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Effects of foliar application of potassium dihydrogen phosphate on the physiological responses of rice seedlings under high temperature stress

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Abstract: This study investigated the alleviating effects and physiological responses to foliar-applied potassium dihydrogen phosphate (KDP) on rice seedlings under high-temperature (HT) stress. An early *indica* hybrid rice, YLY17 (high-temperature-sensitive), was used as the planting material. Four treatment groups were set up: (a) NT – normal temperature; (b) NT + KDP – normal temperature with foliar application of different KDP concentrations (0.1, 0.2, 0.3, and 0.4%); (c) HT – high temperature treatment without foliar application of KDP, and (d) HT + KDP – high temperature with foliar application of different KDP concentrations. At the three-leaf stage, rice seedlings were subjected to simulated HT stress (32~38 °C during the day and 26~32 °C at night) for 10 days. Growth indicators, photosynthetic parameters, antioxidant characteristics, osmotic adjustment substances, and related metabolic enzymatic activities of young rice seedlings were quantified, and the alleviating effect of KDP was comprehensively evaluated by principal component analysis (PCA). The results showed that HT stress significantly reduced plant height, fresh weight, and dry weight, decreased chlorophyll content and SPAD value, and decreased the net photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration rate (T_r), while increasing intercellular carbon dioxide (CO_2) concentration (c_i). At the same time, it led to the accumulation of superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), and malondialdehyde (MDA), and induced increases in antioxidant enzyme and osmotic adjustment-related enzyme

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activities. Foliar spraying of KDP could effectively alleviate the above damage caused by HT stress, with 0.3% KDP being the most effective treatment. Compared with HT treatment, 0.3% KDP treatment significantly increased plant height, fresh weight and dry weight by 7.6, 10.6 and 10.2%, respectively, improved chlorophyll content and photosynthetic parameters, enhanced the activities of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and ascorbate peroxidase (APX), reduced the accumulation of reactive oxygen species (ROS) and MDA, and promoted the accumulation of osmotic adjustment substances such as soluble protein (SP), proline (Pro), soluble sugar (SS) and sucrose (SUC), as well as increased the activities of nitrate reductase (NR), glutamine synthetase (GS), sucrose synthase (SUS) and sucrose phosphate synthase (SPS). The PCA results showed that the order of comprehensive physiological activity index was NT + KDP > NT > KDP + HT > HT, indicating that KDP enhances heat tolerance by coordinately regulating photosynthesis, antioxidant defence, and osmotic adjustments. This study provides a theoretical basis and technical reference for using KDP to alleviate HT stress in rice seedlings.

Keywords: *Oryza sativa* L.; climate change; abiotic stress; seedling stage; essential macronutrient

Under global climate change, high-temperature (HT) events are becoming more frequent and intense, posing a major constraint on crop production (Shekhawat et al. 2022). Rice (*Oryza sativa* L.), a staple food for nearly half the world's population, is crucial for global food security (Hassan et al. 2023, Shi et al. 2023). However, rice is a typical warm-season crop highly sensitive to temperature. When subjected to continuous HT stress, especially during the seedling stage, it triggers a series of complex physiological and biochemical disorders, severely inhibiting plant growth and creating hidden risks for later yield formation (Lu et al. 2025). Research indicates that the core damaging mechanism of HT stress lies in disrupting the cellular balance of reactive oxygen species (ROS) metabolism. This leads to the explosive accumulation of ROS, such as the superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2), which then attack the membrane system, causing lipid peroxidation. A hallmark product of this process, malondialdehyde (MDA), increases significantly, resulting in increased cell membrane permeability and damage to structural integrity (Al-Zahrani et al. 2022). Concurrently, HT stress severely damages the photosynthetic system in rice leaves. Chlorophyll degradation is a prominent manifestation, involving mechanisms such as inhibited synthesis, damage to the photosystem II reaction centre, and disruption of thylakoid membrane structure. Studies point out that under HT stress, non-stomatal limitations often play a dominant role, for example, decreased Rubisco activity and an impaired photosynthetic electron transport chain (Shrestha et al. 2022, Salgotra and Chauhan 2023). Therefore, an in-depth analysis of the physiological mechanisms underlying rice seedling responses to HT stress, and the exploration of effective agronomic control measures, are of urgent practical significance for ensuring stable rice production.

Facing the increasingly severe challenge of HT stress, foliar regulation using exogenous chemical substances is a rapid, efficient, and environmentally friendly mitigation strategy. In recent years, researchers have tested various plant growth regulators, such as salicylic acid and brassinolide, to enhance crop heat tolerance (Chen et al. 2022, Waadt et al. 2022). Among these, potassium dihydrogen phosphate (KDP), a high-purity, fully water-soluble binary compound fertiliser of phosphorus and potassium, is widely used in agricultural production (Jančaitienė et al. 2023). Studies have confirmed that KDP not only provides plants with essential phosphorus and potassium nutrients but also acts as an effective inducer of stress tolerance, showing great potential for coping with various abiotic stresses (Akram and Ashraf 2011, Xu et al. 2024). Specific research indicates that spraying an appropriate concentration of KDP can significantly increase the activities of antioxidant enzymes, such as SOD, POD, and CAT, in rice leaves under HT stress, while effectively reducing MDA content and alleviating membrane lipid peroxidation damage. Furthermore, it helps maintain higher chlorophyll content and net photosynthetic rate, enhances carbon and nitrogen metabolism, and promotes dry matter accumulation, thereby comprehensively improving the heat tolerance of rice seedlings (Yang et al. 2022).

Phosphorus is a core component of energy carriers, such as adenosine triphosphate. HT stress

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can disrupt photophosphorylation and affect ATP synthesis. Spraying KDP directly provides a phosphorus source for leaves, ensuring the energy supply needed for photosynthesis. Potassium ions can rapidly traverse biological membranes and activate various physiological metabolic enzymes by inducing conformational changes (Sardans and Peñuelas 2021, Jančaitienė et al. 2023). Adequate potassium supply helps maintain guard cell turgor, thereby alleviating, to some extent, the excessive stomatal closure caused by HT, which is beneficial for CO_2 absorption (Kapoor et al. 2022). Simultaneously, potassium's activating effect on enzymes may also involve the antioxidant enzyme system, thereby enhancing the plant's ability to scavenge ROS. Soluble proteins are important osmotic regulators and functional proteins. Research shows that under HT stress, spraying KDP increases soluble protein (SP) content in rice leaves. Its mechanism is primarily attributed to the potassium ions it contains. K^+ rapidly enters cells due to its high membrane permeability and activates enzymes involved in protein synthesis by inducing conformational changes, thereby directly regulating protein synthesis (Chérel et al. 2014).

Although preliminary evidence suggests that KDP can alleviate HT damage in rice, existing studies have mostly focused on reproductive growth stages or individual physiological processes. There remains a lack of a systematic, integrative analysis of how KDP coordinately regulates photosynthesis, antioxidant defence, and carbon-nitrogen (C-N) metabolism at the seedling stage under HT stress. Therefore, this study aims to address this critical research gap.

MATERIAL AND METHODS

Plant material and growth conditions. The high-temperature-sensitive, early *indica* hybrid rice cv. YLY17, was used as plant material. It was bred and provided by Anhui Yuanliang Seed Science Research Institute. Rice seeds with plump grains and uniform size were selected, disinfected with 5% NaClO solution, washed with distilled water, and placed in a growth incubator for germination. The temperature inside the incubator was set at 30 °C. After radicle protrusion, rice seeds were sown in plastic pots and covered with about 1 cm thick cultivation substrate, gently pressed, and thoroughly watered. The substrate consisted of a standard nutrient soil mixture with adequate NPK supply. Each pot contains 5 kg of soil with a loamy texture. The soil had a pH of 6.5, organic carbon of 1.16%, total nitrogen of 0.12%, available phosphorus of 12 mg/kg, and exchangeable potassium of 145 mg/kg. Each pot contained 9 rice seedlings. All the pots were transferred to an artificial climate chamber and grown under normal temperature (NT) conditions (day/night temperature ranges 24–30 °C/18–24 °C, 12 h light/12 h dark, humidity 70–80%, light intensity approximately 1 000 μmol/m^2/s). Regular watering kept the soil moist. When seedlings grew to the three-leaf stage, disease- and pest-free seedlings with consistent plant height were selected for the experiment.

