

## Article

# Effect of Mixed Spraying of SA and ABA on the Growth and Development of Winter Oilseed Rape (*Brassica napus* L.) During the Post-Waterlogging Podding Period

Mingyu Shao <sup>1,2</sup>, Yejun He <sup>1,2</sup>, Xinran Han <sup>1,2</sup>, Hongyue Qu <sup>1,2</sup>, Xiaoyang Zhang <sup>1,2</sup>, Changqiang Chen <sup>1,2</sup>, Jiamin Zhang <sup>1,2</sup>, Qinxu Song <sup>1,2</sup>, Jinghua Zhou <sup>3</sup>, Yucheng Jie <sup>1,2,4,\*</sup> and Hucheng Xing <sup>1,2,4,\*</sup> 

- <sup>1</sup> Ramie Research Institute of Hunan Agricultural University, Changsha 410128, China; shaomingyu@stu.hunau.edu.cn (M.S.); hyejun@163.com (Y.H.); hanxinran@stu.hunau.edu.cn (X.H.); sboping@stu.hunau.edu.cn (H.Q.); zhangxiaoyang@stu.hunau.edu.cn (X.Z.); chenchangqiang@stu.hunau.edu.cn (C.C.); zhangjiaminn@yeah.net (J.Z.); songqinxu@stu.hunau.edu.cn (Q.S.)  
<sup>2</sup> College of Agronomy, Hunan Agricultural University, Changsha 410128, China  
<sup>3</sup> Hunan Anxiang County Agricultural Extension Centre, Changde 415600, China; jinghua06101@163.com  
<sup>4</sup> Hunan Provincial Engineering Technology Research Center of Grass Crop Germplasm Innovation and Utilization, Changsha 410128, China  
\* Correspondence: ibfcjyc@vip.sina.com (Y.J.); xinghucheng@hunau.edu.cn (H.X.)

**Abstract:** Winter oilseed rape is particularly vulnerable to waterlogging stress during its growth and development stages, especially at the podding stage, leading to impaired photosynthesis, reduced antioxidant enzyme activity, and significant declines in yield and oil content. Previous studies have demonstrated that exogenous plant growth regulators, such as salicylic acid (SA) and abscisic acid (ABA), enhance crop resistance to abiotic stresses. Nevertheless, their combined application for winter oilseed rape recovery under waterlogging stress remains underexplored. In this study, a pot experiment was conducted to investigate the effects of SA, ABA, and their combination on the growth, photosynthesis, antioxidant enzyme activity, and yield of winter oilseed rape at the podding stage following waterlogging stress. The results showed that mixed spraying of SA and ABA significantly improved plant height, effective branching number, yield per plant, and thousand-grain weight of winter oilseed rape, surpassing the effects of individual treatments. Structural equation modeling revealed that mixed spraying enhanced yield components through direct improvements in photosynthesis and indirect regulation of antioxidant enzyme activities. This study is the first to systematically evaluate the role of mixed spraying of SA and ABA in mitigating waterlogging stress and restoring yield and quality in winter oilseed rape. This approach effectively alleviates the adverse effects of waterlogging and provides a valuable reference for post-waterlogging management of other crops. These results hold significant implications for addressing the impacts of climate change and ensuring global food security.

**Keywords:** oilseed rape; waterlogging stress; salicylic acid; abscisic acid; yield per plant



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## 1. Introduction

As global warming increases the probability of extreme weather events, it is projected that globally 17 million km<sup>2</sup> of land and 19 per cent of crop yields will be affected by waterlogging stresses [1]. Flooding is the most frequent and widespread disaster in China, with the affected areas in the Yangtze River Basin and the Huang-huai-hai Plain accounting for about 75 per cent of the total area of China's national disaster areas [2]. Hunan is located

in the middle and lower reaches of the Yangtze River basin, and flooding will occur in Hunan every year from 2019 to 2023 [3]. Waterlogging stress disrupts plant processes such as photosynthesis, protein synthesis, and antioxidant enzyme activities, which negatively affects plant growth and can reduce crop yields by 40–80% [4–6]. Oilseed rape, a major oilseed crop in China, is particularly vulnerable to these conditions, especially in Hunan, a key producing region [7]. The subtropical monsoon climate in Hunan brings heavy spring and autumn rains, often exceeding the water requirements of oilseed rape [8]. When stress occurs during the seedling, shoot, flowering, or podding stages, it reduces photosynthesis and antioxidant enzyme activities, resulting in decreased plant height, flower number, seed number, thousand-seed weight, and both seed yield and quality [9–11]. Therefore, it is crucial to identify effective measures to mitigate yield and quality losses in oilseed rape due to waterlogging damage.

Traditional measures to mitigate the adverse effects of flooding primarily include soil and crop management practices [12]. In soil management, the most common techniques are deep plowing and subsoil fertilization [13,14]. However, both methods have limitations. Deep plowing is often short-term in nature and less effective in saline soils, while subsoil fertilization faces challenges such as high upfront costs (approximately \$1200/ha) and lack of specialized equipment [12]. As a result, these techniques are not suitable for widespread implementation. In crop management, common practices include selecting flood-tolerant varieties, adjusting sowing timing, and applying fertilizers. However, breeding flood-tolerant varieties is time-consuming, and the timing of internal flooding is uncertain, which, along with the risk of nutrient imbalances affecting soil ecology, makes these methods less effective in addressing waterlogging stress [15]. Consequently, plant growth regulators are gaining attention as a promising alternative for mitigating the damage caused by waterlogging to crops.

Studies have shown that plant growth regulators can mitigate the damage caused by waterlogging and increase the yield of winter oilseed rape [16]. These regulators play a crucial role in modulating plant physiological responses and enabling adaptation to unfavorable environmental conditions [17]. Salicylic acid (SA) is particularly important in helping plants cope with stress, as it enhances chlorophyll content, photosynthetic rate, and overall photosynthetic activity [18,19]. Absciscic acid (ABA), a well-known stress tolerance factor, regulates plant responses to adverse conditions by promoting adventitious root growth, improving leaf photosynthetic rate, and boosting antioxidant enzyme activities [20–22]. It has been shown that exogenous SA helps maize seedlings and sunflowers to increase yield under waterlogging stress by protecting the photosynthetic system and antioxidant enzyme activities [23,24]. Exogenous ABA reduces the negative effects of waterlogging stress on muskmelon and increases dry matter content [25]. Furthermore, the combined application of plant growth regulators is more effective than individual treatments under stress conditions [26–28]. For instance, Zhang et al. [29] found that the combined use of auxin and ethyl tricosanoate improved root growth, antioxidant enzyme activity, and biomass in crops under drought stress. However, the synergistic effects of these two plant growth regulators following mixed application, as well as their recovery ability after flooding in oilseed rape, remain unexplored. Based on previous findings, we hypothesize that the combination of SA and ABA may have synergistic effects on plant adaptation to abiotic stresses such as flooding.

