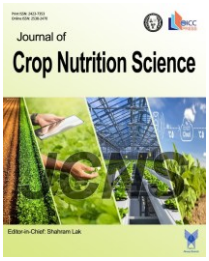

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Research Article

Protective Role of Sodium Nitroprusside (SNP) in Mitigating Chilling Stress Effects in Wheat: Nutrient Homeostasis and Photosynthetic Light Reactions

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Abstract

Background: Cold stress presents a serious challenge to global crop production, particularly affecting cereals such as wheat during early developmental stages. SNP enhances wheat stress tolerance by modulating nitric oxide signalling, improving antioxidant defences, growth, and yield.

Objectives: The present study aimed to explores the physiological impacts of cold stress on nutrient homeostasis and photosynthetic efficiency in wheat, with emphasis on the potential mitigating effects of sodium nitroprusside (SNP).

Methods: Wheat seedlings were grown under controlled conditions. The experiment was conducted using a completely randomized design with four treatments and ten replicates. The treatments included: (1) control, (2) cold stress, (3) SNP, (4) cold stress + SNP. Each replicate consisted of one pot containing ten plants.

Result: Cold stress significantly reduced shoot and root growth, impaired nutrient acquisition, and disrupted photosynthetic performance, as evidenced by altered OJIP fluorescence transients and declines in key JIP-test parameters. Cold treatment led to the formation of L^-, K^-, and J^- bands, indicating structural damage to photosystems and impaired electron transport. Nutrient uptake of essential elements such as N, P, K, Mg, and micronutrients declined notably under chilling conditions. However, SNP application significantly alleviated these detrimental effects, improving biomass accumulation, enhancing nutrient homeostasis, and partially restoring chloroplast electron transport efficiency. SNP-treated plants under cold stress exhibited higher quantum yields, better photosystem stability, and increased performance index (PItotal), suggesting enhanced resilience of the photosynthetic machinery.

Conclusions: These results support the role of nitric oxide as a central player in plant stress physiology and highlight the potential of SNP as an effective treatment to enhance cold tolerance in wheat. This work provides new insight into strategies for improving crop performance under low temperatures, contributing to more resilient agricultural systems in the face of climate variability.

Keywords: Chlorophyll a fluorescence, JIP-test, Mineral nutrition, Nitric oxide

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1. Background

Cold stress is a significant environmental factor that adversely affects agricultural production worldwide. This phenomenon occurs when plants are exposed to temperatures below their optimal growth range, leading to adverse physiological and biochemical effects (Wang et al., 2024). Cold stress can occur in various forms, including chilling (the exposure to non-freezing low temperatures) and freezing stress, each with distinct effects on plant growth, development, and yield (Yadav, 2010). The duration of exposure and the developmental stage of the plant play critical roles in determining the extent of damage. Younger seedlings are often more vulnerable to cold stress than mature plants, making timing crucial for successful cultivation (Soualiou et al., 2022). Globally, the impacts of cold stress on agriculturally sensitive crops such as wheat are profound. Cold stress can reduce germination rates, disrupt flowering processes, impair fruit and seed development, and ultimately lead to lower crop yields (Mesa et al., 2022). The physiological effects of cold stress on plants are complex. Exposure to chilling temperatures can lead to the production of reactive oxygen species (ROS), triggering oxidative stress and damaging cellular components. Additionally, cold stress impacts several important physiological processes in plants, including nutrient absorption and photosynthesis (Ritonga and Chen, 2020). Photosynthesis is one of the most important physiological processes that is negatively affected by chilling stress. Cold stress reduces the content of photosynthetic pigment content in plants. This reduction in chlorophyll content contributes significantly to the overall decline in photosynthetic efficiency under chilling stress (Xu et al., 2022). Chilling stress causes changes in chloroplast ultrastructure, often leading to the damage to thylakoid integrated protein complexes and electron carriers, and reduces the efficiency of the photosynthetic electron transport and light reaction (Wang et al., 2024). The chloroplast electron transport system is highly susceptible to chilling stress. Studies revealed that the primary target for chilling stress is the reaction center of photosystem II (PSII). Furthermore, under chilling stress, the diffusion of plastoquinone in the membranes is restricted, inhibiting the electron transport (Gururani et al., 2015). At the molecular level, chilling can cause the downregulation of light-harvesting complex genes of photosystems, altering the organization of the photosynthetic apparatus, leading to a decrease in photosynthetic light capture and quantum yield (Liu et al., 2022; Pu et al., 2024). Nutrient uptake is severely inhibited under cold conditions due to impairment of root growth and development, leading to reduced root length and exploration capacity (Hussain et al., 2018), decreased root hydraulic conductivity (Hassan et al., 2021), and reduced membrane permeability (Qari et al., 2022). Nutrient content of plants plays an important role in plant cold tolerance. For example, potassium can enhance cold tolerance by improving antioxidant capacity, regulating osmotic potential, and reducing electrolyte leakage (Wang et al., 2013). Limitation in nutrient acquisition affects overall plant metabolism, as essential elements are critical for maintaining cellular functions under stress. For instance, cold stress decreases magnesium uptake, which in turn reduces chlorophyll synthesis and further exacerbates photosynthesis efficiency (Qari et al., 2022). Sodium nitroprusside (SNP), serves as an exogenous nitric oxide (NO) donor in plants. NO functions as a key signaling molecule that mediates numerous physiological processes, including growth, development, and stress responses (Zhang et al., 2024). The primary role of NO in plant stress responses is triggering a cascade of physiological and biochemical responses that enhance stress tolerance. These responses include improvements in water relations, maintenance of membrane integrity, regulation of osmotic balance, enhancement of antioxidant defense systems, and modulation of gene expression related to stress adaptation (Kaya et al., 2024; Yildiz et al., 2020). Through these pathways, SNP helps mitigate stress-induced damage and promote plant survival under challenging conditions. The beneficial effects of SNP application have been observed across various plant species and crops, making it a promising tool for sustainable agriculture in the face of increasing environmental challenges due to climate change (Acosta-Motos et al., 2020). It has been reported that the SNP treatment maintains or enhances photosynthetic efficiency under stress conditions by improving chlorophyll content, gas exchange parameters, photosystem structure and functionality, quantum yields of photosystem II, and electron transfer efficiency (Marques et al., 2023; Vital et al., 2019; Mirzaei Chegeni et al., 2024). In addition, numerous studies have demonstrated the beneficial role of SNP in enhancing nutrient uptake and maintaining ion homeostasis in plants under adverse environmental conditions (Al-Jarah et al., 2019; Zangani et al., 2023). Wheat (*Triticum aestivum* L.) is one of the most important crops worldwide, providing a major source of food for the global population. Its adaptability to a wide range of climatic conditions has enabled its cultivation across diverse regions. However, it remains vulnerable to various abiotic stresses, particularly cold stress during early growth stages in temperate climates. Cold stress can severely affect wheat by reducing seed germination, impairing seedling establishment, limiting nutrient uptake, and suppressing photosynthetic capacity, leading