There were four treatment groups (Table 1); among which, group 1 (NT only) and group 2 (NT + KDP) were maintained under NT conditions throughout the experiment and sprayed with distilled water and

Table 1. Different treatment groups and different foliar concentrations

Treatment group		Treatment	Foliar application description
1	NT only	NT	distilled water only
2	NT + KDP	0.1% KDP 0.2% KDP 0.3% KDP 0.4% KDP	different concentrations of KDP solution
3	HT only	HT	distilled water only
4	HT + KDP	0.1% KDP + HT 0.2% KDP + HT 0.3% KDP + HT 0.4% KDP + HT	different concentrations of KDP solution

NT – normal temperature; NT + KDP – normal temperature + different concentrations of potassium dihydrogen phosphate; HT – high temperature; HT + KDP – high temperature + different concentrations of potassium dihydrogen phosphate

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Table 2. Effects of potassium dihydrogen phosphate (KDP) on growth parameters and malondialdehyde (MDA) content of rice seedling leaves under high temperature (HT) stress

Treatment	Seedling height (cm)	Plant fresh weight	Plant dry weight	MDA (µmol/g FW)
		(mg/plant)		
NT	25.5 ± 0.33^{d}	275.6 ± 5.26^{bc}	35.3 ± 0.97^{bcd}	4.63 ± 0.10^{d}
0.1% KDP	26.2 ± 0.29^{cd}	288.3 ± 8.82^{ab}	37.1 ± 1.37^{abc}	4.42 ± 0.10^{e}
0.2% KDP	26.8 ± 0.20^{bc}	293.2 ± 7.00^{ab}	37.9 ± 0.92^{ab}	4.32 ± 0.12^{ef}
0.3% KDP	27.7 ± 0.32^{a}	302.4 ± 7.14^{a}	39.0 ± 1.01^{a}	4.01 ± 0.06^{g}
0.4% KDP	27.1 ± 0.17^{ab}	297.9 ± 6.83^{a}	38.5 ± 1.08^{a}	4.18 ± 0.12^{fg}
HT	22.3 ± 0.32^{g}	242.3 ± 4.58^{d}	31.5 ± 0.72^{e}	6.92 ± 0.14^{a}
0.1% KDP + HT	22.7 ± 0.30^{g}	256.3 ± 7.18^{cd}	33.1 ± 0.96^{de}	6.64 ± 0.06^{b}
0.2% KDP + HT	23.1 ± 0.18^{fg}	260.5 ± 7.35^{cd}	33.4 ± 1.24^{de}	6.62 ± 0.09^{b}
0.3% KDP + HT	24 .0 ± 0.21^{e}	268.1 ± 7.25^{c}	34.7 ± 0.87^{cd}	6.20 ± 0.09^{c}
0.4% KDP + HT	23.6 ± 0.12^{ef}	265.9 ± 6.27^{c}	34.4 ± 0.73^{cde}	6.50 ± 0.13^{b}

NT – no KDP treated and no high temperature stress; 0.1% KDP – 0.1% KDP treated with no high temperature stress; 0.2% KDP – 0.2% KDP treated with no high temperature stress; 0.3% KDP – 0.3% KDP treated with no high temperature stress; 0.4% KDP – 0.4% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; 0.1% KDP + HT – 0.1% KDP treated with high temperature stress; 0.2% KDP + HT – 0.2% KDP treated with high temperature stress; 0.3% KDP + HT – 0.3% KDP treated with high temperature stress; 0.4% KDP + HT – 0.4% KDP treated with high temperature stress; FW – fresh weight

different KDP concentrations (0.1, 0.2, 0.3, and 0.4% KDP) on leaves, respectively; while group 3 (HT only) and group 4 (HT + KDP) were transferred to controlled conditions for high temperature stress treartment and were sprayed with distilled water and different concentrations of KDP (0.1, 0.2, 0.3, and 0.4% KDP) on leaves, respectively. Foliar spraying was carried out 1 day before the high-temperature stress treatment, with applications at three different times of day (morning, noon and evening) using a hand-knapsack sprayer until a layer of water mist formed on the leaves and a slight runoff occurred from the leaf surface. It is understood that the foliar application was uniformly applied to all treated pots. The HT stress treatments (32–38 °C day/26–32 °C night, 12 h light/12 h dark, 70–80% humidity) (Figure 1) were continued for 10 days. After 10 days, relevant morphological indicators of rice seedlings and photosynthetic parameters of the third fully expanded leaf were measured in all groups. Leaf samples were collected, immersed in liquid nitrogen, and stored at –80 °C for subsequent determination of physiological

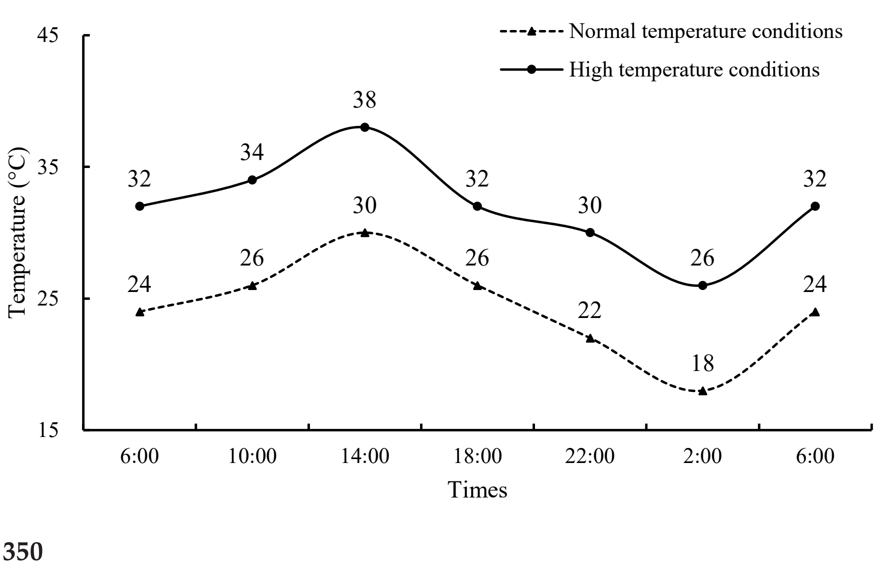

Figure 1. The temperature dynamics in the artificial climate chamber during high temperature processing

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indicators, including chlorophyll content, antioxidant activities, and osmotic adjustment substances.

Assay of seedling height, fresh weight, and dry weight. After the HT treatment, five representative pots of rice seedlings were randomly selected from each treatment. The vertical distance from the ground surface to the highest point of natural leaf growth was measured using a ruler. The average seedling height per pot was recorded. Then, sampled seedlings were blotted dry with absorbent paper to remove surface moisture and immediately weighed on an ME204E electronic balance (Mettler-Toledo Instruments Co., Ltd., Shanghai, China); the recorded data represented fresh weight per plant. After measurement, seedlings were placed in a DHG-240L oven (Hefei Youke Instrument and Equipment Co., Ltd., Hefei, China). They were initially heated to 105 °C for 30 min, then dried at 80 °C for a few days until constant weight was achieved, which was recorded as the dry weight.