Although previous studies have reported that combined treatments of SA or ABA with other plant growth regulators can benefit crops subjected to abiotic stresses [30–32], there is a lack of attention on the effects of combined application of SA and ABA on yield, quality, photosynthesis, and antioxidant enzyme activities of oilseed rape after waterlogging. The aim of this study was to investigate the changes in yield, quality, photosynthesis, and

antioxidant enzyme activities of oilseed rape and the effects of combined application of SA and ABA on the recovery of oilseed rape after waterlogging by spraying SA, ABA, and a mixture of SA and ABA regulators. These results will help to determine whether the combined application of SA and ABA can mitigate the adverse effects of flooding in oilseed rape. They may provide methods for post-flooding recovery measures during pod development in oilseed rape. This provides a reference for the flood-resistant cultivation of rapeseed in the Yangtze River basin of China, which can improve the yield and seed quality of rapeseed and promote its sustainable development.

## 2. Materials and Methods

### 2.1. Test Subjects and Experimental Location

The oilseed rape variety used in this study was 'Fengyou832'. It is developed by the Crop Research Institute of Hunan Provincial Academy of Agricultural Sciences. The variety is characterized by good adaptability, high yield, high oil content, etc. This variety is widely planted in the southern region, especially in Hunan. The main planting time in Hunan is 21–23 years. The pot experiment was conducted from 2020 to 2023 at the experimental base of Hunan Agricultural University (28°18' N, 113°08' E).

### 2.2. Experimental Design

Oilseed rape was sown on September 10 in a silty loam soil seedbed. Fifty seedlings were transplanted on October 25 (at the six-leaf stage) into each experimental plastic pot. The seedlings were placed into plastic pots containing 5 kg of quartz sand, with an inner diameter of 230 mm and a height of 210 mm, with one plant per pot. Each pot received 5 g of composite fertilizer (N:P:K = 15:15:15), 1 g of urea, and 4 g of calcium superphosphate before transplanting. When the oilseed rape reached the pod stage, 50 plant pots were randomly divided into five groups: one group was grown under well-drained conditions (CK1), while the remaining four groups were placed in non-porous plastic pots with an inner diameter of 300 mm and a height of 295 mm. These four groups were flooded with water to maintain a soil surface submergence of more than 3 cm. The waterlogging duration was 10 days, and at the end of each waterlogging period, all remaining water was drained from the soil surface. Three of the groups were sprayed with one of the following solutions, according to Xia Wenrong and Wang Xuefu et al. [33,34], and based on the optimal concentrations identified in previous experiments: 2 mmol/L salicylic acid (SA), 0.16 g/L abscisic acid (ABA), or a mixture of 2 mmol/L salicylic acid and 0.16 g/L abscisic acid (SA + ABA) (Table A1). The final group was sprayed with fresh water, termed CK2.

The agronomic traits, yield per plant, and seed oil content of oilseed rape were investigated over three growing seasons: 10/2020–05/2021, 10/2021–05/2022, and 10/2022–05/2023. The net photosynthetic rate and chlorophyll content (SPAD) were measured in sessile leaves (the first sessile leaf counting down from the flower bud) during the 2022–2023 growth season. Additionally, sessile leaves of all treated plants were harvested on days 0 and 10 after flooding during the 2022–2023 growing season, frozen in liquid nitrogen, and stored at −80 °C. Subsequently, they were assayed for peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT).

### 2.3. Feature Evaluation

The oilseed rape used in the pot experiments was harvested in early May. At physiological maturity, all oilseed rape plants in the pots were evaluated for eight agronomic traits: plant height (Ph), stem thickness (St), number of effective branches (Ebn), number of effective pods (Enp), number of seeds per pod (Nps), oil content (Oc), 1000-grain weight (Tgw), and yield per plant (Ypp).

Plant height was defined as the distance from the stem base to the tip of the main inflorescence. Stem thickness was measured at the first stem node, counted upward from the stem base. The effective number of hornbeams was determined by counting the branches bearing hornbeams and those assessed as fully developed. The number of seeds per pod refers to the average number of seeds from ten randomly sampled individual plants. Thousand-grain weight was measured as the weight of 1000 well-developed seeds. Finally, plants from each plot were harvested for yield evaluation. Seed oil content was assessed using the FOSS-NIR System 5000.

#### 2.3.1. Net Photosynthetic Rate and Chlorophyll

For the 50 pots of oilseed rape in the pot experiment, three fully expanded leaves per plant were randomly selected on Days 0 and 10 of waterlogging to measure the net photosynthetic rate ( $\phi_2$ ) and SPAD using a multifunctional plant meter (PhotosynQ, Michigan State University, East Lansing, MI, USA).

#### 2.3.2. Assays of POD, SOD, and CAT Enzyme Activities

For physiological index measurements, following the approach of Ping Yuan et al. [35], Peroxidase (POD), Superoxide dismutase (SOD), and Catalase (CAT) contents were determined using the spectrophotometry POD, SOD and CAT Kits (Boxbio, Beijing, China), respectively. This was performed separately following each kit's instructions and repeated thrice.

#### 2.4. Statistical Analysis

Morphological, physiological, and biochemical data were analyzed using analysis of variance (ANOVA) with Origin software (version 9.5.1.195; OriginLab, Northampton, MA, USA). Because we are making comparisons between multiple groups, Tukey's HSD is able to effectively control for Type I errors (false positives) caused by multiple comparisons. Differences between treatments were assessed using Tukey's Honest Significant Difference (HSD) test at the  $p < 0.05$  level.