to diminished crop productivity (Hassan et al., 2021). Understanding the physiological and biochemical responses of wheat to cold stress has become a critical area of research for ensuring food security and sustainable agriculture.

2. Objectives

The present study aims to investigate the impact of chilling stress on photosynthesis and particularly the impacts on photosynthetic light reactions and nutrient uptake in wheat and to examine the potential protective role of SNP in alleviating the adverse effects of cold stress in wheat seedlings.

3. Materials and methods

3.1. Plant materials and growing conditions

Seeds of Wheat were sourced from the Plant Improvement Institute of Iran. After sterilization (immersion in 70% ethanol for 2 minutes, followed by a 5-minute soak in a 6% sodium hypochlorite solution and rinsed with distilled water), seeds were sown in plastic pots (20 cm diameter, 25 cm height) filled with a mixture of peat moss and perlite (2:1 v/v). The pots were placed in a growth room with controlled conditions of temperature (25 ± 2°C), humidity (60 ± 5%), and a photoperiod of 16 h light 8 h dark. After germination, the seedlings were thinned to ten per pot. Each pot was irrigated at two-day intervals and received a half-strength Hoagland solution weekly.

3.2. Experimental setup, cold and SNP treatment

The experiment was conducted using a completely randomized design with four treatments and ten replicates. The treatments were: (1) control, (2) cold stress, (3) SNP, (4) cold stress +SNP. Each replicate consisted of one pot containing ten plants. The SNP treatment was applied 15 days after sowing to the SNP and SNP + Cold treatment twice a week at 50 µM concentration. The control and cold stress treatments received distilled water. The cold treatment was initiated 30 days after sowing by transferring the pots from the cold stress and SNP + cold stress treatments into a growth chamber at 10 ° C for 8 hours each night (after dark) and transferring them back to the growth room at the start of the day (turning the light on). Sampling was conducted 15 days after the imposition of cold stress (45 days after sowing).

3.3. Measurement of growth indices

Root and shoot fresh weight and height were determined at harvest. To calculate the dry weights, samples were dried at 72 °C for 48 hours, and the dry weight was determined using digital scale.

3.4. Determination of nutrient content

The determination of nutrient content was carried out based on Guo et al. (2007). After digestion of the samples with HNO_3-$HClO_4$ (2:1 v/v), the nutrient content was assessed by induced plasma atomic emission spectroscopy (ICP-AES) instrument (Agilent 5100, California, USA).

