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Regulatory Mechanisms of Exogenous ABA and NDGA on Photosynthetic and Antioxidant Physiology in Waterlogging-Stressed *Brassica napus* L.

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Abstract

The seedling stage is a critical period for the morphological development of rapeseed, and waterlogging stress seriously affects yield and rapeseed quality. Reasonable use of plant growth regulators can increase crop yield, improve quality, and enhance crop stress tolerance. ABA is an important signaling molecular for stress response, and play key role in enhancing plant stress tolerance. Two *Brassica napus* varieties with different waterlogging tolerance were used materials to investigate the effects and physiological mechanisms of ABA and its inhibitor NDGA in regulating waterlogging tolerance. The results indicated that waterlogging significantly inhibited the growth of rapeseed, leading to lower plant height, root length, biomass, leaves yellowing and shedding, and a higher MDA and reactive oxygen species (H_2O_2 , O_2^-) content. The results of phenotypic observation and waterlogging tolerance coefficient indicated that ABA treatment before waterlogging stress improved the waterlogging tolerance of rapeseed, but NDGA treatment exacerbated the waterlogging damage and increased plant mortality rate. NDGA treatment resulted in more stomatal closure in waterlogging sensitive ZS6 compared to waterlogging tolerant rapeseed HYZ50 during waterlogging stress. However, there is no significant difference in the effect of ABA treatment on stomatal behavior of rapeseed with different waterlogging tolerance. For the two lines treated with ABA or NDGA before waterlogging, there were significant differences in the degree of membrane lipid peroxidation, photosynthetic pigment content, antioxidant activity, osmotic regulation substance content, and ROS metabolite content. HYZ50 showed better physiological response to waterlogging than that of ZS6, with stronger antioxidant capacity (POD, CAT activity) and osmotic regulation (proline, soluble sugar accumulation). The correlation analysis between the waterlogging tolerance index (WTI) and growth and physiological indicators revealed WTI was significant negative correlation with MDA content, POD activity, H_2O_2 and O_2^- content, but positive correlation with CAT activity, underground fresh weight, root vitality, plant height, root length, number of green leaves, aboveground fresh weight, aboveground dry weight, and underground dry weight and WTI. Principal component analysis and waterlogging tolerance index analysis found that ABA treatment before waterlogging stress improved the waterlogging tolerance of rapeseed, while NDGA treatment exacerbated the waterlogging damage. This study systematically investigated the role of ABA treatment before waterlogging in alleviating waterlogging damage, laying the foundation for green and efficient cultivation of rapeseed.

Keywords ABA · NDGA · *Brassica napus* · Waterlogging tolerance · Membrane lipid peroxidation · ROS metabolism · Waterlogging tolerance index

Introduction

Brassica napus L. is a pivotal oilseed crop in China with multiple agronomic functions, serving as a source of edible oil, vegetable, ornamental flower, nectar, green manure, and livestock forage (Zhai et al. 2022; Zhou et al.

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2026). Despite the continuous expansion of planting area and improvement in unit yield of rapeseed in China, a substantial domestic supply shortage remains. Statistical data indicate that China's rapeseed self-sufficiency rate is approximately 70%, with an annual import volume of 3.54 million tons (Huang et al. 2023). Accordingly, high-quality development of the rapeseed industry, based on high and stable yield and oriented toward green and efficient production, is a critical approach to safeguarding national grain and edible oil security, increasing farmers' income, and facilitating rural revitalization in China.

Waterlogging stress represents one of the major abiotic constraints restricting agricultural production. From 1949 to 2020, China recorded an annual average flood-affected area of 946,068 hectares, equivalent to approximately 13.5% of the national total cultivated land (Li et al. 2024). Among all provinces, Anhui, Jiangxi and Hubei suffered the most severe flood hazards. Winter rapeseed (*B. napus* L.) dominates rapeseed production in China, with a total planting area of roughly 6.098 million hectares distributed across the Yangtze River Basin and Huanghuai River Basin; over 80% of national rapeseed acreage is concentrated in the Yangtze River Basin (Zhou et al. 2026; Xiang et al. 2026). Abundant water resources, subtropical monsoon climate, and prevailing paddy-upland rotation patterns (rice–rapeseed, rice–rice–rapeseed, and rice–ratoon rice–rapeseed) jointly render the Yangtze River Basin highly susceptible to frequent waterlogging events (Dennis et al. 2000; Wang et al. 2021). Waterlogging stress suppresses root development and even triggers root rot, accompanied by stunted aboveground growth, premature leaf senescence and complete plant death, ultimately inducing severe yield penalties. Additionally, waterlogging elevates lodging risk, exacerbates pest and disease outbreaks, reduces seed oil concentration, and impedes mechanical harvesting operations (Wu et al. 2024; Hong et al. 2024).

Traditional strategies to mitigate the adverse effects of crop waterlogging primarily rely on the adoption of high-yielding and waterlogging-tolerant cultivars and integrated green cultivation technologies. However, the breeding of tolerant cultivars demands substantial time and manpower inputs, failing to deliver desirable improvements in the short term (Manik et al. 2019). Conventional cultivation measures, including optimized tillage, fertilization and sowing management, robust seedling cultivation, and pest and disease prevention, often exhibit limited efficacy against waterlogging stress. This insufficient performance is mainly attributed to the unpredictable occurrence of waterlogging events and the potential risk of soil ecological nutrient imbalance induced by these agronomic practices (Shao et al. 2025). In this context, plant growth regulators have emerged as a promising alternative approach to alleviate waterlogging-induced crop damage, garnering increasing research attention.

Plant growth regulators (PGRs), also referred to as exogenous phytohormones, are synthetic bioactive substances with functions analogous to endogenous plant hormones. They can directionally regulate crop growth and development and have been widely and effectively applied for plant stress resistance (da Silva Junior et al. 2018; Sasaki et al. 2013). Absciscic acid (ABA) is a multifunctional phytohormone that serves as a vital signaling molecule in plant stress responses and a core regulator of plant water stress adaptation (Shao et al. 2025). 9-cis-epoxycarotenoid dioxygenase (NCED) is the rate-limiting enzyme for ABA biosynthesis, and its activity is modulated by nordihydroguaiaretic acid (NDGA) (Klingler et al. 2010; Peng et al. 2017). Under stress conditions, *NCED* genes induce the accumulation of endogenous ABA, thereby improving plant stress tolerance (Klingler et al. 2010; Peng et al. 2017; Qin and Zeevaart. 1999). As a specific inhibitor of ABA biosynthesis, NDGA primarily blocks stress-induced ABA accumulation by suppressing the activity of key enzymes involved in ABA synthesis, including NCED (Sun et al. 2012). NDGA mediates plant stress responses by regulating endogenous ABA levels through inhibiting ABA biosynthesis (Sun et al. 2012). In plant species such as soybean, *Arabidopsis thaliana*, cotton, and wheat, waterlogging stress significantly increases endogenous ABA content (Kim et al. 2015; Liu et al. 2012; Zhang et al. 2016; Nan et al. 2002). The accumulated ABA induces stomatal closure via signaling molecules including Ca^{2+} , reactive oxygen species (ROS), and nitric oxide (NO), which reduces water transpiration loss,

improves water use efficiency, and ultimately enhances plant waterlogging tolerance (Kim et al. 2015; Liu et al. 2012; Zhang et al. 2016; Nan et al. 2002). Nevertheless, accumulating evidence has demonstrated that ABA can also act as a negative regulator of plant waterlogging tolerance (Pan et al. 2021; Eerdekens et al. 2025). Under waterlogging stress, ABA-induced stomatal closure constrains photosynthetic efficiency, thereby compromising plant resistance to waterlogging (Ahmed et al. 2012).

Studies on the regulatory function of ABA in mediating rapeseed responses to waterlogging stress are limited, and the underlying regulatory mechanisms remain elusive. In the present study, waterlogging incubation was performed to simulate waterlogging stress. Two *B. napus* cultivars with contrasting waterlogging tolerance at the seedling stage were treated with ABA or NDGA (an inhibitor of ABA). We monitored their growth performance under waterlogging stress and conducted systematic physiological and biochemical assays. This study aims to elucidate the regulatory effects and functional mechanisms of ABA and NDGA on waterlogging tolerance in *B. napus* seedlings, and lay a theoretical basis for the waterlogging-resistant cultivation of rapeseed.

Materials and methods

Experimental Design

The experimental materials were two *B. napus* L. cultivars: Zhongshuang No.6 (ZS6, waterlogging-sensitive genotype) and Huayouza 50 (HYZ50, waterlogging-tolerant genotype), which were provided by the Rapeseed Research Team of Yangtze University.