The Partial Least Squares Structural Model is a suitable model for dealing with complex multivariate path models, independent of sample size requirements. By evaluating the model's goodness-of-fit (GOF),  $R^2$  values, path coefficients and other metrics, we can validate the quality of the model's fit and ensure the model's effectiveness in fitting and predicting the data. It is therefore well suited to our smaller sample size datasets. Path modeling analysis, bootstrap simulations, and determination of relationships between treatments and variables such as antioxidant enzyme activities, photosynthesis, yield components, and yield were performed in R (version 4.1.3; <https://www.r-project.org>. Accessed on 25 November 2024.) using the plspm and vegan packages. The ggplot2 package (version 3.5.1) was used to visualize the results.

### 3. Results

#### 3.1. Exogenous SA + ABA Mixed Plant Growth Regulator Restores Damage to the Agronomic Trait of Oilseed Rape After Waterlogging

Waterlogging affected the morphological characteristics of rapeseed plants. Plant height (Ph), number of pods (Np), number of pod seeds (Nps), and 1000-grain weight (Tgw) were reduced after the plants were subjected to waterlogging for ten days at the pod stage (Figures 1A–C and 2A–I). However, spraying exogenous salicylic acid (SA), abscisic acid (ABA), and a mixture of SA + ABA after waterlogging improved these morphological traits, reducing the damage induced by waterlogging stress. Compared with the waterlogged treatment (CK2), spraying the SA + ABA mixture after waterlogging caused an increase in plant height. During the 2021–2022 and 2022–2023 growth seasons, plant height increased

significantly by 7.35% ( $p < 0.05$ , Figure 1B,C). However, stem thickness and effective branching number were not significantly affected by SA, ABA, SA + ABA, or waterlogging.

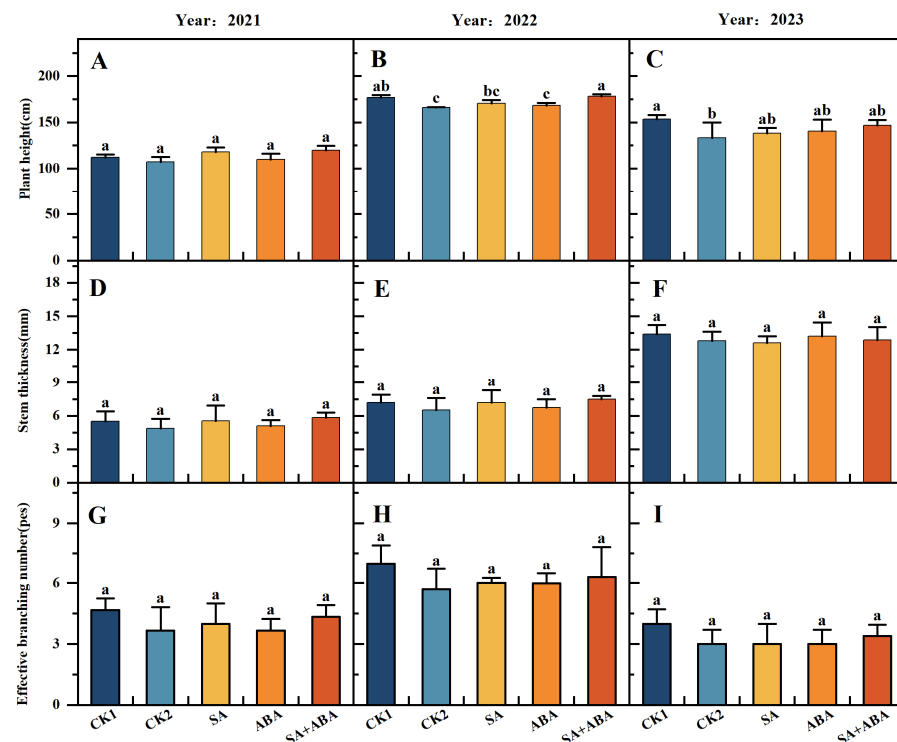


**Figure 1.** Effects of external application of salicylic acid (SA), abscisic acid (ABA), and SA + ABA on potted oilseed rape during the 2021–2023 growth seasons. (A): plant height in 2020–2021 growing season, (B): plant height in 2021–2022 growing season, (C): plant height in 2022–2023 growing season, (D): stem thickness in 2020–2021 growing season, (E): stem thickness in 2021–2022 growing season, (F): stem thickness in 2022–2023 growing season, (G): effective number of branches in 2020–2021 growing season, (H): effective number of branches in 2021–2022 growing season, (I): effective number of branches in 2022–2023 growing season. The mean values are shown with standard errors ( $n = 10$ ). Different letters indicate significant differences according to Tukey's HSD multiple comparison test ( $p < 0.05$ ). CK1 means no waterlogging treatment, CK2 means waterlogging treatment.

Figure 2 shows that waterlogging significantly affected the number of pods, number of grains per pod, and 1000-grain weight. Significant reductions of 22.61%, 17.62%, and 26.10% in the number of pod seeds (Nps), and 43.99%, 32.78%, and 33.08% in the 1000-grain weight (Tgw) were observed after flooding, compared to the control treatment (CK1), during the 2020–2021, 2021–2022, and 2022–2023 growing seasons ( $p < 0.05$ , Figure 2D–I). During the 2021–2022 and 2022–2023 growing seasons, the number of pods (Np) was significantly reduced by 13.19% and 43.23%, respectively ( $p < 0.05$ , Figure 2B,C). Compared to the flooding treatment (CK2), spraying SA + ABA significantly increased the number of pods, number of grains per pod, and 1000-grain weight of rapeseed. Specifically, the number of pods increased by 62.69%, and the 1000-grain weight increased by 70.15% in the 2022–2023 season. The number of pod seeds significantly increased in all three growing seasons, with increases of 20.98%, 17.38%, and 40.10%, respectively. Although spraying SA + ABA after flooding did not eliminate the effects of flooding, it mitigated the impact, to the point where the effects were no longer statistically significant. Additionally, spraying either SA or ABA alone improved Np, Nps, and Tgw, but the differences were not significant.