3.5. Measurement of polyphasic chlorophyll a fluorescence curve and fast fluorescence induction kinetics (JIP-test)

The OJIP fluorescence transient, also known as the Kautsky effect, is a characteristic pattern of chlorophyll fluorescence emitted by photosynthetic organisms when they transition from darkness to light (Kalami et al., 2025). The study of chlorophyll fluorescence became a fundamental tool in photosynthesis research, allowing the exploration of the kinetics of the fast fluorescence rise during dark-light transitions. The OJIP fluorescence transient is characterized by a polyphasic rise in chlorophyll fluorescence when dark-adapted photosynthetic samples are exposed to saturating light. This rise follows a distinct pattern with four key inflection points: O (origin, minimum fluorescence at 50 µs), J (at approximately 2 ms), I (at approximately 30 ms), and P (peak, maximum fluorescence at 200-300 ms). The measurement of chlorophyll (Chl) a fluorescence was performed on dark adapted fully expanded attached leaves at room temperature. A plant efficiency analyzer (Handy PEA, Hansatech instrument Ltd, Lynn, UK) was used to measure Chl a fluorescence at a high resolution of 10 μsec. The obtained data were analyzed by the biolyzer HP software (the fluorescence analyzing program by the bioenergetics laboratory, University of Geneva, Geneva, Switzerland). Table 1 presents the definitions and calculations of JIP-test parameters extracted from the chlorophyll a fluorescent transient.

3.6. Statistical Analysis

Analysis of variance and mean comparisons were done via SPSS (Ver.22) software and Duncan multiple range test at 5% probability level.

4. Results and discussion

4.1. Growth indices and nutrient content

The imposed cold stress significantly ($p \leq 0.05$) affected the plants' growth parameters (Table 2). Shoot and root fresh weights as well as shoot and root dry weights, were significantly reduced by cold stress by 34%, 43%, 46%, and 50%, respectively. The shoot and root length were also negatively affected by cold by 28.3% and 28.2%, respectively. The application of SNP significantly improved the adverse impacts induced by cold stress and

Table 1. Abbreviations, formulae, and glossary of selected JIP-test parameters.

Parameter	Explanation
Data extracted from OJIP transient curve	
F_0	Minimal fluorescence, when all PSII RCs are open
F_{300} µs	Fluorescence intensity at 300 µs
F_J	Fluorescence intensity at the J-step (2 ms) of OJIP
F_I	Fluorescence intensity at the I-step (30 ms) of OJIP
F_P (F_M)	Maximal recorded fluorescence intensity, at the peak P of OJIP. All PSII RCs are closed.
Ft	Fluorescence at time t after onset of actinic illumination
Parameters calculated based on data extracted from OJIP transient	
VJ = (FJ−Fo)/(Fm−Fo)	Relative variable fluorescence intensity at the J-step
VI = (FI−Fo)/(Fm−Fm)	Relative variable fluorescence intensity at the I-step
VK = (FK−Fo)/(Fm−Fo)	Relative variable fluorescence intensity at the K-step
Mo = 4(F300µs−Fo)/(Fm − Fo)	Approximated initial slope of the fluorescence transient
Flux ratios of PSII	
$\varphi P_o = TR_o/ABS = [1-(F_o/F_m)]$	Quantum yield for primary photochemistry(at t = F_o)
$\psi_{o=} ET_o/TR_o = (1-V_J)$	Quantum yield for electron transfer fromQ_A to Q_B(at t = F_o)
$\varphi E_o = ET_o/ABS = [1-(F_o/F_m)]\psi_o$	Quantum yield for electron transport (at t = F_o)
Fv/Fm	Quantum yield of Photosystem II
N	Turn over number of Q_A
Flux ratios of PS I	
$\varphi R_o = RE/ABS = TR_o/ABS\ (1-V_I)$	Quantum yield for reduction of end electron acceptors at the PSI acceptor side (at t = F_o)
δRo = REo/ETo = (1−VI)/(1–VJ)	The efficiency with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side
Vitality indexes (performance indexes) and their components	
$\varphi P_o /(1- \varphi P_o) = [1 - (F_0 / F_M)]/ 1-[1 - (F_0 / F_M)]$	Efficiencies of light reactions
$\psi_o /(1- \psi_o) = (1 - V_J)/1-(1 - V_J)$	Efficiencies of redox reactions
$\delta R_o /1- \delta R_o = \varphi P_o \times (VJ/M0) = (ABS/RC)^{-1}$	Efficiency of PSI to reduce the last electron acceptors
$\gamma RC/(1 - \gamma RC) = (1-F_0/F_M)/M_0/V_J$	Density of the active reaction centers
$PI_{total} = (\varphi P_o/1- \varphi P_o)\times (\psi_o /1- \psi_o)\times (\delta R_o /1- \delta R_o)\times (\gamma RC /1- \gamma RC)$	The performance index for energy conservation from photons absorbed by PSII until the reduction of PSI end electron acceptors

significantly increased the growth parameters in wheat plants. Under cold stress, the uptake of essential nutrients, including N, P, K, Mg, Ca, Zn, Fe, Cu, and Mn was significantly ($p \leq 0.05$) decreased under cold stress (Table 3).