Seeds with plump grains, uniform size, and free of disease and pest injuries were selected and spot-sown into plastic pots (top diameter $\times$ bottom diameter $\times$ height = 7 cm $\times$ 7 cm $\times$ 7.5 cm). The seeds were first incubated in darkness for 3 d at 25 °C with 80% relative humidity, and then cultivated under a 16 h light / 8 h dark photoperiod at a light intensity of 52 $\mu\text{mol m}^{-2} \text{s}^{-1}$ until seedlings developed to the 5–6 leaf stage.

Four treatments were designed in the experiment: CK (normal water supply), T1 (waterlogging treatment + foliar spraying with distilled water), T2 (waterlogging treatment + foliar spraying with 20 mg·L⁻¹ ABA), and T3 (waterlogging treatment + foliar spraying with 100 mg·L⁻¹ NDGA inhibitor of ABA). Foliar sprays of ABA or NDGA were carried out at the 5–6 leaf stage. Both adaxial and abaxial leaf surfaces were sprayed uniformly until fully moistened without water dripping, and the spraying was performed once per day for 3 consecutive days. On the 3rd day after the final spray of ABA or NDGA, all pots were placed into blue plastic trays (60 cm $\times$ 42 cm $\times$ 12 cm). The water level was adjusted to match the height of the soil surface in each pot to establish waterlogging stress. Normal water management was resumed after 9 days of continuous waterlogging.

Light and temperature conditions were maintained consistent throughout all the above treatments, and each treatment was set up with three biological replicates.

Indicator determination and method

Agronomic traits were surveyed before ABA or NDGA application, at 0 d and 9 d after waterlogging stress. The 2nd and 3rd fully mature leaves of seedlings under each treatment were sampled for the determination of physiological indices. Six biological replicates were set for agronomic trait investigation in each treatment; three biological replicates (with three technical replicates per biological replicate) were used for stomatal observation and physiological index measurement.

Agronomic Trait Investigation Six plants were randomly selected from each treatment to determine agronomic traits, including plant height, root length, number of green leaves, fresh weight and dry weight. The counting criteria for green leaves were defined as follows: a fully unfolded central leaf of seedling was counted as one leaf, and a leaf was classified as green leaf if its green area exceeded half of the total leaf area. Plant water content was

calculated using the formula below:

$$\text{Water content} = (\text{Fresh weight at sampling} - \text{Dry weight}) / \text{Fresh weight at sampling} \times 100\%$$

Determination of Root Activity Root activity was measured using the 2,3,5-triphenyl tetrazolium chloride (TTC) reduction method (Liu et al. 2015). Root samples were collected before ABA or NDGA spraying, at 0 d and 9 d of waterlogging stress. Residual seedling substrate adhering to the roots was thoroughly rinsed, and root activity was determined immediately afterward. Three biological replicates were included for each treatment.

Observation of Stomatal Characteristics Temporary leaf epidermal slides were prepared following the method of Maciel et al (Maciel et al. 2025). Specimens were examined under an upright BX63 microscope coupled with a DP73 digital camera. Stomatal numbers were counted to calculate stomatal density using CellSens Standard software. Stomatal length and guard cell width were measured, and micrographs were captured simultaneously.

Measurement of photosynthetic pigment content Photosynthetic pigment contents were determined using the ethanol-acetone method (Dunkerley et al. 2008).

Determination of antioxidant enzyme activity and malondialdehyde content Peroxidase (POD, EC 1.11.1.7) using the guaiacol method, catalase (CAT, EC 1.11.1.6) using ultraviolet absorption, and malondialdehyde (MDA) content using the thiobarbituric acid method (Ma et al 2025).

Determination of osmotic adjustment substance content Soluble sugar content using the anthrone colorimetric method, soluble protein content using the Coomassie blue staining method, and proline content using the acidic indole-3-carboxaldehyde method.

Measurement of O_2^- and H_2O_2 contents Superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2) contents were determined referring to the methods reported by Thordal Christensen et al. (Thordal Christensen et al 1997; Al Mahmud et al 2020).

Waterlogging Tolerance Evaluation

The waterlogging tolerance index (WTI) was calculated using a slightly modified method reported by Xu et al (Xu et al. 2016). $WTI = \text{Measured trait values of the waterlogging treatment} / \text{Measured trait values of the control treatment}$.

Data Processing and Statistical Analysis

Raw data were entered, calculated, and organized using Microsoft Excel. Statistical analyses were performed with the DPS 7.05 data processing system, and graphs were generated using GraphPad Prism 9 software. A one-way analysis of variance (ANOVA) with replication was conducted for each sampling time point, and multiple comparisons between treatments were performed using Fisher's least significant difference (LSD) test.

Results

Effects of ABA and NDGA treatments on seedling growth of *B. napus* under waterlogging stress

Figure 1A illustrates that prior to ABA or NDGA application and at the onset of waterlogging (0 d), seedlings of genotypes ZS6 and HYZ50 displayed comparable growth vigor across all treatment groups. Throughout waterlogging exposure, seedlings subjected to waterlogging treatments (T1, T2, T3) progressively developed leaf wilting, chlorosis and abscission, alongside retarded new leaf outgrowth and diminished leaf size. At 9 days post waterlogging for genotype ZS6: T1 exhibited severe leaf chlorosis and extensive leaf abscission; T2 showed alleviated chlorosis and leaf shedding but suffered significantly suppressed growth relative to the control (CK); T3 sustained more severe leaf injury than T1, accompanied by obvious plant lodging. After a 7-day recovery phase, only a fraction of T1 seedlings retained young apical leaves; nearly all T2 seedlings survived yet maintained markedly inferior growth compared with CK; all T3 seedlings ultimately wilted and perished entirely. For HYZ50

harvested at 9 days post waterlogging: T1 displayed global growth retardation, coupled with chlorosis, leaf abscission and shortened plant height; T2 presented mild yellowing and leaf loss; T3 developed aggravated leaf damage plus slight lodging relative to T1. Following seven days of recovery, all HYZ50 seedlings remained viable. T1 and T3 possessed significantly lower plant height than CK, while T2 achieved relatively robust recovery, albeit with marginally weaker growth performance than the control.

Prior to foliar pretreatment with ABA or NDGA, no statistically significant differences in total biomass were observed across all treatments for genotypes ZS6 and HYZ50. For ZS6 at 0 days post waterlogging (DPW), both root fresh weight (FW) and dry weight (DW) exhibited descending tendencies in T2 and T3 groups. At 9 DPW, shoot and root FW and DW were markedly suppressed in T1. Relative to T1, T2 displayed 73.72% higher shoot FW, 18.55% higher shoot DW, 196.67% higher root FW and 114.04% higher root DW; all biomass metrics of T2 were comparable to those of the untreated control (CK). In addition, T3 possessed a significantly greater root FW (an 86.67% increase) than T1. Pre-waterlogging application of ABA or NDGA exerted negligible effects on the early growth of HYZ50, and FW and DW did not differ statistically among all groups at 0 DPW. At 9 DPW, shoot FW and DW of T1 were substantially reduced. T2 showed 17.06% higher shoot FW and 50.78% higher shoot DW than T1, with both parameters significantly exceeding those of T1 yet remaining lower than CK. T3 suffered further drastic declines in fresh biomass; its dry weight was significantly inferior to CK and showed no statistical discrepancy from T1 (Figure 1B and C).

Collectively, pre-stress foliar spraying of ABA sustained seedling growth and enhanced waterlogging tolerance of *B. napus* seedlings under hypoxic waterlogging conditions. In contrast, NDGA pretreatment failed to alleviate waterlogging-derived injury and instead exacerbated stress-associated damage to rapeseed seedlings.

