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Growth and physiological responses of wheat plants to polyphosphate and orthophosphate fertilizers supply under salt stress

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ABSTRACT

Phosphorus (P) availability is significantly reduced under salt-stress conditions. Appropriate P fertilization can effectively alleviate its negative impact on plant growth and development. This study examines the impact of two P fertilizer forms (Ortho-B and Poly-B) on durum wheat tolerance to salinity ($S1 = 3$ dS m^{-1} and $S2 = 6$ dS m^{-1}) under hydroponic conditions. A completely randomized design with six treatments and five replicates per treatment was used. At S2 salinity level, Poly-B outperformed Ortho-B ($p < 0.05$) by increasing shoot and root dry weights by 867 % and 127 %, respectively. It also improved root morphology (length, surface area, and crossings) by up to 353 %, enhanced chlorophyll content by 41 %, and raised shoot phosphorus content by 20 %, indicating superior stress resilience. These findings suggest that polyphosphate fertilizers are more effective in mitigating salt stress effects in wheat. Future long-term field studies are recommended to confirm these results and assess their agronomic applicability at scale.

1. Introduction

Salinity has been considered a major constraint on plant growth and productivity worldwide, mainly in arid and semi-arid regions (FAO, 2024). It limits water uptake and causes ion toxicity which severely affects crucial physiological and biochemical processes in plants (Kumari et al., 2022). Durum wheat (*Triticum durum* Desf.) is a key cereal crop of considerable economic and agronomic importance, primarily grown across the Mediterranean region. Morocco is the third-largest wheat-producing country in terms of cultivated area, with an average annual yield of around 24 million quintals between 2018 and 2021 (Rezzouk et al., 2022). Importantly, approximately 45 % of wheat production in Morocco takes place in arid and semi-arid zones, which are frequently exposed to salinity stress. In this regard, wheat growth is severely affected by high salt concentrations, leading to reduced germination rates, stunted root and shoot growth (Loudari et al., 2023), impaired photosynthesis (Loudari et al., 2022b), and lower biomass accumulation (Robin et al., 2016), ultimately decreasing grain yield (Merwad, 2020).

Plant roots serve as the primary sensors for detecting elevated concentrations of Na^{+} and Cl^{-} ions in the surrounding growth medium, triggering a series of adaptive response including changes in root length, surface area, root hair density, and xylem vessel development, which contribute to ion exclusion and compartmentalization (Robin et al., 2016). Numerous studies have been conducted on the changes in root morphology under salt stress (Loudari et al., 2022a; Demiral, 2017; Robin et al., 2016), and the results showed that the roots adapt to ensure efficient absorption of water and nutrients and subsequently transport them efficiently to the leaves. Additionally, research on different plant species under varying degrees of salinity has shown that salt stress can lead to nutrient deficiencies, which can affect the spatial architecture of the roots (Merwad, 2020).

To mitigate the negative effects of salinity on plant growth, it is important to develop and adopt sustainable strategies to optimize the growing conditions, including nutrient availability under salt-stress conditions (Shabala and Munns, 2017). Phosphorus (P) is the second most essential nutrient for plant growth and development after Nitrogen (N), playing a critical role in energy transfer and cell division (Demiral, 2017). However, P availability can be limited under salinity due to its interaction with other ions in the soil-plant system (Khan et al., 2018;

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Belouchrani et al., 2020). Indeed, when plants do not have sufficient P, they often exhibit stunted growth, reduced root development, and poor flowering or fruiting (Carstensen et al., 2018). Additionally, the leaves may turn a dark green color and become brittle or curl at the edges which could severely affect photosynthesis (Kalaji et al., 2018). Thus, while P deficiency can be a significant limiting factor for plant growth and crop production, adequate P fertilization is essential for maintaining healthy and productive plants mainly under salt-stress conditions (Khan et al., 2018; Mohamed et al., 2021). Different studies have shown that the combined effect of salinity and P on plant growth can be either synergistic or antagonistic depending on specific experimental conditions and plant species like wheat (Loudari et al., 2022a, 2022b, 2023), common bean (Mohamed et al., 2021), sorghum (Belouchrani et al., 2020), tomato (Loudari et al., 2020), as well as quinoa, sugar beet, and red pepper (Bouras et al., 2021, 2022, 2024). However, phosphorus (P) deficiency has been shown to intensify the adverse effects of salinity stress on plant development (Mohamed et al., 2021). Indeed, improving nutrient management practices can also help to improve crop production under stressful conditions (Merwad, 2020).

Hydroponics has gained popularity in recent years as it allows for more efficient and sustainable agriculture, particularly in areas where arable land is limited (Saha et al., 2021). While these systems may not fully replicate the complexity of field soils—where phosphorus fixation, microbial interactions, and soil structure influence nutrient dynamics—they offer a highly controlled environment to isolate specific stress responses (Wang et al., 2016, El-Mejjaouy et al., 2022). Although extrapolation to soil-based agriculture requires caution and further field validation, the insights gained provide a valuable foundation for understanding key physiological traits related to P-use efficiency under salt stress and can inform future breeding and agronomic strategies. Few studies have explored strategies to mitigate this interactive effect in hydroponics, using nutrient solutions with adjusted salinity levels and targeted phosphorus supplementation (Loudari et al., 2020).