Exogenous application of SNP significantly improved the nutrient homeostasis of wheat seedlings under cold stress. Cold stress represents one of the most significant environmental challenges for plants, affecting their growth, development, and survival through several physiological and biochemical limitations. Based on our results, a significant decrease in uptake of both macronutrients (N, P, K) and micronutrients (Ca, Mg, Fe, Cu, Mn, Zn), each playing important roles in plant metabolism, was observed under cold stress. Consistent with our results, Yoon et al. (2019) reported a decline in nutrient content of spinach plants in response to exposure to cold stress condition. Cold stress significantly impairs

nutrient uptake in plants through several physiological mechanisms. One of the main impacts is the reduction in root hydraulic conductivity, which severely limits water uptake and subsequently affects nutrient transport to shoots. The disruption in water uptake limits nutrient absorption rates and restricts nutrient transport throughout the plant (Panda et al., 2021). Membrane damage is another important factor affecting nutrient uptake under cold stress. Low temperatures affect membrane structure and fluidity, negatively affecting the properties necessary for nutrient and water uptake (Qari et al., 2022). The plasma membrane proton pump, essential for nutrient transport across membranes, is particularly affected by cold temperatures (Reda et al., 2025). Cold stress significantly impairs root growth and development by reducing root length, biomass. This reduction in root volume severely limits the plant's ability to access water and nutrients from the soil (Qari et al., 2022). Our findings revealed that root biomass (fresh and dry weight) and length of wheat plants were significantly affected by cold treatment, which contributes to the reduced nutrient absorption in wheat plants. Reduction in essential nutrient uptake can minimize the shoot growth rate, as observed in the present study. Furthermore, a decrease in nutrient content, such as K, Mg, Ca, Zn, Fe, Cu, and Mn, which are important to the structure and functionality of the photosynthetic apparatus, can lead to photosynthetic dysfunction. SNP has emerged as an effective protective agent against cold tolerance when applied exogenously. It works by releasing nitric oxide (NO), which acts as a signaling molecule, triggering various protective mechanisms in plants (Wang et al., 2024).

In our experiments, application of SNP alleviated the negative impacts of cold treatment on growth parameters, nutrient homeostasis, and photosynthetic machinery in wheat plants. SNP treatment enhances root function and nutrient absorption capacity under stress conditions (Dong et al., 2023). It has been reported that SNP improves the uptake and concentration of several nutrients such as K, Ca, Mg, and NO3 in plants by stimulating the selective transporters (Amiri et al, 2015; Dong et al., 2023). SNP also supports nitrogen metabolism under stress, promoting plant growth (Kim et al., 2022). These are consistent with the higher content of nutrients in the wheat plant treated with SNP before the cold treatment.

4.2. Chlorophyll a fluorescence transient curves

The impact of cold stress and SNP on the chlorophyll fluorescence transient curve is presented in Fig. 1. Cold stress led to an increase in O step, followed by a decline in fluorescence intensity at J, I, and P step. However, the SNP application diminishes the changes in fluorescence intensity of stressed plants at the O, J, I, and P phases. In the Fig. 2, the L-band was calculated by the normalization of the relative fluorescence between O and K steps [WOK= (Ft−Fo)/(FK−Fo)].

The K-band was visualized by the normalization of fluorescence intensity between O and J steps [WOJ= (Ft−Fo)/(FJ−Fo)]. To visualize the J-band, fluorescence intensity between O and I steps was normalized [WOI= (Ft−Fo)/(FI−Fo)].

Table 2. The growth indices of wheat plants under control, cold stress, SNP treatment, and cold stress + SNP treatment. Values are the mean of ten independent replications. Different letters indicate significant difference (P≤ 0.05)

Treatment	Shoot fresh weight(g)	Root fresh weight(g)	Shoot dry weight(g)	Root dry weight(g)	Shoot length (cm)	Root length (cm)
Control	26.41 ± 2.4 a	9.23 ± 0.99a	3.56 ± 0.45 a	0.95 ± 0.17a	10.43 ± 1.13 a	7.91 ± 1.43a
Cold	17.44 ± 0.93 d	5.25 ± 0.51c	1.92 ± 0.49c	0.47 ± 0.99 d	7.48 ±1.16b	5.68 ± 0.75 c
SNP	24.53 ± 0.79 b	9.44 ± 0.76 a	3.98 ± 0.14 a	0.78 ± 0.11 b	9.17 ± 1.3a	6.44 ±0.58 a
Cold+SNP	20.94 ± 1.44c	7.62 ± 0.93 b	2.91 ± 0.33 b	0.61 ± 0.16 c	7.94 ± 1.69 b	6.04 ± 0.57 b