Assay of chlorophyll content and photosynthetic parameters. Chlorophyll content and photosynthetic parameters were determined as described by Song et al. (2025). The chlorophyll contents of the third expanded leaf were determined using the extraction method. The leaf tissue was cut into pieces, mixed thoroughly, and 0.2 g was weighed, then extracted with 5 mL of N_2-dimethylformamide. The mixture was extracted for 24 h at 4 °C in the dark until the leaves turned completely white. After filtering, the OD values at 647, 664, and 470 nm were measured using a UV-1800 UV-Visible Spectrophotometer (Shimadzu Corporation, Kyoto, Japan) for the filtered extract. The chlorophyll content (the sum of chlorophyll *a* and chlorophyll *b*) was calculated. The relative chlorophyll content was measured using a SPAD-502 chlorophyll meter (Konica Minolta, Tokyo, Japan). For each of the third fully expanded leaves, measurements were taken at three different leaf parts: upper, middle, and lower. The average SPAD value was recorded for that leaf. Subsequently, the photosynthetic parameters of the third fully expanded leaf were measured using a Li-6400 portable photosynthesis system (Li-COR, Lincoln, USA). The leaf chamber conditions were set as follows: light intensity of 1 000 $\mu mol/m^2/s$, CO_2 concentration of 400 ppm, and leaf temperature at the growth temperature. Once the readings stabilised, data on net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (c_i), and transpiration rate (T_r) were recorded. All the measurements were recorded after the stabilisation period of approximately 2–3 min following leaf insertion into the chamber.

Assay of antioxidant enzyme activities. Zhang et al. (2025) reported that antioxidant enzyme activities were measured using the spectrophotometric method. Fresh leaf samples (0.5 g) were ground in an ice bath with 5 mL pre-cooled 50 mmol/L KDP buffer (pH 7.0) and centrifuged at 10 000 × *g* for 10 min (4 °C). The supernatant was used to measure absorbance changes at 560 nm (SOD), 470 nm (POD), and 240 nm (CAT) using a UV759 visible-ultraviolet spectrophotometer (Shanghai Jingke Scientific Instrument Co. Ltd., Shanghai, China). Leaf APX activity was extracted using 50 mmol/L KH_2PO_4 buffer (pH 7.5) and measured at 290 nm.

Assay of reactive oxygen species (ROS). The MDA contents in the leaves of rice seedlings were determined according to the thiobarbituric acid (TBA) method described by Hodges et al. (1999). The leaf samples (1.0 g) were homogenised using KH_2PO_4 buffer (pH 7.8) and then centrifuged at 12 000 × *g* for 10 min at 4 °C. Subsequently, the supernatant was collected, and the absorbance at 532, 600, and 450 nm was recorded using a UV759 visible-ultraviolet spectrophotometer to determine the MDA content. Leaves of rice seedlings were ground with pre-cooled phosphate buffer (pH 7.8), centrifuged, and the supernatant was used as the enzyme extract. The enzyme extract was added to a reaction mixture containing NBT, methionine, riboflavin, and EDTA, and the reaction was carried out under light for a certain time. The O_2^- radical production rate was calculated by measuring the absorbance change of the reaction system at 560 nm (Dhindsa et al. 1981). Hydrogen peroxide (H_2O_2) contents were determined using the titanium sulfate complex colourimetric method (Jia et al. 2017). Titanium sulfate reagent and concentrated ammonia water were sequentially added to the supernatant to precipitate the H_2O_2-titanium complex. The precipitate was dissolved in diluted sulfuric acid, and absorbance was measured at 415 nm to calculate H_2O_2 contents.

Assay of osmotic adjustment substances. Soluble protein contents were determined using the Coomassie Brilliant Blue G-250 staining method (Bradford 1976). Leaves of rice seedlings (0.5 g) were ground and extracted with phosphate buffer (pH 7.5), centrifuged, and the supernatant collected. An appropriate amount of supernatant was mixed with Coomassie Brilliant Blue G-250 reagent, allowed to stand for several minutes, and the absorbance was measured at 595 nm to calculate SP content. Pro content was determined using the acidic ninhydrin colourimetric method (Bates et al. 1973). Leaves of rice seedlings (0.5 g) were ground and extracted with 3% sulfosalicylic acid solution, extracted in a boiling water bath for 10 min, centrifuged, and the supernatant collected. Acidic ninhydrin reagent and glacial acetic acid were added to the supernatant, which was then heated in a boiling water bath for 40 min. After the reaction, the mixture was cooled, and the red product was extracted with toluene. The absorbance of the toluene phase was measured at 520 nm to calculate the proline content.

Assay of nitrate reductase, glutamine synthetase, sucrose synthase, and sucrose phosphate synthase activities. Leaves of rice seedlings (1.0 g) were ground in an ice bath with HEPES-NaOH buffer (pH 7.5) and centrifuged at low temperature to obtain the supernatant. Sucrose synthase (SUS) activity was assayed in a reaction system containing UDPG, fructose, and enzyme extract. After a certain reaction time, enzyme activity was calculated by measuring the SUC produced (Kato 1995). Sucrose phosphate synthase (SPS) activity was assayed in a reaction system containing UDPG, fructose-6-phosphate, and enzyme extract, and activity was calculated by measuring the sucrose phosphate produced (Hubbard et al. 1991). The activities of nitrate reductase (NR) and glutamine synthetase (GS) were calculated following Yu and Zhang (2012).

Statistical analysis. Data analysis was performed using one-way analysis of variance (ANOVA) and Duncan's new multiple range test for multiple comparisons ($P < 0.05$) through SPSS software 22.0 (IBM, Chicago, USA). Before ANOVA, data were examined for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene's test. The results indicated that the variance among the treatment groups was homogeneous; therefore, the original data were used for subsequent statistical analysis. Data are presented as the mean ± standard error of five replicates.

RESULTS

Effects of KDP on growth parameters and MDA content under HT. Compared with the NT, HT significantly increased MDA accumulation in rice seedling leaves and reduced seedling height and biomass (Table 2). Compared with NT, the HT treatment significantly reduced seedling height, fresh weight per plant, and dry weight per plant by 12.7, 12.1, and 10.8%, respectively, and exhibited a higher MDA content (49.4%). Compared to HT, HT + KDP treatments significantly reduced MDA accumulation in leaves and increased plant height and biomass (Table 2). Among HT + KDP treatments, 0.3% KDP + HT showed the best results. Compared with HT treatment, seedling height, fresh weight per plant, and dry weight per plant of 0.3% KDP + HT significantly increased by 7.6, 10.6, and 10.2%, respectively, and MDA accumulation significantly decreased by 10.5%. Thus, HT stress limited rice seedling growth, while KDP reduced MDA accumulation and promoted plant growth.

Effects of foliar KDP on chlorophyll content and SPAD value under HT. Figure 2 shows that

Table 3. Loading value of each variable and the initial Eigen values and contribution rate of principal component 1 in different treatments

Indicator	Loading value
Seedling height (X_1)	0.988
Plant fresh weight (X_2)	0.995
Plant dry weight (X_3)	0.998
Malondialdehyde (X_4)	–0.943
Chlorophyll content (X_5)	0.985
Soil plant analysis development value (X_6)	0.994
Net photosynthetic rate (X_7)	0.996
Stomatal conductance (X_8)	0.989
Intercellular CO_2 concentration (X_9)	–0.876
Transpiration rate (X_{10})	0.982
Superoxide dismutase (X_{11})	0.973
Peroxidase (X_{12})	0.981
Catalase (X_{13})	0.964
Ascorbate peroxidase (X_{14})	0.952
O_2^- (X_{15})	–0.821
H_2O_2 (X_{16})	–0.899
Soluble protein (X_{17})	0.960
Proline (X_{18})	0.945
Soluble sugar (X_{19})	0.952
Sucrose (X_{20})	0.940
Nitrate reductase (X_{21})	0.932
Glutamine synthetase (X_{22})	0.926
Sucrose synthase (X_{23})	0.912
Sucrose phosphate synthase (X_{24})	0.852
Eigen value	21.456
Variance contribution rate	89.40%
Cumulative variance contribution rate	89.40%