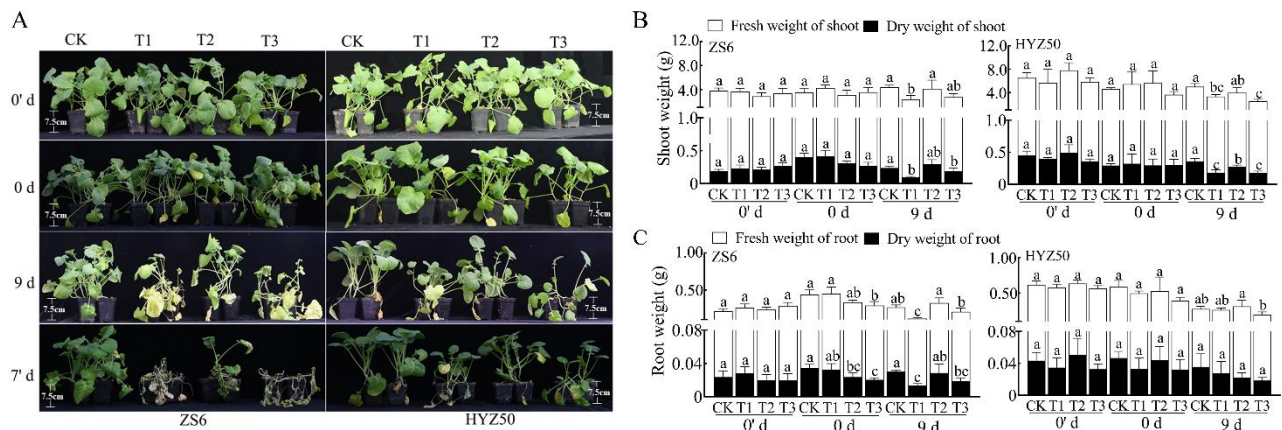


Fig. 1 Effect of ABA or NDGA on the growth of rapeseed under waterlogging stress

Note: CK: normal water supply; T1: waterlogging stress + spraying distilled water; T2: waterlogging stress + spraying ABA; T3: waterlogging stress + spraying NDGA. 0' d: Before ABA or NDGA treatment; 0 d: waterlogging 0 d; 9 d: waterlogging 9 d; 7' d: Resume growth for 7 d. At the same time point, different lowercase letters indicate significant differences between treatments at the 0.05 probability level.

Agronomic traits, plant water content and root activity

As shown in Table 1, prior to foliar pretreatment with ABA or NDGA, no statistically significant differences in plant height, root length, green leaf number, plant water content and root activity were detected for genotypes ZS6 and HYZ50 across all treatment groups. However, upon exposure to waterlogging stress, prominent variations in these agronomic indicators emerged among treatments for the two rapeseed genotypes with contrasting waterlogging tolerance.

At 0 DPW, root length and root activity of ZS6 showed descending tendencies in T2 and T3 treatments. The root length of T2 was significantly lower than that of CK and T1, with respective decreases of 15.85% and 18.97%; meanwhile, root activity in T2 and T3 was markedly suppressed relative to CK and T1. Additionally, T2 and T3 had no obvious impacts on plant height and green leaf number of ZS6 at 0 DPW, yet T2 induced a significant reduction in plant water content, which declined by 2.04% and 2.79% compared with CK and T1, respectively. At 9 DPW, T1

treatment triggered dramatic reductions in plant height, root length, green leaf number and root activity of ZS6, whereas no statistical discrepancy in plant water content was observed between T1 and CK. Relative to T1, ZS6 seedlings subjected to T2 exhibited elevated plant height (+12.58%), root length (+62.02%), plant water content (+2.19%) and root activity (+60.28%). All these indicators were comparable to CK values except root activity. Under T3 treatment at 9 DPW, all measured agronomic parameters of ZS6 were significantly inferior to CK apart from plant water content. Compared with T1, only root length and root activity displayed statistically significant differences: root length increased by 35.35%, while root activity dropped by 23.41%.

At 0 DPW, no statistically significant differences in plant height, green leaf number and root activity were observed among all treatments for genotype HYZ50. However, root length and plant water content of T3 were markedly lower than those of the other groups. Compared with CK and T1, root length of T3 decreased by 13.48% and 14.25%, and plant water content dropped by 2.19% and 2.90%, respectively. At 9 DPW, plant height, root length, green leaf number and root activity of HYZ0 seedlings were all significantly suppressed relative to CK. Root activity under T2 was elevated by 50.89% compared with T1, though it failed to recover to the level of CK. The remaining agronomic indices displayed increasing trends in T2 versus T1, yet no statistically significant differences were detected. In contrast, T3 treatment caused a dramatic 57.74% reduction in root activity relative to T1; slight declines were found in plant height, root length and plant water content of T3, but these parameters showed no statistical discrepancy from T1.

Table 1 Effect of ABA or NDGA on agronomic traits of rapeseed under waterlogging stress

Cultivar	Treatment	Number	Plant height (cm)	Root length (cm)	Number of green leaves	Plant moisture content (%)	Root activity (μg $\text{g}^{-1} \text{h}^{-1}$)
ZS6	0' d	CK	19.83 $\pm$ 1.30 a	12.60 $\pm$ 0.71 a	5.92 $\pm$ 0.64 a	94.67 $\pm$ 0.29 a	366.90 $\pm$ 17.41 a
		T1	20.50 $\pm$ 1.61 a	13.50 $\pm$ 2.05 a	5.67 $\pm$ 0.85 a	94.10 $\pm$ 0.84 a	370.70 $\pm$ 10.22 a
		T2	19.97 $\pm$ 0.90 a	13.00 $\pm$ 0.70 a	5.75 $\pm$ 0.60 a	93.12 $\pm$ 1.40 a	397.67 $\pm$ 58.71 a
		T3	20.93 $\pm$ 1.71 a	12.70 $\pm$ 1.02 a	5.92 $\pm$ 0.49 a	93.36 $\pm$ 2.10 a	409.60 $\pm$ 29.62 a
	0 d	CK	20.83 $\pm$ 1.42 a	11.17 $\pm$ 1.10 a	6.33 $\pm$ 0.47 a	92.28 $\pm$ 1.79 ab	439.67 $\pm$ 25.04 a
		T1	20.88 $\pm$ 2.06 a	11.60 $\pm$ 0.54 a	6.33 $\pm$ 0.47 a	92.99 $\pm$ 0.51 a	431.10 $\pm$ 43.81 a
		T2	21.43 $\pm$ 0.74 a	9.40 $\pm$ 0.63 b	6.00 $\pm$ 0.58 a	90.40 $\pm$ 0.66 b	258.17 $\pm$ 17.29 c
		T3	20.15 $\pm$ 1.34 a	10.93 $\pm$ 0.58 ab	6.17 $\pm$ 0.37 a	93.55 $\pm$ 1.20 a	345.43 $\pm$ 27.12 b
	9 d	CK	19.64 $\pm$ 1.20 a	11.42 $\pm$ 1.22 a	5.67 $\pm$ 1.25 a	93.05 $\pm$ 0.39 ab	489.23 $\pm$ 9.36 a
		T1	16.46 $\pm$ 1.01 b	6.45 $\pm$ 2.62 c	2.50 $\pm$ 0.50 bc	92.39 $\pm$ 0.62 b	232.57 $\pm$ 35.40 c
		T2	18.53 $\pm$ 1.52 a	10.45 $\pm$ 0.74 ab	3.33 $\pm$ 0.47 b	94.41 $\pm$ 1.23 a	372.77 $\pm$ 19.66 b
		T3	17.00 $\pm$ 1.22 b	8.73 $\pm$ 1.14 b	1.83 $\pm$ 0.69 c	93.43 $\pm$ 0.61 ab	178.13 $\pm$ 7.02 d
HYZ50	0' d	CK	21.07 $\pm$ 1.59 a	15.20 $\pm$ 1.57 a	5.83 $\pm$ 0.69 a	92.50 $\pm$ 0.80 a	472.10 $\pm$ 45.53 a
		T1	21.28 $\pm$ 0.73 a	15.40 $\pm$ 1.24 a	6.00 $\pm$ 0.41 a	91.41 $\pm$ 3.90 a	433.40 $\pm$ 34.68 a
		T2	21.38 $\pm$ 1.21 a	14.97 $\pm$ 1.31 a	5.92 $\pm$ 0.49 a	92.88 $\pm$ 2.61 a	455.60 $\pm$ 35.84 a
		T3	21.03 $\pm$ 2.10 a	14.07 $\pm$ 0.45 a	6.00 $\pm$ 0.58 a	93.46 $\pm$ 0.20 a	445.90 $\pm$ 29.52 a
	0 d	CK	20.48 $\pm$ 1.05 a	11.13 $\pm$ 0.76 a	6.33 $\pm$ 0.47 a	93.04 $\pm$ 0.57 a	420.13 $\pm$ 79.65 a
		T1	21.68 $\pm$ 1.84 a	11.23 $\pm$ 1.03 a	6.33 $\pm$ 0.47 a	93.72 $\pm$ 0.76 a	380.40 $\pm$ 26.38 a
		T2	20.93 $\pm$ 1.62 a	10.70 $\pm$ 0.39 ab	6.17 $\pm$ 0.37 a	94.08 $\pm$ 0.85 a	401.73 $\pm$ 56.38 a
		T3	21.37 $\pm$ 1.23 a	9.63 $\pm$ 1.34 b	6.33 $\pm$ 0.47 a	91.00 $\pm$ 1.61 b	393.90 $\pm$ 57.03 a
	9 d	CK	19.88 $\pm$ 1.17 a	12.65 $\pm$ 1.55 a	6.33 $\pm$ 0.75 a	91.88 $\pm$ 0.44 b	619.86 $\pm$ 41.77 a
		T1	18.11 $\pm$ 1.08 bc	9.47 $\pm$ 0.90 bc	4.17 $\pm$ 0.69 b	93.82 $\pm$ 0.70 a	298.43 $\pm$ 52.99 c
		T2	19.20 $\pm$ 2.48 ab	9.97 $\pm$ 1.24 b	4.33 $\pm$ 0.47 b	92.27 $\pm$ 1.72 ab	450.30 $\pm$ 18.88 b
		T3	16.69 $\pm$ 1.54 c	8.45 $\pm$ 0.85 c	4.17 $\pm$ 0.69 b	92.22 $\pm$ 0.21 ab	126.13 $\pm$ 18.01 d

Note: Data in the table are means $\pm$ SEs. Different lowercase letters in the same column indicate significant difference at the 0.05 probability level. Treatments and abbreviations are the same as those given in Figure 1. Same as table below.