Table 3. Changes in nutrient content of wheat leaves under control, cold stress, SNP treatment, and cold stress + SNP treatment. Values are the mean of ten independent replications. Different letters indicate significant difference (P≤ 0.05)

Nutrient (mg/Kg DW)	Content			
	Control	Cold	SNP	Cold + SNP
N	4935.3 ± 129.3 a	4028.82 ± 163.5 c	4965.22 ± 153.2 a	4553.2 ± 121.2 b
P	4325.3 ± 132.7 a	3563.53 ± 114.5 c	4237.2 ± 173.4 a	3727.5 ± 151.3 b
K	4005.5 ± 117.4 a	2631.06 ± 105.6c	3985.3 ± 123.3 a	2872.8 ± 133.2 b
Ca	362.6 ± 110.1 b	388.69 ± 95.4a	3585.3 ± 152.5c	3655.8 ± 143.5 b
Mg	1273.2 ± 115.5 a	1032.78 ± 24.3 c	1143.1 ± 136.2 a	1143.8 ± 126.4 b
Zn	52.7 ± 7.7 a	35.43 ± 6.4c	49.6 ± 2.4 a	44 ± 6.1 b
Fe	43.4 ± 3.2 a	31.02 ± 1.4c	45.2 ± 1.7 a	39.4 ± 4.2 b
Cu	55.3 ± 4.1 b	48.39 ± 2.8 c	57.2 ± 2.2 a	51.7 ± 5.6 b
Mn	24.4 ± 4.5 b	20.02± 4.3c	25.4 ± 1.5 a	22.4 ± 3.2b

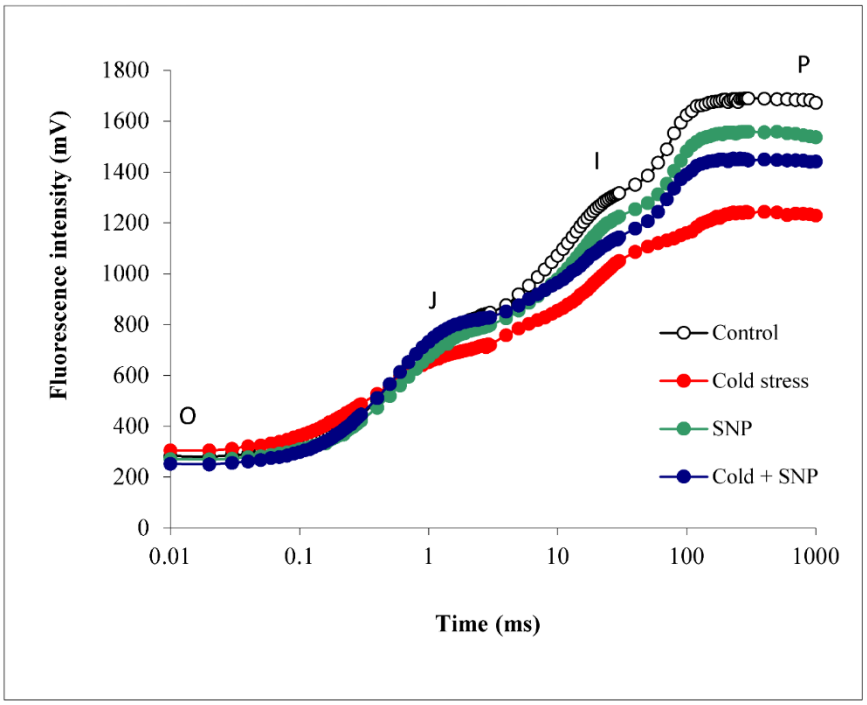

Figure 1. Fast fluorescence induction curves of wheat seedlings under control, cold stress, SNP treatment, and cold stress + SNP treatment