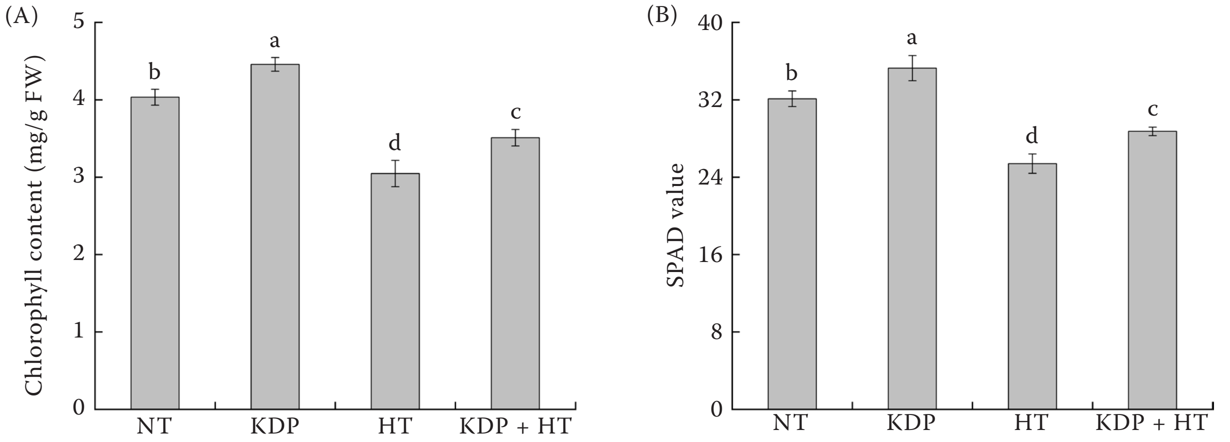

Figure 2. Effects of potassium dihydrogen phosphate (KDP) on (A) chlorophyll content and (B) SPAD value of rice seedling leaves under high temperature (HT) stress. NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress; FW – fresh weight. Different lowercase letters indicate significant differences among treatments according to Duncan's multiple range test at $P < 0.05$

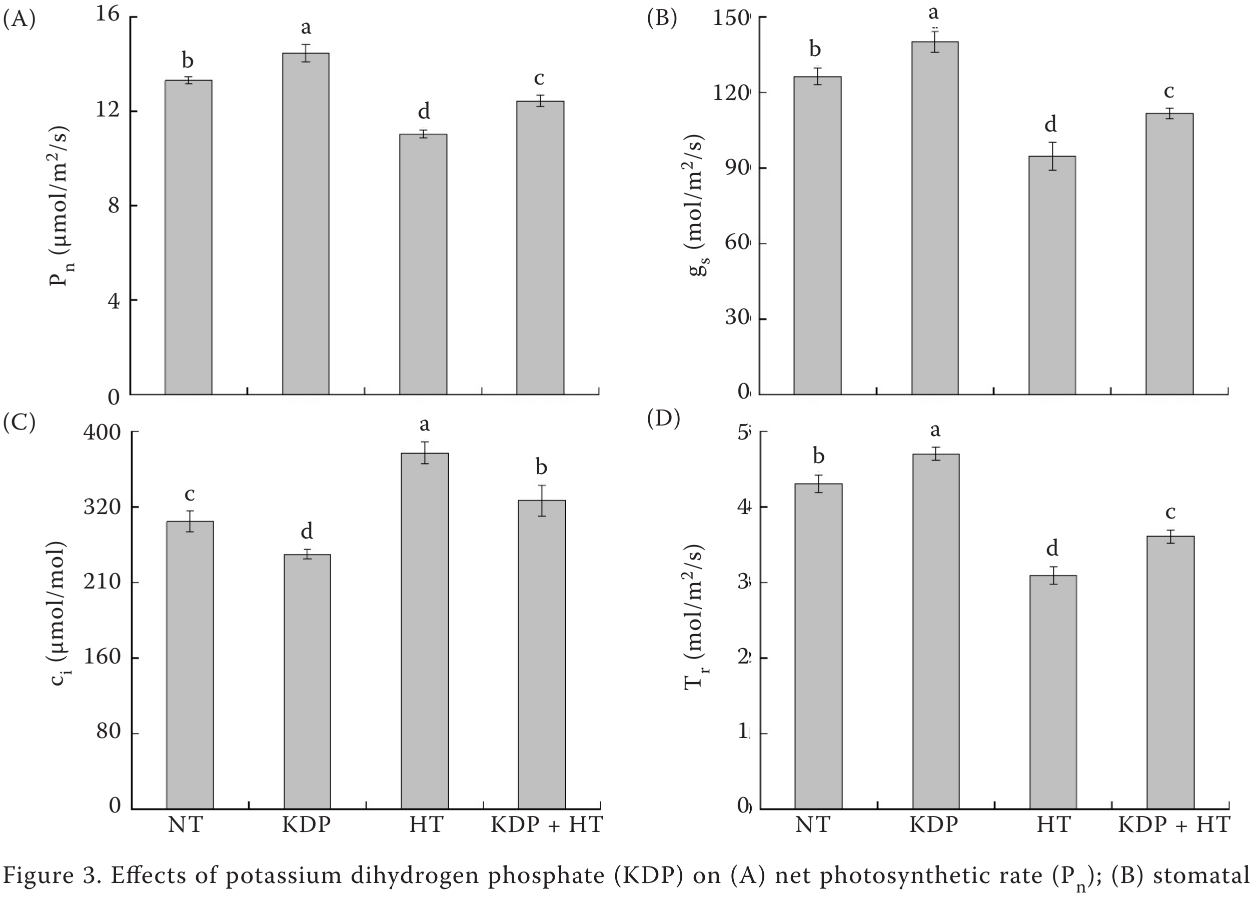

Figure 3. Effects of potassium dihydrogen phosphate (KDP) on (A) net photosynthetic rate (P_n); (B) stomatal conductance (g_s); (C) intercellular CO_2 concentration (c_i), and (D) transpiration rate (T_r) of rice seedling leaves under high temperature (HT) stress. NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress. Different lowercase letters indicate significant differences among treatments according to Duncan's multiple range test at $P < 0.05$