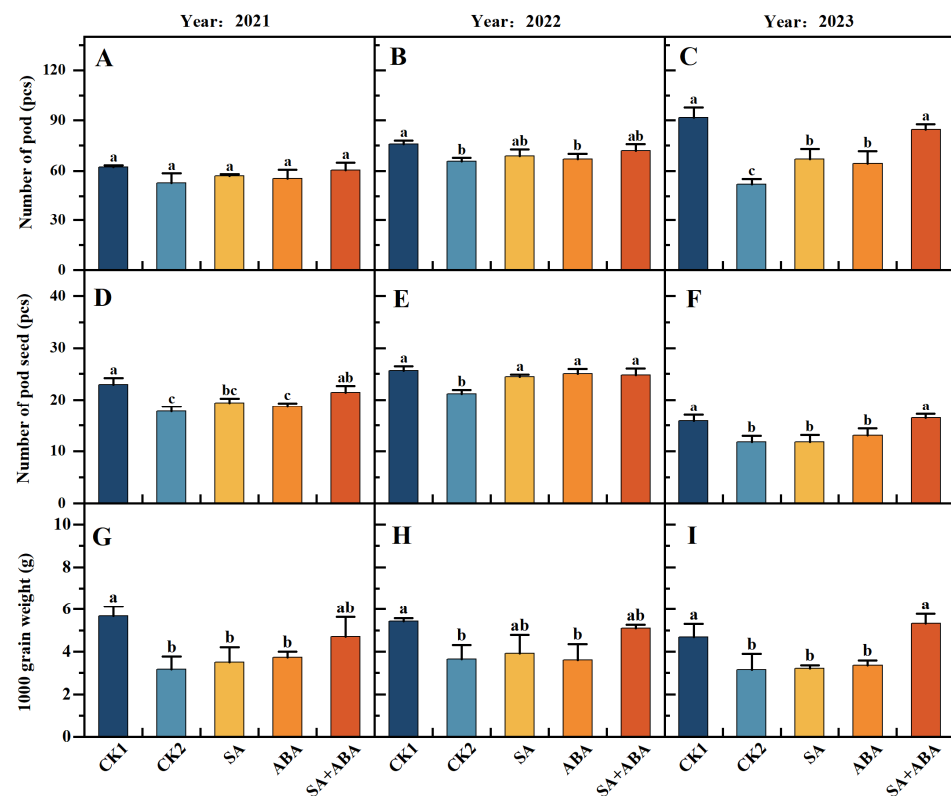


**Figure 2.** Effects of external application of salicylic acid (SA), abscisic acid (ABA), and SA + ABA on potted oilseed rape during the 2021–2023 growth seasons. (A): number of pods in 2020–2021 growing season, (B): number of pods in 2021–2022 growing season, (C): number of pods in 2022–2023 growing season, (D): number of pod seeds in 2020–2021 growing season, (E): number of pod seeds in 2021–2022 growing season, (F): number of pod seeds in 2022–2023 growing season, (G): 1000 grain weight in 2020–2021 growing season, (H): 1000 grain weight in 2021–2022 growing season, (I): 1000 grain weight in 2022–2023 growing season. The mean values are shown with standard errors ( $n = 10$ ). Different letters indicate significant differences according to Tukey's HSD multiple comparison test ( $p < 0.05$ ).

### 3.2. Exogenous SA + ABA Mixed Plant Growth Regulator Restores Damage to the Yield and Oil Content of Oilseed Rape After Waterlogging

Oilseed rape yield and oil content were lower after 10 days of flooding compared to the normal control (CK1). Specifically, compared to CK1, the single-plant yield of oilseed rape was significantly reduced by 28.09% and 22.43% in the 2020–2021 and 2022–2023 growing seasons, respectively, following waterlogging (CK2) ( $p < 0.05$ , Figure 3A,C). Oil content was significantly reduced by 8.48% after waterlogging in the 2022–2023 growing season ( $p < 0.05$ , Figure 3F). The mean values for other years were lower than those of CK1, although the differences were not statistically significant. However, spraying with an exogenous SA + ABA mixture increased both yield and oil content, mitigating the damage caused by flooding stress. Compared to the flooding treatment (CK2), the SA + ABA mixture significantly increased single-plant yield by 32.26% and oil content by 4.34% in 2022–2023 ( $p < 0.05$ , Figure 3C,F). These results demonstrate that waterlogging stress has a significant negative impact on agronomic traits, yield, and oil content of oilseed rape, whereas, the SA + ABA mixture can effectively alleviate the damage caused by waterlogging.

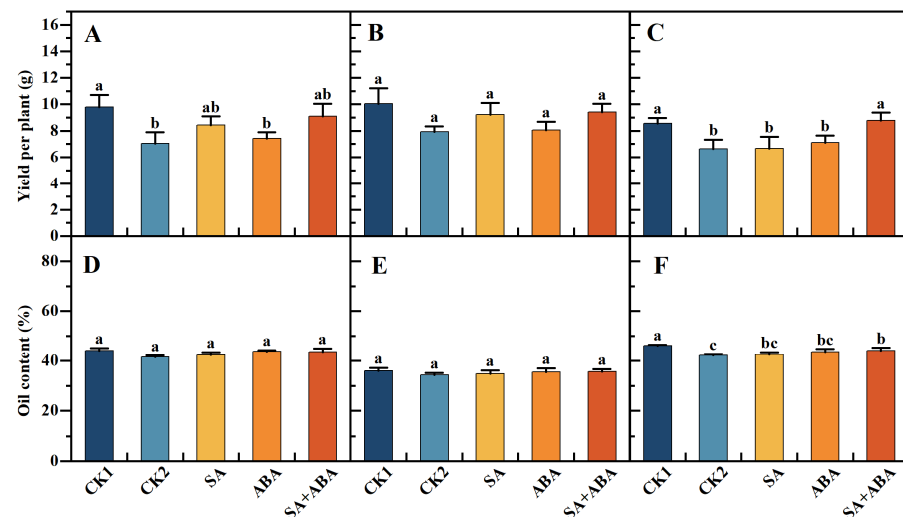


**Figure 3.** Effects of external application of salicylic acid (SA), abscisic acid (ABA), and SA + ABA on potted oilseed rape during the 2021–2023 growth seasons. (A): yield per plant in 2020–2021 growing season, (B): yield per plant in 2021–2022 growing season, (C): yield per plant in 2022–2023 growing season, (D): oil content in 2020–2021 growing season, (E): oil content in 2021–2022 growing season, (F): oil content in 2022–2023 growing season. The mean values are shown with standard errors (n = 10). Different letters indicate significant differences according to Tukey's HSD multiple comparison test ( $p < 0.05$ ). CK1 means no waterlogging treatment.