Collectively, waterlogging stress exerted multiple adverse effects on the growth and development of *B. napus* seedlings, primarily manifested as root rot, leaf chlorosis, and growth retardation. Pre-waterlogging foliar application of ABA induced increasing trends in plant height, root length, and root activity of rapeseed seedlings, which effectively alleviated the adverse damage caused by waterlogging stress. In contrast, pre-waterlogging foliar spraying of NDGA exerted an opposite regulatory effect, failing to mitigate waterlogging stress and even

exacerbating the growth inhibition of rapeseed seedlings under waterlogging conditions.

Effects of ABA and NDGA treatments on stomatal traits of *B. napus* under waterlogging stress

Microscopic observations revealed that stomata of rapeseed are predominantly distributed on the abaxial leaf epidermis, located between mesophyll cells or atop epidermal cells and forming small, compact pores. As illustrated in Figure 2, stomatal traits of the two genotypes exhibited minor variations across all treatments prior to foliar pretreatment with ABA or NDGA and at 0 DPW. At 9 DPW, however, extensive stomatal closure was observed in waterlogging-sensitive ZS6 under T3 treatment, whereas only a small proportion of stomata closed in waterlogging-tolerant HYZ50.

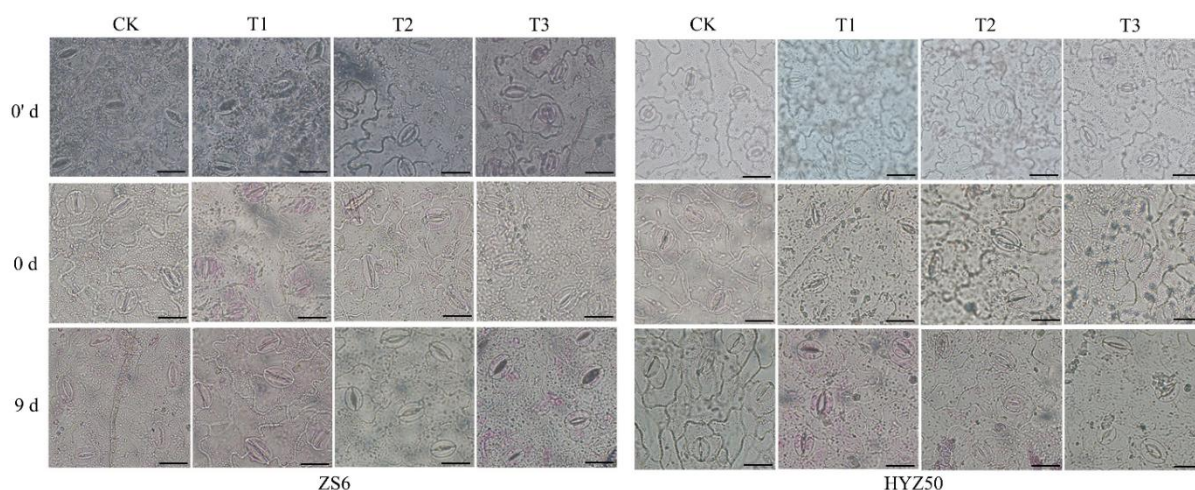


Fig. 2 Observation of stomata in rapeseed under waterlogging stress after ABA or NDGA treatment

Note: Treatments and abbreviations are the same as those given in Figure 1. The scale in the figure is 50 μm .

As shown in Table 2, no statistically significant differences in stomatal density, stomatal length and guard cell width were observed between genotypes ZS6 and HYZ50 prior to foliar pretreatment with ABA or NDGA. At 0 DPW, stomatal length of ZS6 under T3 increased significantly by 10.72% compared with CK. For HYZ50 at 0 DPW, T3 exhibited markedly higher stomatal density than CK, while its stomatal length was significantly lower than that of T1. At 9 DPW, stomatal density and guard cell width of ZS6 displayed ascending trends in all treatments relative to CK. T2 and T3 had significantly higher values of these two indicators than CK, yet no statistical discrepancy was found between T2/T3 and T1. Conversely, stomatal length presented a descending tendency: T1 possessed significantly shorter stomata than CK; T2 and T3 showed no significant difference from each other, but both had remarkably reduced stomatal length relative to T1. At 9 DPW, the variation patterns of all stomatal parameters in HYZ50 differed distinctly from those in ZS6. Stomatal density and guard cell width both exhibited declining trends. Stomatal density followed the sequence $\text{CK} > \text{T1} > \text{T2} > \text{T3}$: T2 had significantly lower stomatal density than CK, and T3 displayed markedly reduced density relative to both CK and T1. Guard cell width showed no statistical difference between CK and T1, and both groups possessed substantially wider guard cells than T2 and T3, whereas T2 and T3 were comparable to each other. Stomatal length exhibited an upward trend, ranking $\text{CK} < \text{T1} < \text{T2} < \text{T3}$. T3 had significantly longer stomata than all other treatments; stomatal length was similar between T1 and T2, and both were significantly higher than CK.

It is thus inferred that stomatal behavior may be closely correlated with waterlogging tolerance of *B. napus*.

Table 2 Effect of ABA or NDGA on stomatal characteristics of rapeseed under waterlogging stress

Cultivar	Treatment	Number	Stomatal density ($\text{NO} \cdot \text{mm}^{-2}$)	Stomatal length (μm)	Guard cell width (μm)
ZS6	0' d	CK	39.91 ± 3.39 a	49.18 ± 2.27 a	33.58 ± 2.74 a
		T1	54.42 ± 8.01 a	48.11 ± 1.27 a	32.66 ± 1.65 a

	0 d	T2	48.98±5.88 a	48.04±1.45 a	32.45±0.89 a
		T3	47.17±3.39 a	49.10±1.70 a	33.92±1.57 a
		CK	48.30±5.30 a	45.54±2.58 b	34.70±1.48 a
		T1	42.63±7.90 a	45.74±2.24 b	33.44±1.52 a
		T2	59.18±17.55 a	45.54±6.84 b	34.03±1.74 a
		T3	43.99±8.19 a	50.42±3.15 a	33.50±1.56 a
		CK	41.50±1.11 b	50.24±1.77 a	32.51±2.00 b
		T1	48.53±1.40 ab	48.78±1.13 b	33.78±1.78 ab
		T2	51.02±5.47 a	44.97±1.88 c	35.07±1.11 a
		T3	56.46±5.30 a	46.22±1.29 c	34.52±1.97 a
		CK	60.77±4.62 a	43.70±0.41 a	32.31±0.12 a
		T1	51.70±2.22 a	44.23±0.29 a	33.45±0.74 a
HYZ50	0' d	T2	56.24±5.59 a	43.70±0.73 a	31.54±0.51 a
		T3	56.24±10.96 a	43.56±0.07 a	32.26±1.45 a
		CK	44.14±7.98 b	46.92±2.33 ab	34.04±2.57 a
	0 d	T1	37.41±2.72 b	48.30±0.86 a	34.33±1.76 a
		T2	39.00±2.50 b	46.95±1.92 ab	34.66±1.33 a
		T3	58.28±3.16 a	46.17±1.26 b	33.27±2.26 a
	9 d	CK	55.78±2.42 a	44.96±1.64 c	33.64±1.42 a
		T1	52.38±8.89 ab	48.41±2.60 b	32.68±1.18 a
		T2	38.10±3.89 bc	48.95±2.50 b	31.02±1.02 b
		T3	33.56±7.78 c	51.95±4.06 a	31.47±1.35 b

Note: Treatments and abbreviations are the same as those given in Figure 1. Data in the table are means $\pm$ SEs. Different lowercase letters in the same column indicate significant difference at the 0.05 probability level.