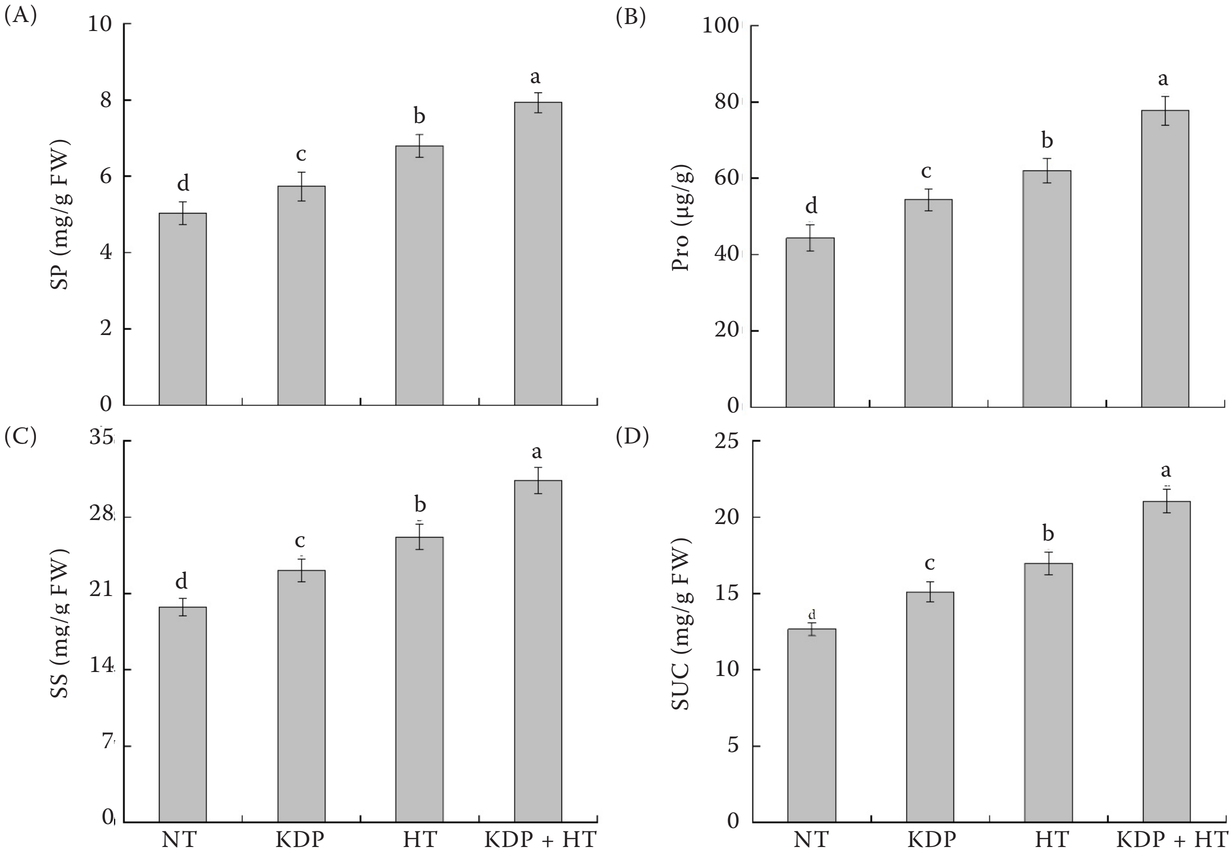

Figure 4. Effects of potassium dihydrogen phosphate (KDP) on (A) soluble protein (SP); (B) proline (Pro); (C) soluble sugar (SS), and (D) sucrose (SUC) of rice seedling leaves under high temperature (HT) stress. NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress; FW – fresh weight. Different lowercase letters indicate significant differences among treatments according to Duncan's multiple range test at $P < 0.05$

HT stress significantly reduced chlorophyll content and SPAD value in rice seedling leaves by 24.5% and 20.9%, respectively, compared with the NT treatment. KDP treatment significantly increased chlorophyll content and SPAD value. Compared with NT treatment, KDP treatment significantly increased chlorophyll content and SPAD value by 10.5% and 9.9%, respectively. KDP + HT significantly increased chlorophyll content and SPAD value by 15.2% and 13.1%, respectively, compared with the HT treatment. In summary, HT stress significantly reduced chlorophyll content and SPAD value in rice seedling leaves, whereas exogenous KDP treatment effectively alleviated HT-induced inhibition of chlorophyll synthesis and leaf greenness, significantly increasing chlorophyll content and SPAD value, demonstrating a clear HT-mitigating effect.

Effects of foliar KDP on photosynthetic parameters under HT. Compared with NT treatment, HT treatment significantly reduced P_n, g_s, and T_r in the leaves of rice seedlings by 17.0, 25.1, and 28.2%, while c_i significantly increased by 23.9% (Figure 3). Foliar KDP treatment significantly increased P_n, g_s, and T_r, and significantly reduced c_i. Specifically, compared with NT treatment, KDP treatment significantly increased P_n, g_s, and T_r by 10.5, 12.0, and 9.2%, respectively, while significantly decreasing c_i by 12.4%. Within high temperature stress treatments, compared with HT treatment, KDP + HT treatment significantly increased P_n, g_s, and T_r by 12.7, 18.0, and 16.7%, respectively, while significantly decreasing c_i by 13.4%. In conclusion, KDP treatment significantly improved the net photosynthetic rate, stomatal conductance, and transpiration rate of rice seedlings under HT stress. It effectively inhibited the increase in CO_2 concentration, thereby improving leaf photosynthetic performance.

Effects of foliar KDP on osmotic adjustment substances under HT. Compared with NT treatment, HT

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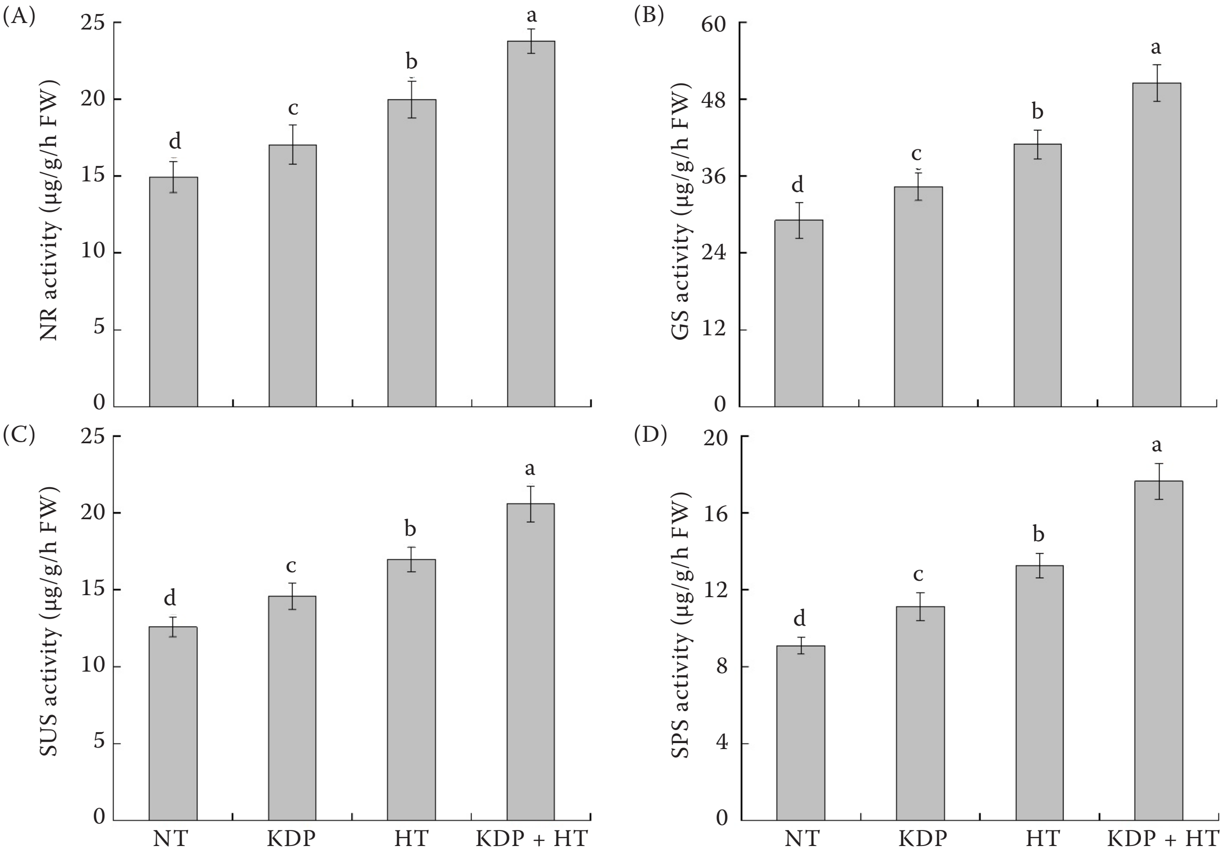

Figure 5. Effects of potassium dihydrogen phosphate (KDP) on (A) nitrate reductase (NR); (B) glutamine synthetase (GS); (C) sucrose synthase (SUS), and (D) sucrose phosphate synthase (SPS) activities of rice seedling leaves under high temperature (HT) stress. NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress; FW – fresh weight. Different lowercase letters indicate significant differences among treatments according to Duncan's multiple range test at $P < 0.05$

treatment caused rice seedling leaves to accumulate higher levels of SP (35.1%), Pro (39.8%), SS (32.6%), and SUC (33.9%) (Figure 4). KDP treatment further increased the accumulation of osmotic adjustment substances. Compared with NT treatment, KDP treatment significantly increased SP, Pro, SS, and SUC contents by 13.9, 22.6, 17.1, and 19.2%, respectively. Compared with HT treatment, KDP + HT treatment significantly increased SP, Pro, SS, and SUC contents by 16.7, 25.3, 19.7, and 24.0%, respectively. It can be seen that KDP treatment significantly increased the accumulation of osmotic adjustment substances in rice seedlings under HT stress, thereby enhancing the plant's osmotic adjustment capacity.