Phosphorus is commonly supplied to crops in the form of orthophosphate (OrthoP) fertilizers (Chtouki et al., 2022). It has been observed that plants absorb less than 30 % of the applied OrthoP fertilizers (Campos et al., 2018). This low P uptake can be attributed to the low mobility of P and its strong adsorption and precipitation in the soil matrix, particularly in soils with high concentrations of metal ions, such as Fe^{3+} and Al^{3+} (McBeath, 2006).

Polyphosphates (PolyP) are a group of condensed compounds that consist of multiple phosphate molecules linked together (Gao et al., 2020). They have several benefits over traditional OrthoP fertilizers in agriculture (Loudari et al., 2022 a,b; Khourchi et al., 2022 a,b). The slow and continuous release property of PolyP can reduce P losses through leaching, which can improve P uptake by plants, reduce the frequency of fertilizer application (Kulakovskaya et al., 2012). Furthermore, PolyP fertilizers are characterized by their chelation capacity of some micronutrients such as Iron, Manganese and Zinc (Wang et al., 2019). However, research on the use of PolyP fertilizers in agriculture is still in its early stages, and several challenges need to be addressed before widespread adoption can occur (Khourchi et al., 2023). In addition, the use of PolyP fertilizers under salt stress could be a promising area of research to improve crop production in saline conditions (Loudari et al., 2022 a,b). Studies in conditions without salinity stress have shown that the application of PolyP fertilizers can improve several growth parameters and the yield of chickpeas plants (Chtouki et al., 2022), wheat (Khourchi et al., 2022a; El-Mejjaouy et al., 2022) and Maize plants (Gao et al., 2020). Similarly, in wheat plants grown in saline soil, the application of PolyP fertilizers increased root morphological, biomass, antioxidant capacity and photosynthetic performance, leading to a significant increase in shoot and root mineral contents and optimal physiological performance under salinity stress conditions (Loudari et al., 2022a, b; 2023). This beneficial effect of PolyP might be due to the improvement of plant nutrient uptake and the alleviation of nutrient imbalances caused by salinity.

Although the beneficial role of P in alleviating salt stress has been well documented, the influence of different soluble P fertilizer forms—specifically orthophosphates and polyphosphates—remains insufficiently explored, particularly in hydroponic systems where nutrient dynamics differ from soil-based cultivation. Considering the limited information available on this topic, we hypothesize that the form of soluble P fertilizer (Ortho-B vs. Poly-B) can significantly affect P uptake efficiency and physiological performance of plants under saline conditions. The present study aimed to evaluate the short-term effects of these two P forms on the growth, nutrient acquisition, and photosynthetic function of durum wheat (*Triticum durum*) subjected to increasing salinity levels in a controlled hydroponic environment.

2. Material and methods

2.1. Plant material and growth conditions

Wheat seeds (*Triticum durum* var KARIM) were used in this experiment. Karim cultivar is known for its adaptation to the bour and irrigated zones, tolerance to rust and *Septoria* and precocity. It was provided by SONACOS (National Seeds Corporation Commercialization, Morocco). Under regulated temperature (23 °C) and total darkness, wheat seeds were germinated in peat. Seedlings with comparable size were placed in ambient conditions with a temperature of 23 ± 2 °C and 18 ± 2 °C during the day and at night, respectively. The daily photoperiod was 16 h. Distilled water was used to irrigate the plants. Seedlings were transferred fifteen days after sowing (DAS) to plastic containers. Each container (with nine seedlings) was filled with 6 L of half-concentrated modified nutritional solution formulated to meet wheat-specific requirements, following established protocols for hydroponic wheat culture (Hoagland and Arnon, 1950, Singh et al., 2019) without any treatment considered as a plant adaptation medium. The nutrient solution consists of the following composition: Nitrogen (N) at 210 ppm, Potassium (K) at 234 ppm, Calcium at 200.39 ppm, Magnesium at 49 ppm, Copper at 0.02 ppm, Manganese at 0.5 ppm, Iron at 2.8 ppm, Zinc at 0.48 ppm, Boron at 0.45 ppm, and Molybdenum at 0.0106 ppm (Hoagland and Arnon, 1950, Singh et al., 2019).