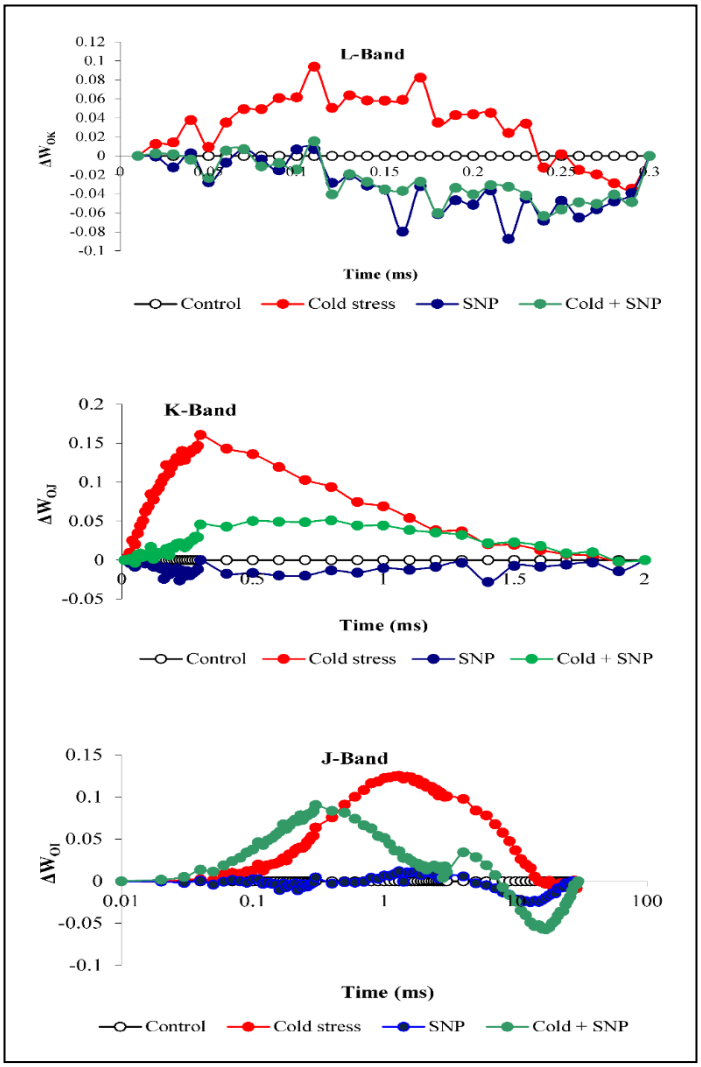

Figure 2. Effects of control, cold stress, SNP treatment, and cold stress + SNP treatment on the formation of L-band, K-band, J-band in wheat seedlings

Our findings revealed a cold treatment led to the formation of a distinct L-band, whereas other treatments did not cause the L-band formation. The K-band was also formed by cold stress; however, the application of SNP attenuated the K-band under cold stress conditions. Similarly, the cold stress and cold stress + SNP treatments exhibited the formation of the J-band.

However, the intensity of J-band was lowered by SNP treatment under cold stress, compared to cold stress alone. Our results demonstrated that the cold stress impaired the structural stability of photosynthetic machinery, PSII and PSI functionality, and electron transport, leading to a decrease in quantum yield and photosynthetic performance indices.

The OJIP transient curve was sensitive to cold stress, and the shape of the curve was flatter compared to the control group, with an increase in fluorescence intensity at the O step, followed by a reduction in J, I, and P steps. At O step (FO), reaction centers (RC) are in an open position, and an increase in FO indicates the inactivation of RCs (Nezamivand Cheginiet al., 2024). Lower rate of fluorescence at J, I and P step suggests an impairment in photochemical efficiency, electron transport rate, and reduction of PSI final electron acceptors, which will be discussed in detail (Ghotbi-Ravandi et al., 2016). Our results revealed a distinct rise and formation of L-band, K-band, and J-band under cold stress. The formation of L-band represents the dissociation of thylakoid structures and lower energetic connectivity between PSII units (Chen et al., 2021). The K-band is linked to the inhibition of the oxygen-evolving complex (OEC) (Kalaji et al., 2016). The J-band is associated with the rate of electron flow from QA to the QB. The formation of the J-band reflects the disruption of electron delivery to the QB site (Toth et al., 2007). Our results revealed a distinct rise and formation of L-band, K-band, and J-band under cold stress. These results suggest that under cold stress, the structure and function of PSII units are hindered, affecting photon absorption, water splitting, and electron delivery to the plastoquinone pool (Borjian et al., 2025). It has been reported that SNP treatment can maintain photosynthetic function under cold stress via several mechanisms. SNP can help preserve chlorophyll content and improve photochemical efficiency (Liang et al., 2018). This can justify the better OJIP transient curves and L, K, and J bands in SNP-treated wheat plants under cold stress.

4.3. JIP test parameters

The imposed cold stress significantly reduced the quantum yield for primary photochemistry (φPo), the quantum yield for electron transfer from QA to QB (ψO), the quantum yield for electron transport (φEo), the quantum yield (φRo) and the efficiency (δRo) for the reduction of end electron acceptors on the PSI acceptor side, quantum yield (FV/FM), and the number of QA turnovers (N) (Fig. 3).