Effects of KDP on osmoregulation-related enzyme activities under HT. Compared with NT treatment, HT treatment caused rice seedling leaves to accumulate higher levels of NR (33.7%), GS (40.8%), SUS (35.0%), and SPS (45.8%) (Figure 5). KDP treatment further enhanced osmoregulation-related enzyme activities. Compared with NT treatment, KDP treatment significantly increased NR, GS, SUS, and SPS activities by 14.1, 18.0, 15.9, and 22.3%, respectively. Compared with HT treatment, KDP + HT treatment significantly increased NR, GS, SUS, and SPS activities by 19.0, 23.3, 21.2, and 32.9%, respectively. This showed that KDP treatment significantly enhanced the activities of osmoregulation-related enzymes in rice seedlings under HT stress, thereby improving the plant's osmotic adjustment and metabolic adaptation capacity.

Effects of KDP on antioxidant enzyme activities under HT. Compared with NT treatment, HT treatment caused rice seedling leaves to accumulate higher levels of SOD (49.2%), POD (58.0%), CAT (40.4%), and APX (30.9%) (Figure 6). KDP treatment further enhanced antioxidant enzyme activities. Compared with NT treatment, KDP treatment significantly increased SOD, POD,

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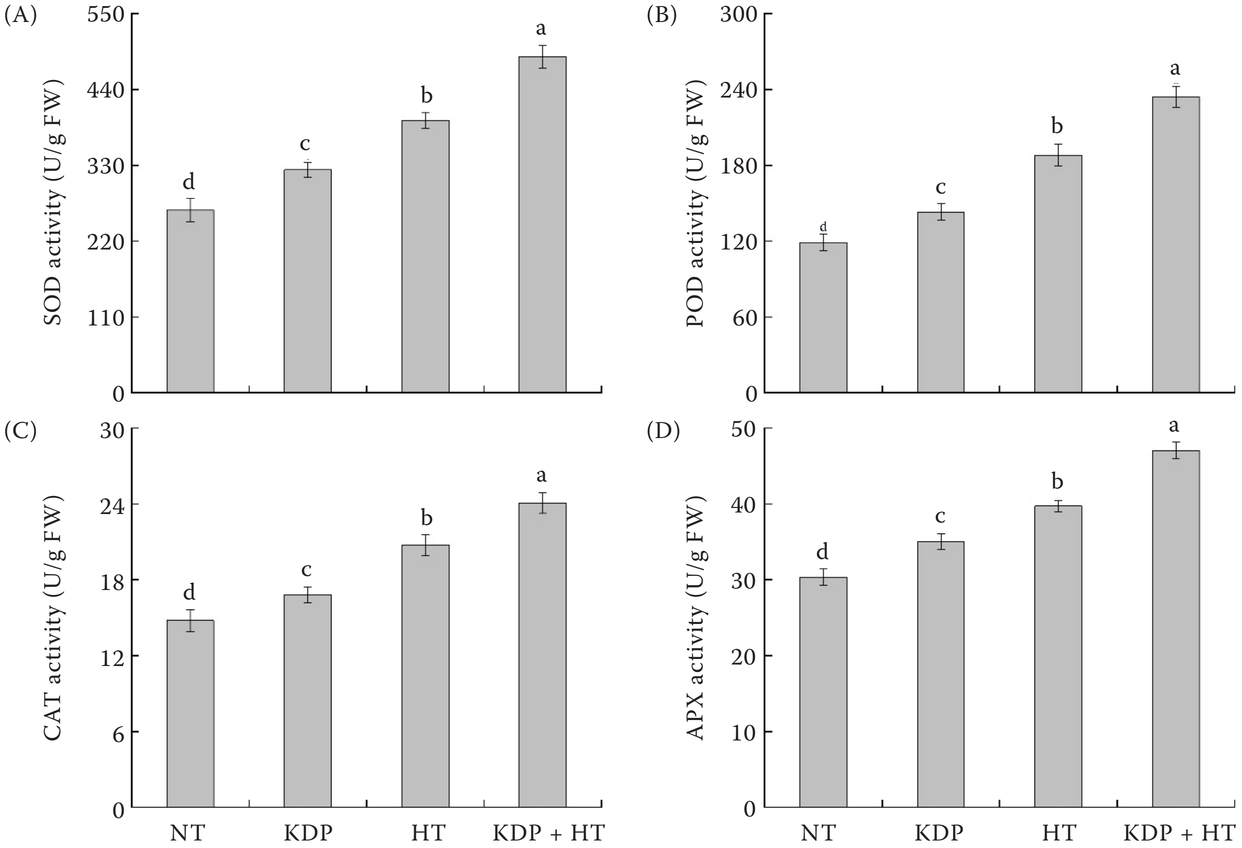

Figure 6. Effects of potassium dihydrogen phosphate (KDP) on (A) superoxide dismutase (SOD); (B) peroxidases (POD); (C) catalase (CAT); (D) ascorbate peroxidase (APX) activities of rice seedling leaves under high temperature (HT) stress. NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress; FW – fresh weight. Different lowercase letters indicate significant differences among treatments according to Duncan's multiple range test at $P < 0.05$

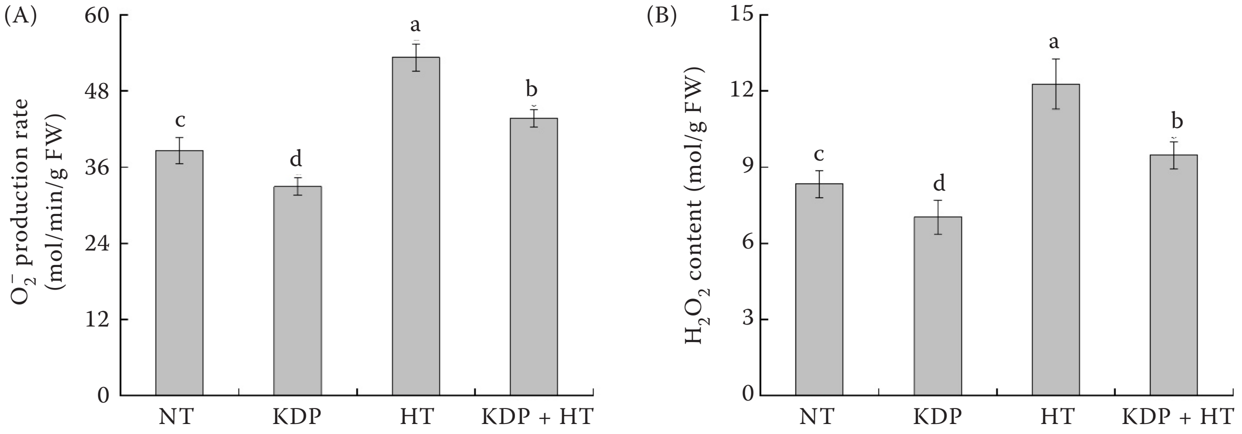

Figure 7. Effects of potassium dihydrogen phosphate (KDP) on (A) superoxide dismutase (SOD), and (B) peroxidases (POD) of rice seedling leaves under high temperature (HT) stress. NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress; FW – fresh weight. Different lowercase letters indicate significant differences among treatments according to Duncan's multiple range test at $P < 0.05$

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Table 4. Principal component score and comprehensive physiological activity index of different treatments

Treatment	Principal component 1 score	Comprehensive physiological activity index	Ranking
NT	1.42	1.27	2
KDP	2.18	1.95	1
HT	–3.05	–2.73	4
KDP + HT	–0.55	–0.49	3

NT – no KDP treated and no high temperature stress; KDP – 0.3% KDP treated with no high temperature stress; HT – no KDP treated and high temperature stress; KDP + HT – 0.3% KDP treated with high temperature stress

CAT, and APX activities by 22.0, 20.2, 13.8, and 15.4%, respectively. Compared with HT treatment, KDP + HT treatment significantly increased SOD, POD, CAT, and APX activities by 23.3, 24.5, 16.1, and 18.5%, respectively. Therefore, KDP treatment significantly enhanced the activities of key antioxidant enzymes in rice seedlings under HT stress, effectively improving the plant's oxidative stress defence capability.