### 3.3. Exogenous SA + ABA Plant Growth Regulators Recovery phi2 and SPAD Reduction in Oilseed Rape After Waterlogging Stress

Phi2 represents the actual photosynthetic capacity of plants. This study demonstrates that waterlogging significantly affects the photosynthetic capacity of oilseed rape. The net photosynthetic rate of CK2 was significantly reduced by 13.65% compared to CK1, 10 days after waterlogging ( $p < 0.05$ , Figure 4A). In contrast, the net photosynthetic rates of plants treated with ABA and SA + ABA after flooding were significantly increased by 6.52% and 9.25%, respectively ( $p < 0.05$ , Figure 4A).

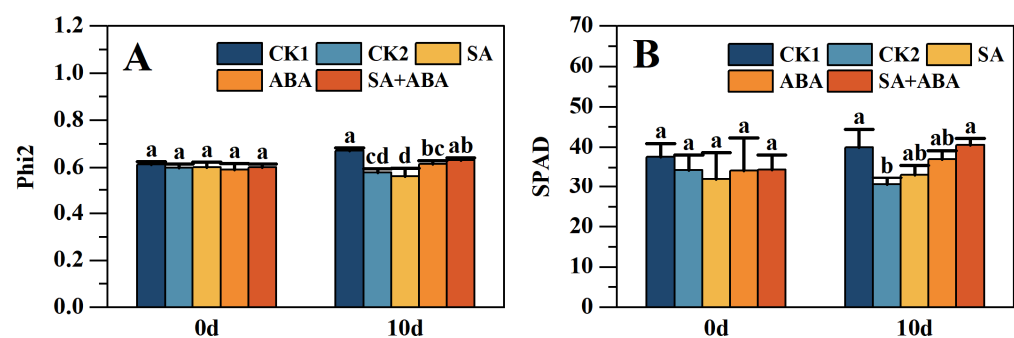


**Figure 4.** Effects of external application of SA, ABA, and SA + ABA on potted oilseed rape. The application effects on phi2 (A) and SPAD (B). The mean values are shown with standard errors (n = 10). Different letters indicate significant differences according to Tukey's HSD multiple comparison test ( $p < 0.05$ ).

SPAD measures leaf greenness and reflects the content of photosynthetic pigments. As waterlogging stress intensifies, the SPAD value decreases. On Day 10, the most significant decrease in SPAD was observed in oilseed rape leaves that received no regulator treatment after waterlogging ( $p < 0.05$ , Figure 4B). In contrast, spraying with ABA, and SA + ABA had a positive effect on SPAD values. Specifically, SPAD increased significantly by 32.82% after spraying SA + ABA, compared to CK2, while spraying with SA and ABA alone resulted in

a difference that was not statistically significant. Additionally, on Day 0 of waterlogging, no significant differences in Phi2 or SPAD values were observed between treatments ( $p < 0.05$ , Figure 4A,B).

### 3.4. Effects of Plant Growth Regulators on POD, SOD, and CAT in Oilseed Rape After Waterlogging Stress

Waterlogging affects the antioxidant capacity of oilseed rape plants. After ten days of waterlogging at the podding stage, the activities of POD, SOD, and CAT decreased significantly (Figure 5A–C). In CK2, the activities of POD ( $p < 0.05$ , Figure 5A), SOD ( $p < 0.05$ , Figure 5B), and CAT ( $p < 0.05$ , Figure 5C) were reduced by 45.54%, 34.48%, and 26.51%, respectively, compared to CK1. However, the application of exogenous SA, ABA, and the SA + ABA mixture solutions significantly increased antioxidant enzyme activities. Specifically, the activities of POD ( $p < 0.05$ , Figure 5A), SOD ( $p < 0.05$ , Figure 5B), and CAT ( $p < 0.05$ , Figure 5C) were significantly increased by 58.44%, 45.44%, and 28.20%, respectively, after spraying with the SA + ABA mixture compared to CK2, though the effects of waterlogging were not entirely alleviated. Notably, there were no significant differences in POD, SOD, and CAT enzyme activities among treatments on Day 0. However, after 10 days of waterlogging, the levels of these enzymes decreased across all treatments compared to Day 0.

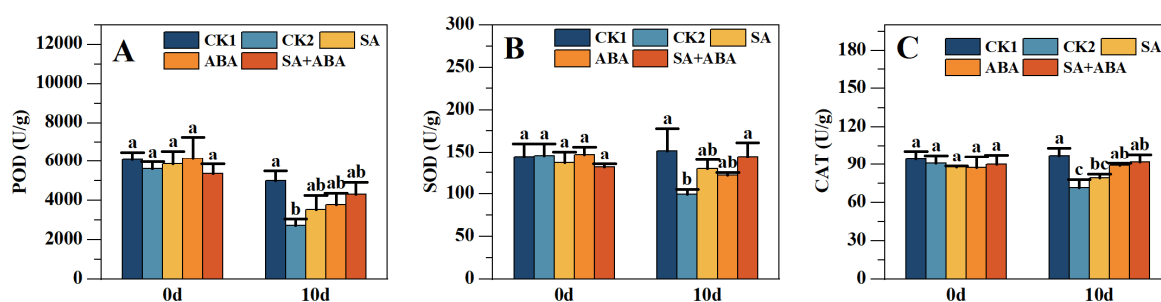


**Figure 5.** Effects of the external application of SA, IBA, and IBA + SA solutions on potted oilseed rape during the 2023 season. The application effects on POD (A), SOD (B), CAT (C). The mean values are shown with standard errors ( $n = 10$ ). Different letters indicate significant differences according to Tukey's HSD multiple comparison test ( $p < 0.05$ ).

### 3.5. Correlation Between Individual and Combined Spraying of Plant Growth Regulators on Recovery of Oilseed Rape After Waterlogging

Pearson's correlation analysis revealed that combined spraying was highly positively correlated with Np, Nps, Tgw, Ypp, as well as with Phi, SPAD, and antioxidant enzyme activities (Figure 6). In contrast, spraying with SA or ABA alone showed a significant negative correlation ( $p < 0.05$ ). Additionally, yield components such as NP and Tgw were highly positively correlated with Ypp in oilseed rape ( $p < 0.001$ ). Furthermore, SPAD was significantly positively correlated with antioxidant enzyme activities, including Nps, Tgw, POD, SOD, and CAT ( $p < 0.01$ ), with POD showing a highly significant correlation with SPAD ( $p < 0.001$ ). From the perspective of agronomic traits, the yield of oilseed rape after waterlogging stress is closely related to number of pods and thousand-grain weight. An increasing number of pods and thousand-grain weight is the main goal for restoring the yield of oilseed rape after waterlogging stress. From the physiological indicators, increasing the values of SPAD and antioxidant enzymes (POD, SOD, CAT) can effectively enhance the photosynthetic and antioxidant capacities of oilseed rape, thereby increasing the yield of oilseed rape.