Effects of ABA and NDGA treatments on photosynthetic pigment contents of *B. napus* under waterlogging stress

As shown in Figure 3, no statistically significant differences in chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and total chlorophyll concentrations were detected between the two genotypes with contrasting waterlogging tolerance prior to foliar pretreatment with ABA or NDGA. At 0 DPW, Chl *a* and total chlorophyll concentrations of ZS6 under T3 were markedly lower than those of CK, with respective reductions of 24.78% and 23.23%. By contrast, T2 treatment significantly elevated Chl *a*, Chl *b* and total chlorophyll contents of HYZ50 relative to CK, increasing by 23.33%, 37.14% and 33.74%, respectively. At 9 DPW, Chl *a* and total chlorophyll levels of ZS6 were significantly suppressed in T1, T2 and T3 compared with CK. The greatest decline in Chl *a* was observed in T3, which decreased by 61.26% and 36.76% relative to CK and T1, respectively, with both differences statistically significant. Nevertheless, Chl *a*, Chl *b* and total chlorophyll concentrations of HYZ50 showed no statistical discrepancy from CK across all treatments.

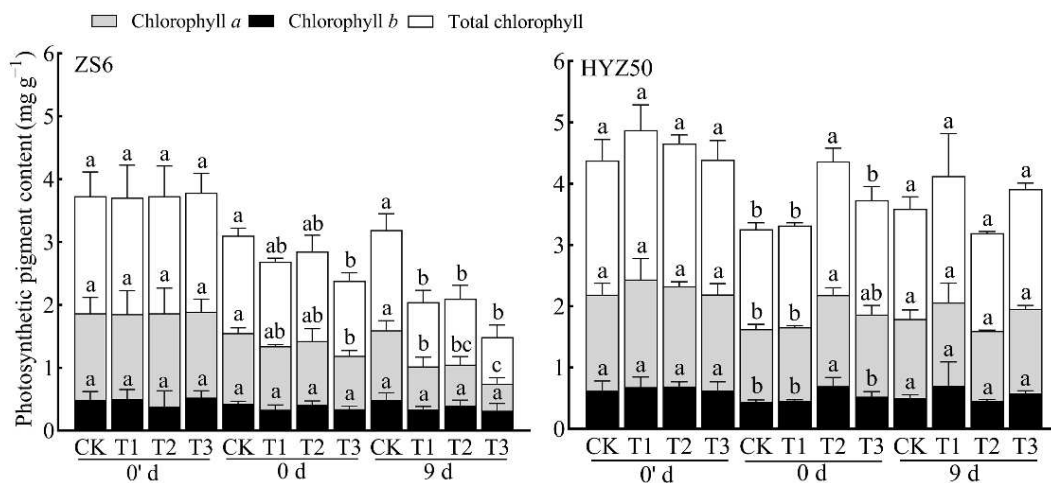


Fig. 3 Effect of ABA or NDGA on the content of photosynthetic pigments in leaves of rapeseed under waterlogging stress

Note: Treatments and abbreviations are the same as those given in Figure 1. At the same time point, different lowercase letters indicate significant differences between treatments at the 0.05 probability level.

Overall, the pigment measurements revealed divergent variation trends of Chl *a* and total chlorophyll between the two rapeseed genotypes under different treatments, whereas Chl *b* exhibited only minor fluctuations.

Prior to foliar pretreatment with ABA or NDGA and at 0 DPW, no statistically significant differences in MDA concentrations were detected across all treatments for genotypes ZS6 and HYZ50. At 9 DPW, MDA concentrations of both ZS6 and HYZ50 increased markedly under T1 and T3 treatments. Relative to CK, MDA levels of ZS6 in T1 and T3 were elevated by 3.05-fold and 3.66-fold, respectively; the corresponding fold increases for HYZ50 were 0.61 and 1.89. By contrast, MDA concentrations in T2 exhibited no statistical discrepancy from CK for both genotypes (Figure 4A).

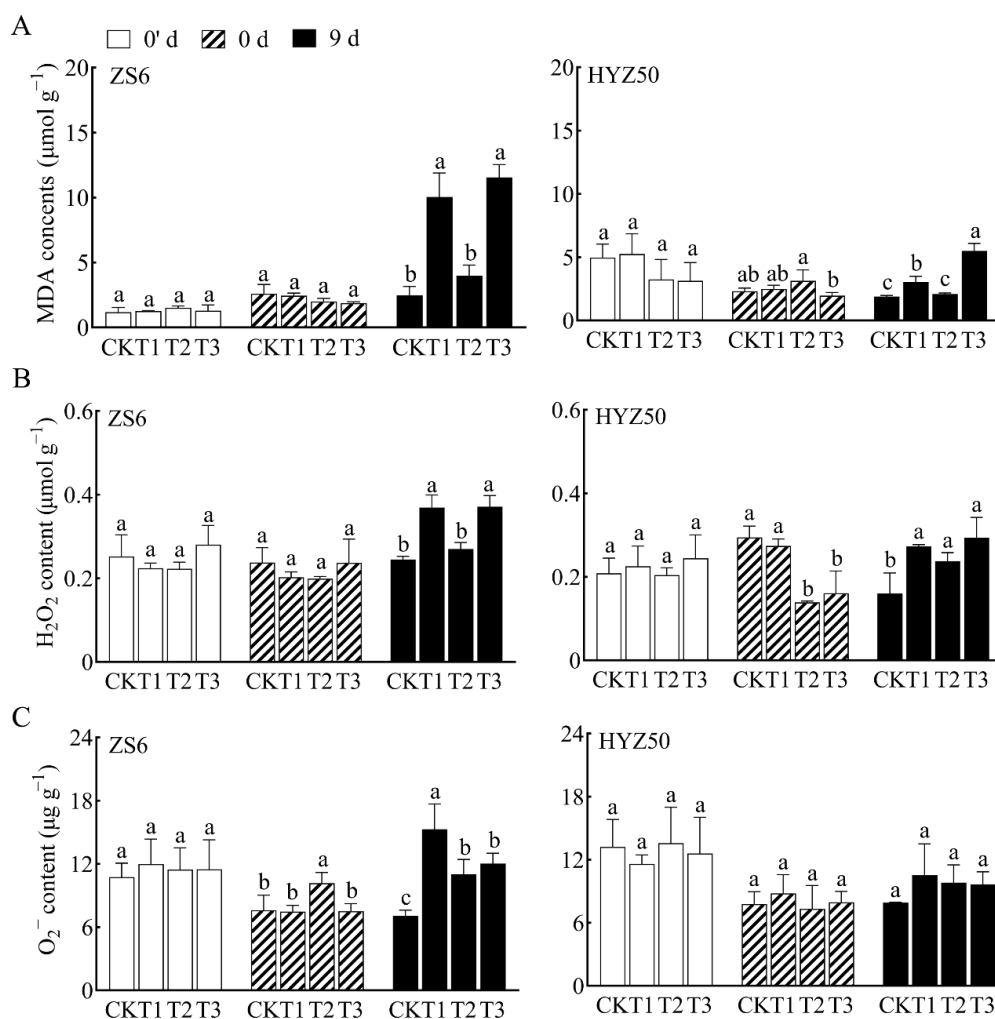


Fig. 4 Effect of ABA or NDGA on the content of MDA and ROS metabolite in leaves of rapeseed under waterlogging stress

For superoxide anion (O_2^-) contents, no significant differences were detected among treatments in ZS6 before foliar application of ABA or NDGA. At 0 DPW, T2 exhibited significantly higher O_2^- levels than all other treatments. By 9 DPW, O_2^- concentrations in ZS6 were significantly increased by 116.14%, 55.91%, and 70.12% in T1, T2, and T3, respectively, compared with CK. In HYZ50, O_2^- contents did not differ significantly among treatments at any time point, though a general increasing trend was observed across all treatments by 9 DPW (Figure 4C).

Effects of foliar pretreatment with ABA or NDGA on variations in antioxidant enzyme activities in *B. napus* leaves under waterlogging stress

Prior to foliar pretreatment with ABA or NDGA and at 0 DPW, no statistically significant differences in CAT activities were detected among all treatments for ZS6. At 9 DPW, CAT activities of T1 and T3 were significantly inhibited, decreasing by 19.47% and 30.94% relative to CK, respectively; CAT activity in T2 showed no statistical discrepancy from CK. For HYZ50, CAT activities did not differ significantly across treatments before ABA or NDGA application and at 0 DPW. At 9 DPW, T1 exhibited markedly lower CAT activity than CK, while the elevated CAT activities in T2 and T3 were comparable to those of CK (Figure 5A).