Effects of KDP on O_2^- and H_2O_2 content under HT. Compared with NT treatment, HT treatment significantly increased the content of O_2^- and H_2O_2 in rice seedling leaves by 37.9% and 47.2%, respectively (Figure 7). KDP treatment significantly reduced O_2^- and H_2O_2 content. Compared with NT treatment, KDP treatment significantly reduced O_2^- and H_2O_2 content by 14.8% and 15.6%, respectively. Compared with HT treatment, KDP + HT treatment significantly reduced O_2^- and H_2O_2 content by 18.0% and 22.8%, respectively. In addition, KDP treatment effectively inhibited ROS accumulation in rice seedling leaves under HT stress, thereby alleviating oxidative damage.

Principal component extraction. To comprehensively evaluate the effects of different treatments on the physiological characteristics of rice seedling leaves, principal component analysis (PCA) was performed on 24 measured morphological and physiological indicators (Table 3). Based on the Eigen value > 1 criterion, only one principal component was extracted, with an Eigen value of 21.456 and a variance contribution of 89.40%, indicating that this component explains most of the total variation. The loading matrix of principal component 1 (Table 3) showed that indicators such as seedling height, fresh weight per plant, dry weight per plant, chlorophyll content, SPAD value, P_n, g_s, SOD, POD, CAT, APX, SP, Pro, SS, SUC, NR, GS, SUS, and SPS had high positive loadings (0.852–0.998) on principal component 1, while indicators such as MDA, O_2^-, and H_2O_2 had negative loadings (–0.943 to –0.821). The PCA provided an integrated assessment of treatment responses and supported the overall conclusion that KDP alleviated the adverse effects of HT stress on rice seedlings by enhancing photosynthetic capacity, antioxidant activity, and osmotic adjustment.

Principal component scores and comprehensive physiological activity index. Based on the principal

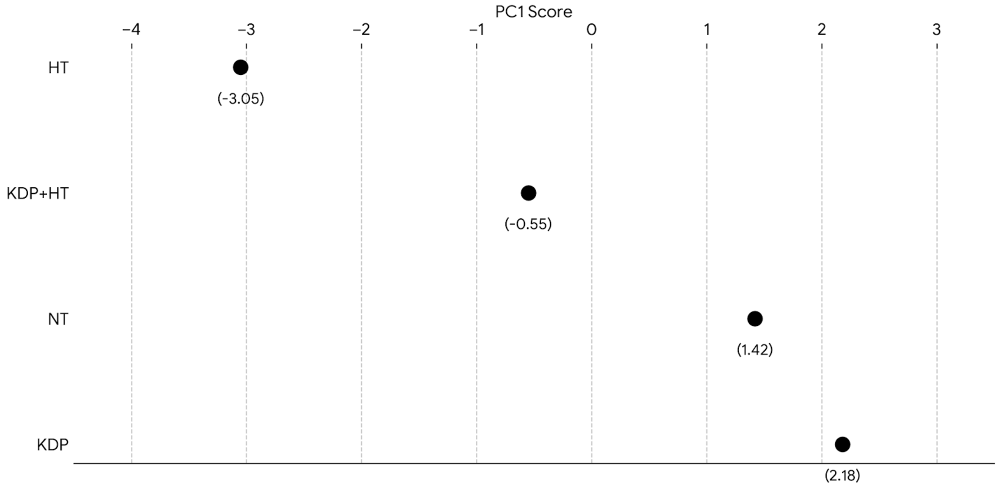

Figure 8. Distribution of principal component 1 scores of rice seedlings under normal temperature and high temperature stress with or without foliar potassium dihydrogen phosphate application

component score coefficients, the principal component 1 score for each treatment was calculated, and the comprehensive physiological activity index (F) was calculated using its variance contribution rate as the weighting coefficient, with the following formula:

$$\begin{gathered} F1 = 0.041X1 + 0.041X2 + 0.042X3 - 0.039X4 + \\ + 0.041X5 + 0.041X6 + 0.042X7 + 0.041X8 - \\ - 0.037X9 + 0.041X10 + 0.041X11 + 0.041X12 + \\ + 0.040X13 + 0.040X14 - 0.034X15 - 0.037X16 + \\ + 0.040X17 + 0.039X18 + 0.040X19 + 0.039X20 + \\ + 0.039X21 + 0.039X22 + 0.038X23 + 0.035X24 \\ F = 0.8940 \times F1 \end{gathered}$$

The comprehensive physiological activity index and ranking for each treatment are shown in Table 4. To facilitate visualisation of the PCA results, the distribution of the PC1 scores for all treatments is presented in supplementary Figure 8. The ranking based on the PC1 scores was consistent with the comprehensive physiological index, with KDP > NT > KDP + HT > HT. The ranking results were: KDP > NT > KDP + HT > HT. This indicates that KDP treatment promoted seedling growth and enhanced photosynthesis and antioxidant capacity, while HT treatment showed the lowest physiological activity; KDP + HT treatment still showed some regulation under HT stress.

DISCUSSION

Effects of KDP on the morphology and photosynthetic parameters of rice seedlings under HT stress. HT stress is an important abiotic stress factor that severely inhibits the growth and photosynthetic performance of rice seedlings, posing a major threat to rice production under global climate change. Morphological indicators such as plant height, fresh weight, and dry weight directly reflect plant growth status. At the same time, photosynthetic parameters, including chlorophyll content, SPAD value, P_n, g_s, and T_r, are core indicators of photosynthetic system functional integrity (Zuo et al. 2025). This study showed that, compared with normal temperature treatment, HT stress significantly inhibited rice seedling growth, reducing plant height by 12.7%, fresh weight by 12.1%, and dry weight by 10.8%. Simultaneously, HT decreased chlorophyll content by 24.5%, SPAD value by 20.9%, and significantly reduced P_n, g_s, and T_r by 17.0, 25.1, and 28.2%, respectively, while c_i increased by 23.9%. These results are consistent with existing research conclusions that HT stress damages chloroplast structure, impairs photosystem II reaction centres, ultimately leading to decreased photosynthetic capacity and growth retardation (Song et al. 2021, Kan et al. 2023).

Foliar spraying of KDP effectively alleviated the adverse effects of HT on rice seedling morphology and photosynthesis. Among the concentrations tested in this experiment, 0.3% KDP showed the most significant effect. Compared with the HT treatment, it increased rice seedling height, fresh weight, and dry weight by 7.6, 10.6, and 10.2%, respectively. Additionally, KDP + HT treatment significantly increased chlorophyll content (15.2%) and SPAD value (13.1%), enhanced P_n (12.7%), g_s (18.0%), and T_r (16.7%), while decreasing c_i (13.4%). The intrinsic mechanism underlying these improvement effects may be related to the dual nutritional functions of phosphorus and potassium contained in KDP. Phosphorus is an important component of ATP and chloroplast membranes; exogenous phosphorus application can stabilise photosynthetic membrane structure, promote photophosphorylation, and ensure energy supply for photosynthesis under HT stress. Potassium regulates stomatal movement, maintains appropriate stomatal conductance to facilitate CO_2 absorption, while activating various photosynthetic enzymes to enhance carbon assimilation efficiency. The results of this study are consistent with previous findings. Li et al. (2023) found that spraying KDP increased chlorophyll content and photosynthetic rate in wheat flag leaves under HT stress, while Yang et al. (2024) demonstrated that phosphorus application enhanced rice photosynthetic capacity by maintaining chloroplast integrity.

