, SP) to maintain water balance, and mitigates chlorophyll loss while aiding PSII/PSI repair. Among the treatments, 3 μ mol/L ABA exhibited the most pronounced impact, but it could not fully counteract all the physiological and biochemical damage caused by long-term severe waterlogging. These findings provide a solid theoretical and technical foundation for the protection and application of *L. megaphylla* in flood-prone environments.

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