No obvious inter-treatment variations in POD activities were observed in ZS6 before ABA or NDGA pretreatment and at 0 DPW. At 9 DPW, POD activities were significantly increased by 53.26% and 60.08% under T1 and T3 compared with CK, whereas POD activity of T2 was statistically equivalent to CK. HYZ50 presented largely consistent dynamic patterns of POD activity with ZS6 at all sampling stages (pre-treatment, 0 DPW and 9 DPW). However, HYZ50 has superior waterlogging tolerance, which alleviates cellular damage and restricts excessive ROS accumulation in seedling tissues. Consequently, no significant differences in POD activity were found among all treatments of HYZ50 (Figure 5B).

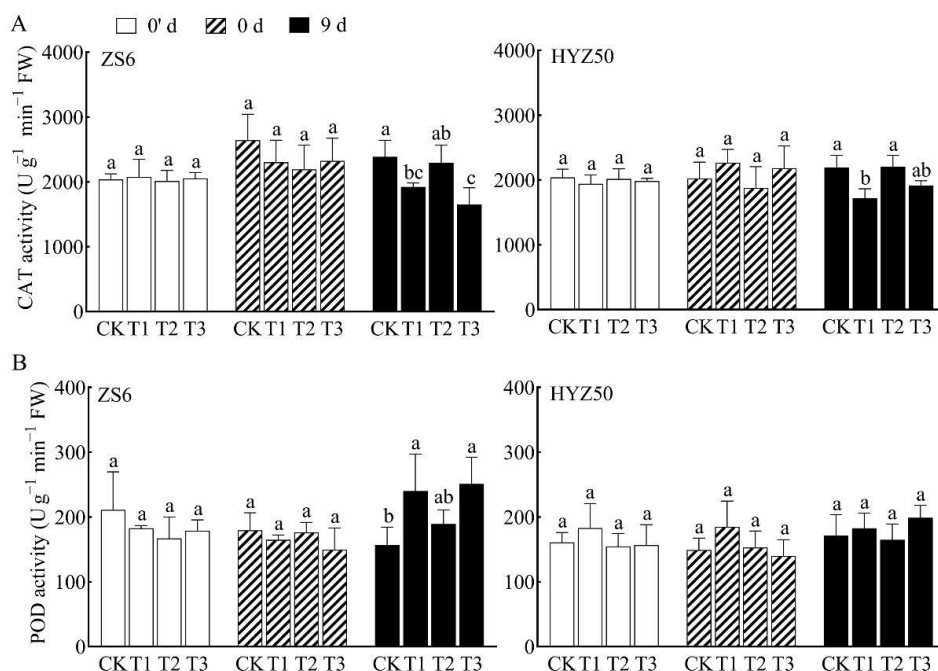


Fig. 5 Effect of ABA or NDGA on the activities of protective enzyme in leaves of rapeseed under waterlogging stress

Note: Treatments and abbreviations are the same as those given in Figure 1. At the same time point, different lowercase letters indicate significant differences between treatments at the 0.05 probability level.

Effects of foliar pretreatment with ABA or NDGA on variations in concentrations of osmotic adjustment substances in *B. napus* leaves under waterlogging stress

Prior to foliar pretreatment with ABA or NDGA, no statistically significant differences in the concentrations of soluble sugars, soluble proteins and proline were observed across all treatments for genotypes ZS6 and HYZ50.

At 0 DPW, soluble sugar concentrations declined under T3 treatment. For ZS6, soluble sugar levels showed no statistical discrepancy relative to CK, whereas those of HYZ50 were markedly reduced by 15.54% compared with CK. At 9 DPW, soluble sugar concentrations of ZS6 exhibited ascending trends in all treatments versus CK. T2 possessed the highest soluble sugar concentration, which was significantly greater than CK, T1 and T3; T3 also displayed substantially higher soluble sugar levels than CK, yet no significant difference was detected between T3 and T1. Soluble sugar contents of HYZ50 also presented upward tendencies across treatments, with no statistical differences among groups (Figure 6A).

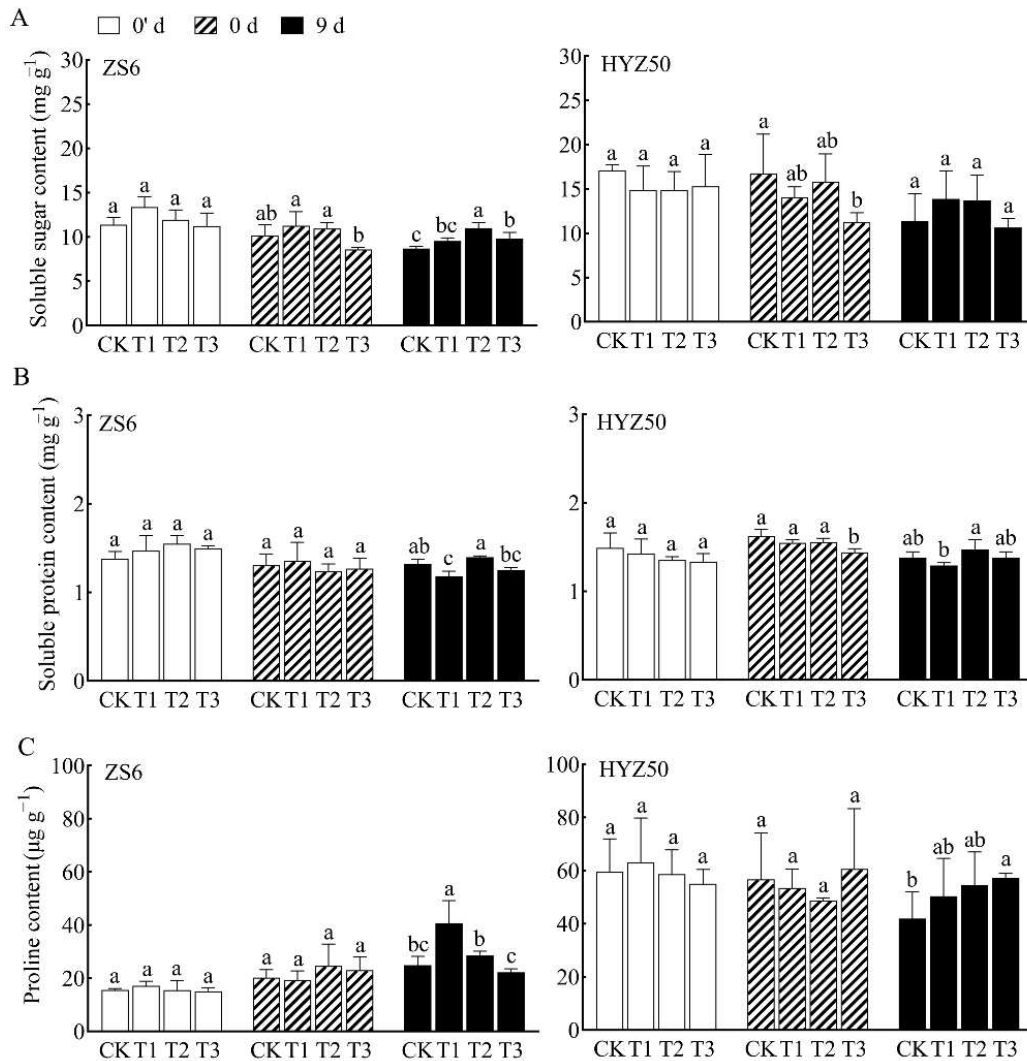


Fig. 6 Effect of ABA or NDGA on the permeation regulating substances content of rapeseed under waterlogging stress

Note: Treatments and abbreviations are the same as those given in Figure 1. At the same time point, different lowercase letters indicate significant differences between treatments at the 0.05 probability level.

At 0 DPW, soluble protein concentrations of ZS6 exhibited no statistical discrepancy from CK across all treatments. By comparison, soluble protein levels of HYZ50 in T3 were significantly reduced by 11.11% relative to CK. At 9 DPW, soluble protein concentrations of ZS6 under T1 decreased markedly by 10.60% compared with CK. T2 had the highest soluble protein concentration, which was significantly elevated by 15.71% versus T1 and comparable to CK. T3 showed no statistically significant differences in soluble protein content relative to either CK or T1. For HYZ50 at 9 DPW, the overall variation pattern of soluble proteins was largely consistent with that of ZS6. However, no treatments differed significantly from CK; T2 contained significantly higher soluble protein concentrations (an increase of 12.24%) than T1 (Figure 6B).