The phenomenon of increased c_i under HT stress indicates that the main reason for decreased photosynthetic rate at this time is non-stomatal limitation, such as damage to the photosynthetic apparatus and decreased enzyme activity, rather than insufficient CO_2 supply. After KDP + HT treatment, the net photosynthetic rate of rice seedlings increased while c_i decreased. This result demonstrates that it can effectively alleviate the aforementioned non-stomatal limitation by protecting the photosynthetic system. This conclusion is consistent with the research findings of Shangguan et al. (2000), who reported that nutrient supply can alleviate abiotic limitations induced by environmental stress. In summary, this study confirms that KDP can improve morphogenesis and photosynthetic performance of rice seedlings under HT stress by providing essential nutrients, stabilising photosynthetic structure, and regulating stomatal and non-stomatal processes.

Effects of KDP on antioxidant characteristics of rice seedlings under HT stress. Excessive production of ROS, such as O_2^- and H_2O_2, is a characteristic of HT stress, leading to oxidative damage to cell membranes, proteins, and nucleic acids. The plant antioxidant system, composed of enzymatic antioxidants (SOD, POD, CAT, and APX) and non-enzymatic antioxidants, plays a key role in scavenging excess ROS and maintaining cellular redox homeostasis. MDA is widely used to assess the degree of oxidative damage in plants. This study found that HT stress significantly increased O_2^-, H_2O_2, and MDA contents in rice seedling leaves by 37.9, 47.2, and 49.4%, respectively, while inducing compensatory increases in SOD (49.2%), POD (58.0%), CAT (40.4%), and APX (30.9%) activities. This indicates that rice seedlings can respond to HT stress by activating their own antioxidant defence system. Still, this activation is insufficient to eliminate the excessive ROS produced under HT stress, ultimately resulting in oxidative damage (Liu et al. 2022, Fathi et al. 2025).

Foliar spraying of KDP further enhanced the antioxidant capacity of crop seedlings under HT stress, thereby reducing oxidative damage (Lv et al. 2017). Compared with the HT treatment, the KDP + HT treatment significantly increased SOD, POD, CAT, and APX activities by 23.3, 24.5, 16.1, and 18.5%, respectively, while reducing O_2^-, H_2O_2, and MDA contents by 18.0, 22.8, and 10.5%, respectively. The enhancement of antioxidant enzyme activities may be related to the regulatory effects of phosphorus and potassium on plant metabolic processes: phosphorus participates in the synthesis of antioxidant enzymes and coenzymes. In contrast, potassium promotes the activation of antioxidant enzymes by maintaining their conformational stability. Cakmak (2005) emphasised that potassium application can effectively alleviate ROS accumulation in plants under stress conditions by increasing antioxidant enzyme activities. (Li et al. 2023) also found that KDP spraying maintained high SOD, POD, and CAT activities in wheat roots under HT stress, thereby reducing MDA accumulation.

The PCA results showed a significant negative correlation between antioxidant enzyme activities and MDA content, further confirming that KDP can alleviate oxidative damage by enhancing the plant's antioxidant defence system. This conclusion is consistent with the findings of Chen et al. (2024) and Zhang et al. (2025), who reported that phosphorus application alleviated cadmium-induced oxidative damage by increasing antioxidant enzyme activities. Furthermore, KDP reduces ROS levels in plants, protecting cell membranes from peroxidative damage and preventing ROS-induced damage to the photosynthetic apparatus, thereby creating a synergistic protective effect on plant growth and photosynthesis (Li et al. 2023). Therefore, KDP can alleviate oxidative stress by enhancing the antioxidant system's ROS-scavenging capacity, thereby improving the heat tolerance of rice seedlings.

Effects of KDP on osmotic adjustment substances and related enzyme activities in rice seedlings under HT stress. Osmotic adjustment is an important adaptive mechanism for plants to cope with HT stress, primarily through accumulating osmotic adjustment substances such as SP, Pro, SS, and SUC to maintain cell turgor, stabilise cell structure, and prevent water loss (Ahmad et al. 2021, Zubair et al. 2025). Additionally, nitrogen metabolism-related enzymes, including NR and GS, as well as sucrose metabolism-related enzymes, including SUS and SPS, play important roles in regulating the synthesis and accumulation of osmotic adjustment substances (Xu et al. 2023). The coordinated regulation of carbon and nitrogen metabolism plays a central role in stress adaptation. Enhanced NR and GS activities indicate improved nitrogen assimilation, providing substrates for amino acid and protein synthesis, while increased SUS and SPS activities promote sucrose metabolism and carbon allocation. The coordination between C and N metabolism ensures the synthesis of osmolytes and functional proteins, thereby enhancing cellular stability and stress tolerance under HT conditions. This study found that HT stress induced accumulation of SP (35.1%), Pro (39.8%), SS (32.6%), and SUC (33.9%) in rice seedling leaves, while increasing the activities of NR (33.7%), GS (40.8%), SUS (35.0%), and SPS (45.8%). This indicates that rice seedlings can enhance their osmotic adjustment capacity to cope with HT stress by accumulating osmotic adjustment substances and activating related metabolic enzymes.

Foliar spraying of KDP further enhanced the osmotic adjustment capacity of plants under HT stress by promoting the accumulation of osmotic adjustment substances and increasing the activities of related enzymes (Bolat et al. 2024). Compared with the HT treatment, KDP + HT treatment significantly increased SP, Pro, SS, and SUC contents by 16.7, 25.3, 19.7, and 24.0%, respectively, and increased NR, GS, SUS, and SPS activities by 19.0, 23.3, 21.2, and 32.9%, respectively. The promoting effect of KDP on osmotic substance accumulation may be related to potassium ions' regulatory effects on plant metabolic processes. Potassium ions can rapidly cross biological membranes, activate enzymes involved in protein and carbohydrate synthesis, thereby promoting the synthesis of soluble proteins and carbohydrates (Sardans and Peñuelas 2021).

The results of PCA showed significant positive correlations between osmotic adjustment substances, related enzyme activities, and seedling growth indicators. This indicates that KDP can improve rice seedlings' adaptability to HT stress by enhancing their osmotic adjustment capacity. This conclusion is consistent with the findings of Barbhuiya et al. (2024), who found that phosphorus application increased osmotic adjustment substances in rice, enhancing its drought resistance. Furthermore, the increase in NR and GS activities indicates that KDP can promote nitrogen uptake and assimilation by plants, providing sufficient nitrogen sources for the synthesis of osmotic substances and functional proteins, thereby enhancing stress tolerance (Sulaman et al. 2025). Therefore, KDP can enhance the osmotic adjustment capacity of rice seedlings under HT stress by regulating the synthesis of osmotic adjustment substances and the activities of related metabolic enzymes, thereby maintaining intracellular environmental homeostasis and improving stress tolerance.

Agronomic implications and limitations. Foliar application of KDP, particularly at 0.3%, is a practical, cost-effective strategy for mitigating heat stress during the early rice growth stage. However, as this study was conducted under controlled conditions using a single heat-sensitive genotype (YLY17), further field validation across diverse cultivars and environments is required. This study provides a foundation for future research; future studies should evaluate long-term yield responses in different cultivars with contrasting heat tolerance and optimise the KDP application regimes under fluctuating climatic conditions.

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