The (φRo) and (δRo) parameters were most susceptible to the cold stress. The SNP treatment was able to attenuate the adverse effects of cold stress on these flux ratios of the electron transport system. The impact of cold stress and SNP treatment on key photosynthetic efficiencies is presented in Fig. 4.

Cold stress significantly decreased the efficiency of the light reactions [φPo/(1−φPo)], the redox reactions [ψo/(1−ψo)], and the efficiency of PSI in reducing the final electron acceptors [δRo/(1−δRo)], and the density of active reaction centers [γRC/(1−γRC)]. These changes ultimately led to a significant ($p \leq 0.05$) reduction in the performance index [PI total = (φPo/1- φPo)× (ψo /1- ψo)× (δRo /1- δRo)× (γRC /1- γRC)] by 78%. The SNP treatment effectively improved all parameters contributing to the PItotal of wheat seedlings under Cold stress, resulting in a higher performance of the photosynthetic apparatus of Cold-treated plants. Our findings demonstrated that values of φPO, FV/FM, ψO, φEO, φRO, and δRo have been negatively affected by cold stress in wheat plants. These reductions indicate the disruptions in quantum yield of photochemistry, quantum yield, and efficiency of electron transport in the electron transfer chain and reduction of electron acceptors in the PSI acceptor site (Ghotbi-Ravandi et al., 2014). Based on our results, the structural integrity and function of both PSII and PSI were hindered by cold stress. The performance index (PItotal) is the most sensitive marker of the status of photosynthetic apparatus functionality and overall plant health (Ghotbi-Ravandi et al., 2019). Our results demonstrated that the constituents of PI were negatively affected by cold stress, leading to a significant reduction in PI parameter. SNP stimulates the higher rates of φPO, FV/FM, and improves the PsbA (D1) protein repair pathway, contributing to maintaining PSII recovery and functionality under cold stress. In addition, SNP enhances ferredoxin-mediated NADP photoprotection of PSI (Feng et al, 2021). SNP treatment also helps to maintain thylakoid membranes' integrity and stability, which is crucial for the proper functions of membrane-localized electron carriers involved in the electron transfer chain (Fan et al., 2015). In line with our results, Dong et al. (2018) reported that the application of SNP, significantly improved the photochemical efficiency of photosystem II, photochemical quenching, photosystem II photochemical efficiency and non-photochemical quenching of walnut plants under cold stress.

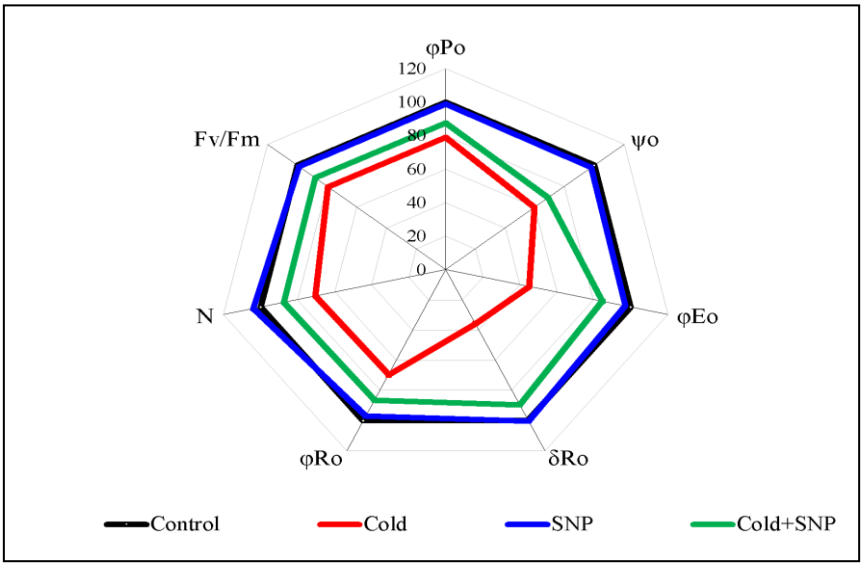

Figure 3. Effects of control, cold stress, SNP treatment, and cold stress + SNP treatment on the changes (%) of JIP test parameters deduced from chlorophyll a fluorescence transient in wheat leaves