At 0 DPW, proline concentrations showed no significant inter-treatment differences for both ZS6 and HYZ50.

Waterlogging stress triggered proline accumulation in rapeseed seedlings. At 9 DPW, proline levels of ZS6 in T1 rose significantly by 63.39% compared with CK. Proline concentrations in T2 and T3 displayed descending trends relative to T1 and were statistically equivalent to CK. In HYZ50, proline concentrations presented ascending tendencies in T1, T2 and T3 treatments, among which T3 achieved the maximum value. Its proline concentration was significantly higher than CK, with an increment of 54.63% (Figure 6C).

Correlations among physiological traits of waterlogged rapeseed treated with ABA or NDGA

Waterlogging tolerance index (WTI) of genotypes ZS6 and HYZ50 was calculated using agronomic traits, stomatal characteristics and physiological indicators. Correlation analysis between each index and WTI revealed that MDA concentration, POD activity, H₂O₂ and O₂⁻ contents were extremely significantly negatively correlated with WTI. CAT activity and underground fresh weight had significant positive correlations with WTI. Root vigor, plant height, root length, green leaf number, shoot fresh weight, shoot dry weight and underground dry weight showed extremely significant positive correlations with WTI. No significant correlations were detected between WTI and the other tested indicators (Figure 7).

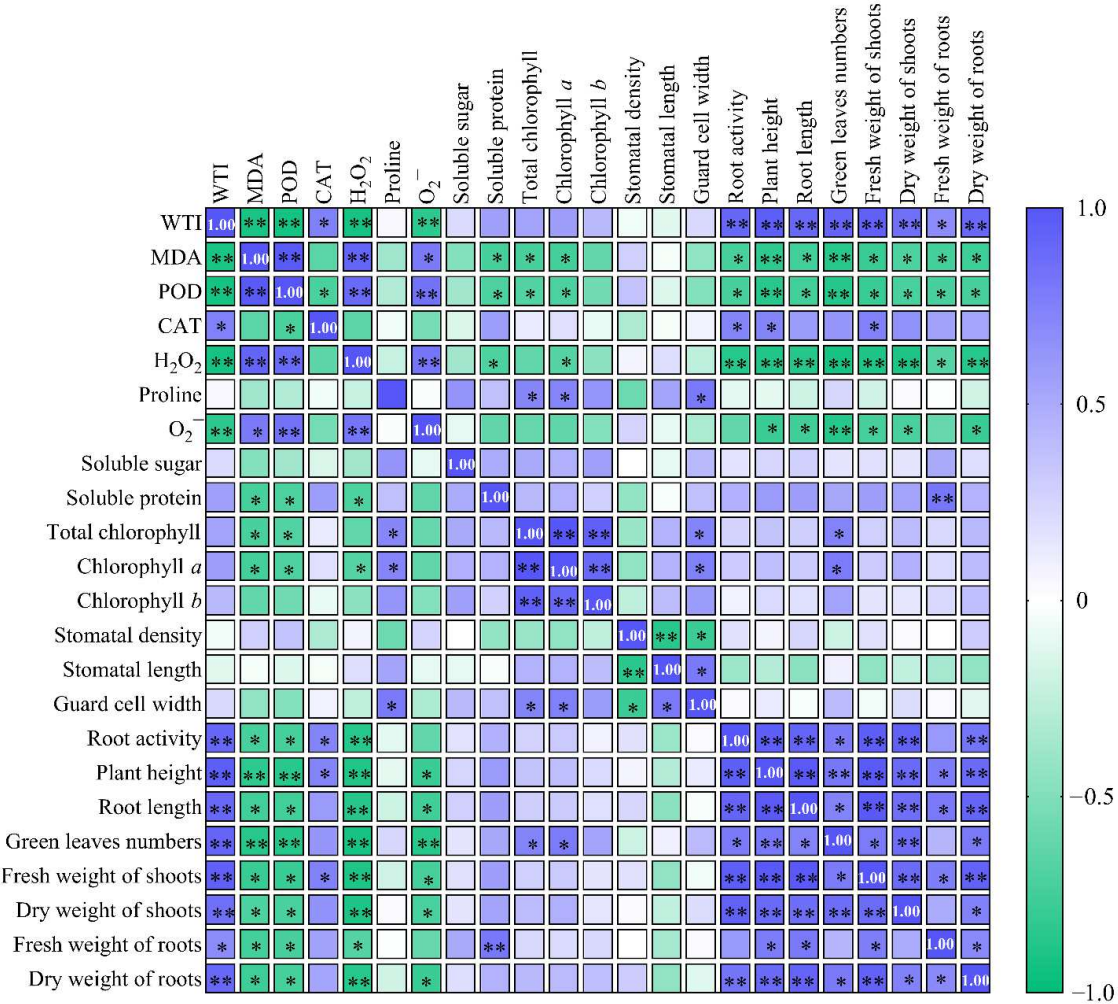


Fig. 7 Correlation analysis between various traits and waterlogging tolerance index of rapeseed under waterlogging stress

Comprehensive assessment of rapeseed waterlogging tolerance with ABA or NDGA pretreatments

Correlation analysis further indicated tight correlations between agronomic traits and physiological indicators, while severe multicollinearity was observed among these measured traits (Figure 7). Therefore, principal component analysis (PCA) was adopted to realize dimensionality reduction of all datasets using DPS 7.05 software. Seven principal components were extracted. The first two principal components accounted for 54.63% and 23.79% of the total variance, respectively, with a cumulative variance contribution rate of 78.42%, which could effectively reflect

the majority of information carried by the 22 indicators (Table 3). Thus, the first two principal components were selected as key factors to judge the waterlogging tolerance of rapeseed.

Table 3 Common factor variance contribution rate of various indicators in rapeseed

Principal component	Eigenvalue	Proportion of variance (%)	Cumulative proportion of variance (%)
PC1	12.02	54.63	54.63
PC2	5.23	23.79	78.42
PC3	1.86	8.43	86.85
PC4	1.41	6.42	93.27
PC5	0.74	3.34	96.62
PC6	0.39	1.78	98.39
PC7	0.35	1.61	100.00

Comprehensive scores of each treatment for genotypes ZS6 and HYZ50 were calculated using the scoring coefficients of the first and second principal components as weights. As shown in Table 4, waterlogging stress reduced the comprehensive scores of both rapeseed genotypes. Compared with CK, the comprehensive scores of ZS6 and HYZ50 under T1 treatment decreased by 297.30% and 55.29%, respectively, indicating that genotype ZS6 was more susceptible to waterlogging stress. Relative to T1, the comprehensive scores of the two genotypes under T2 treatment increased by 82.88% and 111.83%. By contrast, T3 treatment further reduced the comprehensive scores by 15.07% (ZS6) and 54.84% (HYZ50) compared with T1. These results demonstrated that foliar pretreatment with ABA before waterlogging stress effectively improved rapeseed waterlogging tolerance, whereas NDGA pretreatment produced the opposite effect.

Table 4 Ranking of comprehensive scores on the effect of ABA or NDGA treatment on waterlogging tolerance of rapeseed

Treatment	PC scores		Composite score	Composite score ranking
	PC1	PC2		
ZS6	CK	2.95	1.48	1
	T1	-5.44	-2.92	3
	T2	0.29	-0.50	2
	T3	-5.09	-3.36	4
HYZ50	CK	4.71	2.08	1
	T1	0.82	0.93	3
	T2	2.81	1.87	2
	T3	-1.05	0.42	4

Treatments and abbreviations are the same as those given in Figure 1.

In addition, the WTI analysis revealed that waterlogging stress significantly reduced the overall waterlogging tolerance index of the two rapeseed varieties. Specifically, ZS6 showed a decrease of 22.64%, 9.05%, and 24.95% relative to the CK in treatments T1, T2, and T3, respectively. Meanwhile, HYZ50 showed a decrease of 11.45%, 9.64%, and 18.23% relative to CK in treatments T1, T2, and T3, respectively. Compared to treatment T1, the overall waterlogging tolerance index showed an upward trend in treatment T2, with ZS6 exhibiting a significant increase of 17.57% in the overall waterlogging tolerance index in T2 compared to T1. However, in treatment T3, the index showed a downward trend, with HYZ50 exhibiting a significant decrease of 7.65% in the overall waterlogging tolerance index compared to T1 (Table 5). The calculation results were consistent with the principal component analysis and phenotype, further demonstrating that ABA treatment improved the waterlogging tolerance of rapeseed, while NDGA treatment exacerbated the damage caused by waterlogging to rapeseed.