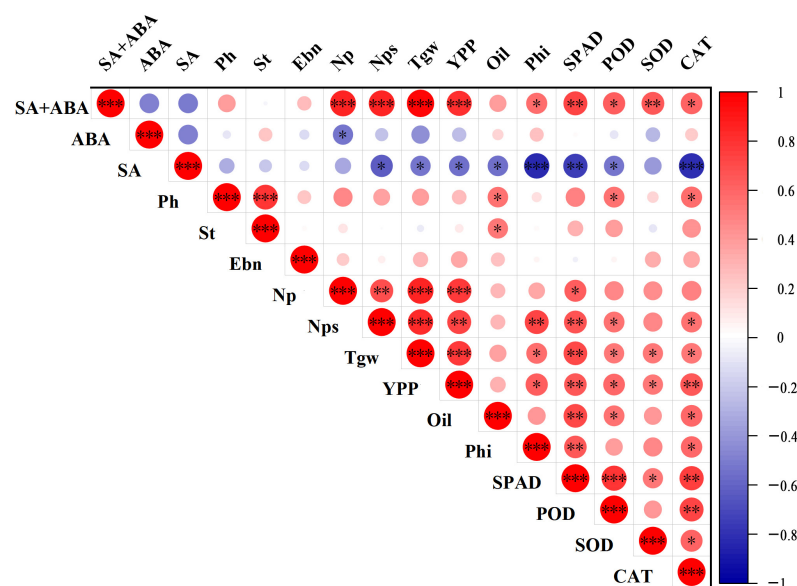


**Figure 6.** Heat map of correlation coefficients between plant growth regulators sprayed alone or in combination with plant growth, photosynthesis, and antioxidant enzymes in oilseed rape after waterlogging. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; blank cells, not significant.

### 3.6. Structural Equations for Yield Recovery in Oilseed Rape Sprayed with Plant Growth Regulators After Waterlogging

The structural equation model suggests that the yield component factors, including the number of pods, number of seeds per pod, and 1000-grain weight, significantly influence oilseed rape yield. Photosynthesis and combined application play key roles in determining these yield components. Both combined and single applications not only directly affect the yield components but also influence them indirectly through antioxidant enzyme activity and photosynthesis (Figure 7).

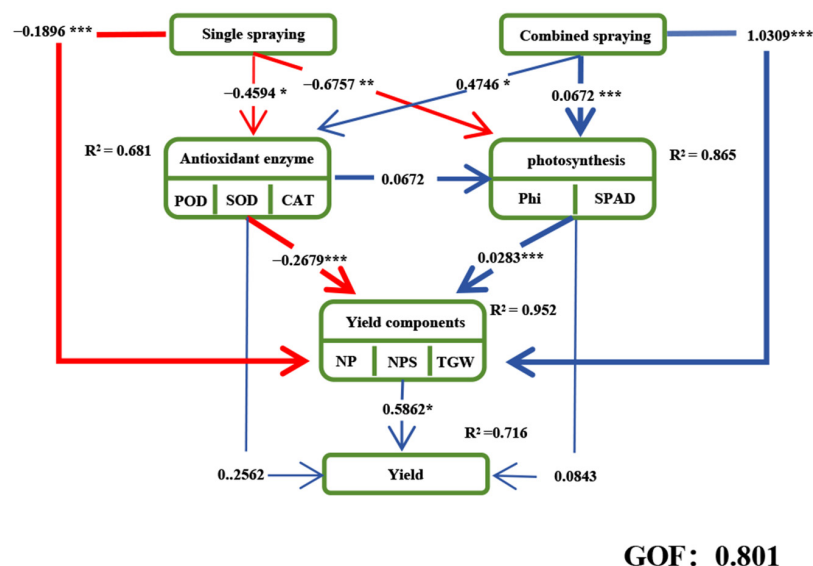


**Figure 7.** Structural equation modeling of the effect of individual and combined spraying on oilseed rape yield. The arrows indicate the hypothesized direction of causality, with blue arrows indicating positive relationships and red arrows indicating negative relationships. The width of the arrow indicates the strength of the relationship. Numbers next to the arrows are standardized path coefficients. Asterisks indicate significance (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ). The proportion of explained variance ( $R^2$ ) appears next to each response variable in the model. The model's goodness-of-fit statistic is  $GOF = 0.801$ .

## 4. Discussion

### 4.1. Effect of Exogenous SA + ABA on Yield per Plant and Oil Content of Oilseed Rape Plants at Podding Stage After Waterlogging

Due to global climate change, extreme weather events, such as prolonged rainfall, are becoming more frequent [30,36]. These events pose a growing challenge to oilseed rape production [37], as the crop is particularly vulnerable to flooding and waterlogging during its growth and development, which negatively impacts both yield and quality [9,10]. Previous studies have demonstrated that waterlogging stress affects oilseed rape at various growth stages [38]. Our study indicates that it significantly reduces plant height (Figure 1A–C), pod number, number of seeds per pod, 1000-grain weight (Figure 2A–I), yield per plant, and oil content (Figure 3A–C) after 10 days of waterlogging. These findings further support the hypothesis that the effects of waterlogging on oilseed rape physiology and yield were susceptible in the flowering and pod-setting stages.