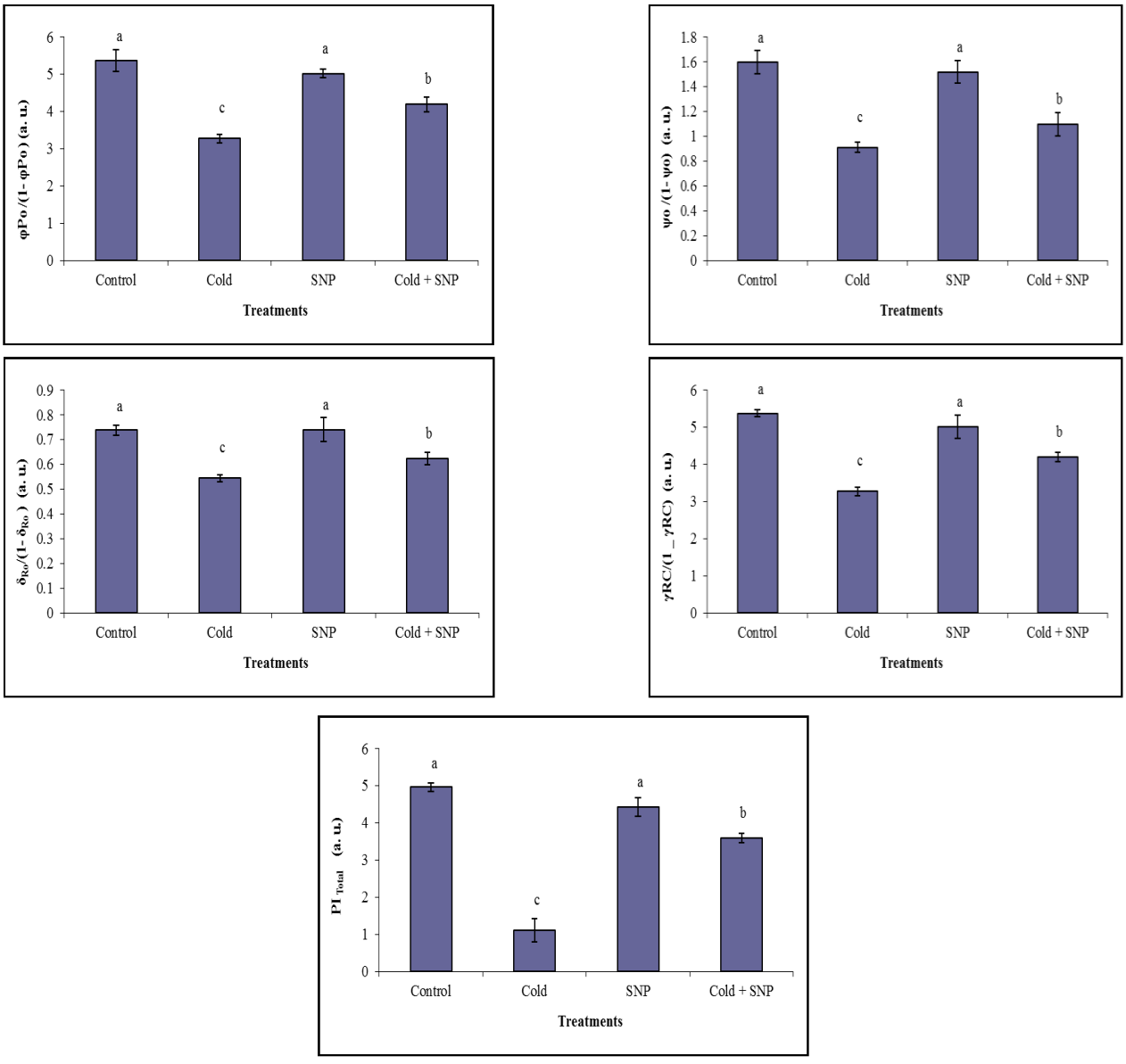

Figure 4. Effects of control, cold stress, SNP treatment, and cold stress + SNP treatment on performance indices and their constituents in wheat seedlings. Values are the mean of ten independent replications. Different letters indicate significant difference (P≤ 0.05)

5. Conclusion

Cold stress imposes complex physiological limitations on wheat, reducing growth, disrupting nutrient uptake, and significantly impairing photosynthetic light reactions and electron transport. Our findings demonstrate that cold stress leads to chloroplast dysfunction, particularly damaging both PSII and PSI performance and reducing overall photosynthetic efficiency. In parallel, the nutrient content of wheat seedlings declined significantly under cold conditions, further exacerbating the stress effects. However, exogenous application of SNP proved to be a promising approach for alleviating cold-induced damage. SNP treatment improved plant growth, restored essential nutrient uptake, and preserved the structure and function of the photosynthetic apparatus under cold stress. It reduced the formation of stress-induced fluorescence bands and significantly enhanced chlorophyll fluorescence parameters and performance indices. The finding of the present study demonstrates the role of SNP in improving nutrient uptake and protecting photosynthetic machinery. These findings suggest that SNP application could serve as an effective agronomic strategy to improve wheat cold tolerance. Future studies may focus on optimizing SNP application rates and timings and exploring their synergistic effects with other protective agents to develop applicable and efficient protocols.

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Authors Contribution

All authors are equally involved.

Conflict of interests

Authors declared no conflict of interest.

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