Table 5 Effect of ABA or NDGA on WTI of rapeseed under waterlogging stress

Treatment	ZS6		HYZ50	
	Total WTI	Order	Total WTI	Order
CK	22.00±0.00 a	1	22.00±0.00 a	1
T1	17.02±0.68 c	3	19.48±0.89 b	3
T2	20.01±0.22 b	2	19.88±0.65 b	2
T3	16.51±0.50 c	4	17.99±0.12 c	4

Treatments and abbreviations are the same as those given in Figure 1. Data in the table are means ± SEs. Different lowercase letters in the same column indicate significant difference at the 0.05 probability level.

Discussion

ABA and NDGA pretreatments regulate rapeseed seedling growth under waterlogging stress

The seedling stage constitutes a critical growth period for rapeseed. Waterlogging stress can induce irreversible damage to rapeseed plants, ultimately deteriorating yield and quality attributes at maturity (Men et al 2020). As a key abiotic stressor, waterlogging substantially inhibits plant growth by disrupting endogenous hormone homeostasis and signal transduction pathways (Yan et al 2010). Exogenous application of plant growth regulators can modulate physiological and biochemical metabolism in plants, thereby effectively mitigating the growth inhibition induced by waterlogging stress (Sasaki et al 2013; Xu et al 2016; Yan et al 2010).

In this study, single waterlogging stress (T1) markedly suppressed the seedling growth of rapeseed, presenting as reduced plant height, shortened root length, decreased number of green leaves, lowered biomass accumulation, and declined root activity. In particular, the waterlogging-sensitive genotype ZS6 exhibited a more pronounced growth inhibition phenotype under waterlogging conditions. Pre-waterlogging foliar pretreatment with ABA effectively alleviated waterlogging-induced damage and improved rapeseed waterlogging tolerance, whereas pre-stress NDGA pretreatment aggravated the adverse effects of waterlogging stress. Consistent with the phenotypic variations, principal component analysis and WTI evaluation further verified the opposing regulatory effects of ABA and NDGA on rapeseed waterlogging tolerance. Collectively, these findings demonstrate that optimal pre-waterlogging ABA pretreatment facilitates the growth and development of waterlogged rapeseed. It enhances the absorption and utilization of water and mineral nutrients, maintains the structural stability of plant cells, sustains normal physiological metabolism, and ultimately relieves the growth suppression caused by waterlogging stress. In contrast, NDGA pretreatment inhibits endogenous ABA accumulation, which exacerbates waterlogging-induced physiological damage and growth retardation in rapeseed seedlings.

Consistent with our results, Shao et al. reported that combined foliar application of salicylic acid (SA) and ABA significantly improved plant height, effective branch number, yield per plant, and 1000-kernel weight of winter rapeseed under waterlogging stress (Shao et al 2025). Additionally, Li et al. confirmed that exogenous ABA application could alleviate waterlogging damage to *Cleistocalyx operculatus* and *Syzygium cumini* plants. Overall, the results of the present study are highly consistent with these previous findings (Li et al 2022).

ABA and NDGA modulate rapeseed stomatal responses to waterlogging stress

Stomata are specialized structures on the epidermal tissues of higher plant organs and play pivotal roles in plant transpiration and photosynthesis (Park et al 2025). Plants exhibit analogous adaptive mechanisms in response to waterlogging and drought stresses. Under waterlogging conditions, root damage in waterlogging-sensitive plants reduces water uptake, resulting in plant water deficit and leaf wilting. To maintain water balance and mitigate cellular damage, plants tend to close stomata under such stress conditions (Bradford and Hsiao 1982). The present study verified this regulatory pattern. Under waterlogging stress, NDGA pretreatment aggravated stress-induced damage in the waterlogging-sensitive rapeseed genotype ZS6, accompanied by extensive stomatal closure.

Previous studies have demonstrated that ABA participates in the regulation of multiple physiological processes in plants, including stomatal movement, stress response, and growth and development (Gomez-Cadenas et al 2015). Castonguay et al. reported that ABA accumulation induces stomatal closure and enhances plant stress tolerance by reducing transpiration water loss (Castonguay et al 1993). However, only a slight degree of stomatal closure was observed in waterlogged rapeseed plants with ABA pretreatment in this study, and the underlying mechanism remains to be further explored. Collectively, our preliminary results indicate that ABA and NDGA mediate rapeseed adaptation to waterlogging stress by modulating stomatal closure, which further alters leaf photosynthesis and

transpiration.

ABA and NDGA modulate rapeseed antioxidant enzyme and ROS homeostasis responses to waterlogging stress

Waterlogging stress triggers excessive ROS accumulation in plant cells. Excess ROS that cannot be scavenged timely will damage biomembrane structure and disrupt normal physiological and biochemical metabolism (Hong et al 2024). O_2^- and H_2O_2 are the major ROS in plant cells. Antioxidant enzymes including POD and CAT serve as core ROS-scavenging systems, which can convert toxic ROS into low-toxic or non-toxic substances to alleviate oxidative damage (Hong et al 2024). MDA, a critical product of membrane lipid peroxidation, is widely used to evaluate the degree of cellular oxidative injury under abiotic stress. In the present study, waterlogging stress significantly increased cellular O_2^- and H_2O_2 concentrations in rapeseed seedlings. Pre-waterlogging ABA pretreatment markedly enhanced CAT activity, thereby efficiently eliminating excess ROS and reducing MDA accumulation. By contrast, NDGA pretreatment exerted the opposite effects and aggravated waterlogging-induced oxidative stress. Additionally, the variation trend of POD activity observed in this study was slightly different from the findings reported by Shao et al., which was speculated to be attributed to the differences in rapeseed genotypes and sampling time points between studies (Shao et al 2025).

ABA and NDGA pretreatments modulate osmolyte accumulation in waterlogged rapeseed

Plants rely on osmotic adjustment to maintain cellular water retention capacity, preserve cell membrane integrity, and sustain normal growth and development under stress conditions (Wang et al 2019). In this study, at 9 days after waterlogging stress, foliar pretreatment with ABA significantly increased the contents of soluble sugars and soluble proteins in rapeseed leaves. In comparison, the accumulation of these two osmotic substances was lower in the NDGA-pretreated group. Moreover, distinct genotypic differences in proline accumulation were observed between the two rapeseed genotypes under ABA and NDGA pretreatments.

Consistent with our findings, He et al. demonstrated that exogenous ABA application could induce osmotic adjustment in soybean under water stress, thereby optimizing leaf water status and water use efficiency, while exhibiting no significant effect on crop yield (He et al 2019). Massive accumulation of osmotic adjustment substances can maintain high cellular osmotic pressure, enhance cellular dehydration tolerance, stabilize plasma membrane structure, and ultimately improve plant resistance to abiotic stress (Tian et al 2019). The results of the present study are largely consistent with these previous conclusions.

In summary, the two rapeseed genotypes exhibited significant differences in waterlogging tolerance and physiological responses to waterlogging stress. Pre-waterlogging foliar application of ABA effectively alleviated waterlogging-induced plant damage, whereas NDGA pretreatment aggravated the adverse effects of waterlogging stress on rapeseed seedlings.

Conclusions

Currently, limited studies have focused on the regulatory effects of ABA and NDGA in plant responses to waterlogging stress. In this study, the differential responses of two rapeseed genotypes with contrasting waterlogging tolerance to ABA and NDGA pretreatments were comprehensively investigated from phenotypic and physiological perspectives. The results demonstrated that pre-stress ABA pretreatment effectively alleviated waterlogging-induced damage in rapeseed, while NDGA pretreatment exacerbated the inhibitory effects of waterlogging stress. The protective role of ABA was mainly attributed to the improved root vigor and regulated stomatal movement. Furthermore, ABA pretreatment enhanced the activities of POD and CAT to eliminate excessive ROS, thereby maintaining cellular ROS homeostasis and normal osmotic pressure. These positive physiological

changes ultimately facilitated rapeseed growth and improved plant adaptability to waterlogging stress. Collectively, the findings of this study provide a theoretical basis for the green and efficient cultivation of waterlogging-tolerant rapeseed.

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Author contributions Yujie Zhao and Leyan Zhao conducted the experiments and wrote the original manuscript. Qin Cai, Fei Tao and Yuying Wang were responsible for plant cultivation, sample collection and partial experimentation. Lingli Xie and Benbo Xu oversaw the whole research, analyzed the results and revised the manuscript. All authors read and approved the final manuscript.

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Data availability Raw data underlying the results presented in this study can be obtained from the corresponding author following reasonable requests.

Declarations Conflict of interest None.

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