Several studies have demonstrated exogenous plant growth. Regulators can enhance plants' ability to withstand adverse stress [39,40]. For example, Ramadan Shemi found that spraying exogenous salicylic acid (SA) improved wheat yield under drought stress [41], while H. Xiang et al. showed that applying exogenous abscisic acid (ABA) effectively alleviated drought and waterlogging-induced damage during the soybean seedling stage, thereby improving soybean yield [42]. These findings are consistent with the results of our experiments. In our study, spraying either SA or ABA effectively improved the agronomic traits of oilseed rape after waterlogging and mitigated the adverse effects of waterlogging on yield. Specifically, spraying SA or ABA enhanced plant height (Figure 1A–C), number of pods, and number of seeds per pod (Figure 2A–F), thus improving the single-plant yield (Figure 3A–C), although the recovery effect was not statistically significant. However, we observed that the combined spraying of SA and ABA (SA + ABA) provided better recovery than spraying either SA or ABA alone. After waterlogging, plant height (Figure 1A–C), number of pods, number of seeds per pod, and 1000-grain weight (Figure 2A–I) were improved with SA + ABA treatment, which likely explains why the single-plant yield was higher in the combined treatment compared to individual treatments. Nonetheless, spraying SA, ABA, or SA + ABA after flooding did not restore oilseed rape to CK1 levels (Figure 3A–C). Additionally, plant growth regulators have been shown to further enhance plant resistance to abiotic stresses through synergistic interactions [43]. Previous research has indicated that the combined spraying of salicylic acid and indolebutyric acid improved garlic yield under drought stress [44], while Huan Li demonstrated that the combination of 6-benzylaminopurine (6-BA) and ABA improved sweet potato yield under drought stress [26]. Furthermore, Qian Feng et al. [45] reported that combining ABA with CaCl<sub>2</sub> enhanced cold tolerance in cucumber seedlings. These studies collectively support the notion that combined applications of plant growth regulators are more effective than individual treatments in improving crop responses to abiotic stresses and restoring agronomic traits.

In large-scale agricultural management, waterlogging stress can significantly negatively affect both the yield and quality of oilseed rape [46]. Therefore, there is an urgent need for more effective countermeasures to mitigate the impacts of waterlogging stress. Our study demonstrated that spraying a mixture of salicylic acid (SA) and abscisic acid (ABA) can partially alleviate the damage caused by waterlogging. By optimizing the concentration and frequency of spraying, the crop's resistance to waterlogging can be enhanced, leading to the restoration of both yield and quality after waterlogging events. This approach is particularly beneficial for agricultural production in southern regions, where waterlogging disasters are frequent. Thus, the combined spraying of SA and ABA offers not only a novel solution for managing waterlogging stress in oilseed rape but also a viable strategy for managing similar stress in other crops.

However, due to certain limitations, our experiments were only conducted in pots, without field validation. Additionally, the mechanistic pathways through which plant growth regulators may enhance plant recovery after flooding were not investigated, nor did the study address the potential medicinal residues of oilseed rape, which could pose risks to human health. In the future, we plan to expand our research into the field to further evaluate the combined application of SA and ABA and explore its underlying mechanisms. Additionally, we will assess whether pharmaceutical residues remain in oilseed rape to ensure the safety and improve the recovery potential of the crop after flooding.

#### *4.2. Effect of Exogenous SA +ABA on SPAD and Phi2 in Oilseed Rape at Podding Stage After Waterlogging*

Previous studies have shown that SPAD is directly proportional to chlorophyll content, which influences the plant's net photosynthetic rate [47]. Correlation heat maps have also revealed a significant positive correlation between SPAD and Phi2 (Figure 6). Waterlogging during the pod development stage of oilseed rape in this study resulted in reduced SPAD values and photosynthetic activity, which negatively affected pod number and grain weight (Figure 2). This may be because under waterlogged conditions most of the photosynthetic products contributing to grain weight in oilseed rape are derived from carbohydrates stored in the stem [48]. Similar effects have been observed in other crops, where waterlogging-induced yield reduction is attributed to decreased carbon assimilation and impaired reactivation of water-soluble carbohydrates [49]. Previous studies have shown that decreased plant yield following waterlogging is directly related to chlorophyll content (SPAD), gas exchange rate, PSII damage, and disruption of photosynthate translocation [50,51].

Exogenous plant growth regulators have been shown to improve photosynthesis in plants under stress. Phytohormones are involved in regulating chloroplast development during the photomorphogenesis of crops under stress conditions [52,53]. Additionally, the role of exogenous ABA in enhancing water stress tolerance has been reported in many species, including barley, wheat, beans, sugar beet, tobacco, and maize [54]. In these species, the application of exogenous ABA has been found to reduce the degradation of photosynthetic pigments [55]. Meanwhile, Hayat et al. [56] reported the positive effects of exogenous SA treatment on photosynthesis in tomato plants by maintaining photosynthetic parameters and chlorophyll levels. Our experimental results align with these findings, as the post-flooding application of exogenous SA or ABA alone restored SPAD and Phi2 in oilseed rape. However, the restoration effect was more pronounced when SA and ABA were applied together (Figure 4). This may be due to hormonal interactions that enhance the restoration of chloroplast content in the plant. GJ Ahammed et al. [57] found that ethylene and brassinosteroids (BRs) regulate photosynthesis through interactions with ABA. Similarly, Lau and Deng et al. [58] observed that interactions between ethylene, growth hormones, and gibberellins play a role in regulating photomorphological processes. While the interaction between SA and ABA in regulating photosynthesis has not yet been fully explored, the mechanisms by which their combined application improves photosynthesis in plants warrant further investigation.

#### *4.3. Effect of Exogenous SA +ABA on POD, SOD, and CAT Antioxidant Enzymes in Oilseed Rape at Podding Stage After Waterlogging*

Reactive oxygen species (ROS) play a crucial role in sensing abiotic stress and activating stress response networks, which contribute to the establishment of defense mechanisms and enhance plant resilience [59]. Plants have evolved complex mechanisms to detoxify ROS, including both non-enzymatic antioxidants and enzymatic scavenging systems [60]. Waterlogging increases ROS levels in plants while simultaneously reducing the activity

of antioxidant enzymes [61]. Our findings also revealed that the levels of SOD, POD, and CAT were significantly lower in the flooded treatment (CK2) compared to the non-flooded treatment (CK1).

Reactive oxygen species (ROS) exist in dynamic equilibrium within plants and play a crucial role in photosynthesis [62,63]. However, waterlogging disrupts this balance by decreasing antioxidant enzyme activity, causing ROS levels to exceed the plant's antioxidant capacity. This imbalance leads to excessive lipid peroxidation, which damages chloroplast membranes [64], and redox signaling may further disrupt the electron transport chain in the chloroplasts [65]. The associated heat map shows significant positive correlations between the activities of POD, SOD, and CAT enzymes, as well as SPAD values. Notably, POD and SPAD levels were highly correlated (Figure 6), which may explain the significant reduction in SPAD and Phi2 values in *Brassica napus* after waterlogging. Previous studies have demonstrated that phytohormones can restore antioxidant enzyme activities under stress conditions [66–68], with hormone co-spraying often yielding more pronounced effects [45,69]. Our results showed that the SA + ABA mixture significantly increased antioxidant enzyme levels in oilseed rape plants (Figure 5). The results demonstrated a close relationship between increased chlorophyll content and enhanced antioxidant capacity in oilseed rape plants (Figure 6). Elevating chlorophyll content not only improves photosynthetic efficiency but also strengthens plant resistance by boosting antioxidant enzyme activity. This provides a theoretical basis for utilizing plant growth regulators to enhance crop resilience in adverse conditions, such as waterlogging. Structural equation modeling also indicated that the combined spraying of SA and ABA not only directly influenced plant photosynthesis but also indirectly improved it through enhanced enzyme activities (Figure 7). These findings suggest that the SA + ABA mixture promotes the production of more antioxidant enzymes in oilseed rape, thereby reducing ROS content and creating an environment conducive to efficient metabolic processes, which in turn supports plant photosynthesis. However, the specific mechanisms underlying the interaction of SA and ABA in restoring antioxidant enzyme activities and enhancing photosynthesis warrant further investigation.

## 5. Conclusions

In conclusion, this study demonstrated that the application of SA + ABA effectively mitigates the damage caused by waterlogging stress in oilseed rape plants, leading to the restoration of both yield and quality. The combined spraying of SA + ABA proved more effective than spraying SA or ABA alone. The exogenous application of the SA + ABA mixture alleviated the negative effects of waterlogging on winter oilseed rape at the podding stage by enhancing antioxidant enzyme activity, increasing chlorophyll content, and improving photosynthetic performance. Large-scale field trials under different climatic conditions, regions, and soil types are needed in the future to verify the effectiveness of SA + ABA application in practical agricultural production, and also to study the effects on oilseed rape yield and quality in combination with other flooding stress mitigation techniques such as other exogenous plant growth regulators or measures such as improving the soil drainage system and increasing soil aeration. These findings may have important implications for managing the recovery of other plants affected by waterlogging.

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## Abbreviations

The following abbreviations are used in this manuscript:

|       |                            |
|-------|----------------------------|
| SA    | Salicylic acid             |
| ABA   | Absciscic acid             |
| POD   | Peroxidase                 |
| SOD   | Superoxide dismutase       |
| CAT   | Catalase                   |
| SPAD  | Chlorophyll dynamics       |
| Ph    | Plant height               |
| Sd    | Stem thickness             |
| Ebn   | Effective branching number |
| Nps   | Number of pod seeds        |
| Tgw   | 1000-grain weight          |
| Phi2  | Net photosynthetic rate    |
| ANOVA | Analysis of variance       |
| ROS   | Reactive oxygen species    |

## Appendix A

**Table A1.** Pre-experimental data on determination of different phytohormone concentrations.

| Treat    | Concentration of Drug | Number of Pod (pcs) | Number of Pod Seed (pcs) | Oil Content (%)   | 1000 Grain Weight (g) | Yield per Plant (g) | RIR (%) | Treatment Options in 2021–2023 |
|----------|-----------------------|---------------------|--------------------------|-------------------|-----------------------|---------------------|---------|--------------------------------|
| CK1      | 0                     | 60.07 ± 1.33 bc     | 22.58 ± 1.15 a           | 42.32 ± 0.98 bcd  | 5.97 ± 0.61 a         | 9.36 ± 0.84 a       | 79.31   |                                |
| CK2      | 0                     | 50.67 ± 4.2 6f      | 17.40 ± 0.74 b           | 41.63 ± 1.02 d    | 3.41 ± 0.28 c         | 5.22 ± 1.09 b       | 0.00    |                                |
| SA       | 1 mmol/L              | 57 ± 0.63 cd        | 17.54 ± 0.96 b           | 43.76 ± 0.58 abcd | 3.5 ± 0.46 bc         | 9.12 ± 0.16 a       | 74.71   |                                |
|          | 2 mmol/L              | 63.60 ± 1.08 b      | 17.73 ± 0.91 b           | 44.46 ± 0.42 abc  | 4.178 ± 0.59 abc      | 9.77 ± 0.96 a       | 87.16   | ✓                              |
|          | 4 mmol/L              | 56.80 ± 0.29 cde    | 18.55 ± 0.64 b           | 44.92 ± 1.03 ab   | 3.37 ± 0.37 c         | 8.62 ± 1.02 a       | 65.13   |                                |
| ABA      | 0.08 g/L              | 35.40 ± 1.18 g      | 18.36 ± 0.90 b           | 42.32 ± 1.13 bcd  | 3.74 ± 1.13 bc        | 7.03 ± 0.88 ab      | 34.67   |                                |
|          | 0.16 g/L              | 38.60 ± 0.39 g      | 18.64 ± 0.63 b           | 42.46 ± 0.36 bcd  | 4.61 ± 0.76 abc       | 9.12 ± 1.13 a       | 74.71   | ✓                              |
|          | 0.32 g/L              | 52.20 ± 1.44 ef     | 19.18 ± 1.35 b           | 43.77 ± 0.63 abcd | 3.43 ± 0.19 c         | 7.04 ± 0.85 ab      | 34.87   |                                |
| SA + ABA | 0.08 g/L + 2 mmol/L   | 61.80 ± 0.26 b      | 13.27 ± 1.15 c           | 44.79 ± 0.88 abc  | 3.44 ± 0.42 bc        | 7.56 ± 2.41 ab      | 44.83   |                                |
|          | 0.16 g/L + 2 mmol/L   | 68.80 ± 1.29 a      | 16.45 ± 0.79 b           | 45.29 ± 1.29 a    | 5.24 ± 0.77 ab        | 8.63 ± 1.06 a       | 65.33   | ✓                              |
|          | 0.32 g/L + 2 mmol/L   | 54.80 ± 0.96 def    | 12.91 ± 0.69 c           | 42.15 ± 0.69 cd   | 4.31 ± 0.62 abc       | 6.91 ± 0.98 ab      | 32.38   |                                |

Note: CK2 for waterlogged plants; RIR (%) =  $(W - CK2)/CK2 \times 100$ , Where RIR is the relative wetness damage index. Different letters in the same column within the same treatment indicate significant differences ( $p < 0.05$ ).

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