As *durum wheat* is a medium-demanding crop in P and K (Ozturk et al., 2005), the dose of 30 ppm of P is the optimal dose of P under normal conditions (without salt stress) according to the COMIFER approach (French Committee for the Study and Development of Reasoned Fertilization), beyond which additional fertilization does not result in significant yield improvement (COMIFER, 2009). Besides, different studies suggested that the availability of P is reduced under salinity. Hence, in a preliminary laboratory trial, we decided to increase the P dose to test the effect on plants exposed to different salinity levels. The 45 ppm P dose revealed positive contrasted responses. Indeed, at a concentration of 45 ppm, P was added to the solution as hydrosoluble P fertilizers: Ortho-B and Poly-B. Ortho-B is an orthophosphate-based fertilizer comprising 62 % P_2O_5 entirely in the form of orthophosphates, whereas Poly-B is a short-chain linear polyphosphate fertilizer containing 47 % P_2O_5, exclusively as tripolyphosphates. Seedlings were exposed to salt stress five days later, with two treatments (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}). The control treatment (S0) corresponds to the baseline EC (S0 = 1.53 dS.m-1) of the complete nutrient solution, ensuring adequate nutrient supply without additional salt stress. A true zero-salinity treatment was not included, as it would involve nutrient omission, potentially introducing nutrient-deficiency stress and confounding the interpretation of salinity-specific effects. EC was measured using an EC meter. The pH level of the solution was daily measured. The KOH and H_2SO_4 reagents were added to adjust the pH to 5.5. Each container's nutrition solution was changed once every five days. To minimize the eventual effect of the surrounding environment, the containers were fully randomized and relocated. Plant growth was monitored until 35 days after sowing (DAS), corresponding to stage BBCH 29 under our experimental conditions. Chlorophyll *a* fluorescence, absorbance and reflectance with some related parameters and indexes, root morphological parameters, biomass and mineral content were analyzed.

2.2. Chlorophyll content index

The chlorophyll content index (CCI) was measured by a non-destructive instrument: chlorophyll meter SPAD-502 (Konica Minolta). Fully mature and expanded functional leaves were used for measurement (the third leaf counted from the top). The CCI was measured at 35 DAS from the middle part of 15 independent leaves kept in dark for 1 min before measurement.

2.3. Leaf chlorophyll a fluorescence

Before the measurements, wheat plants were kept in the dark for 15 min. At least, 20 measurements were taken for each treatment from fully mature and functional independent leaves (the third leaf counted from the top) using a handheld fluorometer (Handy PEA+, Hansatech instruments). A single 1 s light pulse was generated by an array of six light-emitting diodes (peak 650 nm) to guarantee the closure of all PSII reaction centers (the excitation intensity reaches 3000 μmol s^{-1} m^{-1}). A typical chlorophyll fluorescence curve was obtained. This curve is known as the OJIP fluorescence curve with three distinct phases (OJ, JI, and IP) that represent different light reduction reactions. This curve has been utilized to indicate the photosynthetic apparatus because each phase corresponds to the reduction of a different electron chain transporter (Strasser et al., 2004). The following fluorescence parameter was estimated from the OJIP fluorescence transient obtained during the first-second illumination:

Performance index (PI_{tot})

$$PI_{tot} = [\gamma_o/(1-\gamma_o)].[\varphi_{Po}/(1-\varphi_{Po})].[\psi_o/(1-\psi_o)].\ [\delta_{Ro}/(1-\delta_{Ro})]$$

Where:

- φ_{Po} is the maximum quantum yield of primary photochemistry (at t = 0) which corresponds to the trapping efficiency of the PSII reaction centers of an absorbed photon, φ_{Po} is expressed as:

$$\varphi_{Po} = 1-(F_0/F_M) = F_V/F_M$$

Where:

F_0 corresponds to the initial Chl *a* fluorescence.
F_M corresponds to the maximum Chl *a* fluorescence.
F_V corresponds to the maximum variable Chl fluorescence.

- $\gamma_o/(1-\gamma_o)$ is identical to the ratio of reaction centers and the absorbance (RC/ABS) estimated by JIP phase.
- ψ_o (=$1-V_J$) is the probability that the energy of an exciton trapped by the reaction centers (RC) of the PSII is used for the transport of electrons beyond Q_A.
- $\delta_{Ro} = (1-V_I)/(1-V_J)$ indicates the efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end electron acceptors.

2.4. Leaf spectral reflectance

In our experiment, leaf spectral response was measured using CI-710S SpectraVue Leaf version 0.9.26.0 (CID Bio Science, Inc. Felix Instruments – Applied Food Science) from the middle part of five fully mature and functional independent leaves (the third leaf counted from the top). The leaf spectral response was measured at 35 DAS. SpectraVue Leaf measures the light transmission, absorption, and reflectance in a large range of wavelengths covering the visible and Near Infra-Red (NIR). Based on the data collected, different indexes were calculated using the equations below:

Normalized Difference Vegetation Index (*NDVI)*:

$$NDVI= (R_{800} - R_{680}) / (R_{800} + R_{680})$$

Chlorophyll Normalized Difference (*CNDVI)*:

$$CNDVI = (R_{750} - R_{705}) / (R_{750} + R_{705})$$

Photochemical Reflection Index (*PRI)*:

$$PRI= (R_{531} - R_{570}) / (R_{531} + R_{570})$$

Where: R refers to reflectance, and the subscripts refer to a specific wavelength.

2.5. Biomass parameters

Shoots and roots were carefully washed and oven-dried at 75 °C for 48 h, until constant shoot dry weight (SDW) and root dry weight (RDW) were achieved. Five independent replicates per treatment were considered.

2.6. Roots morphology parameters

Roots were carefully washed and spread over a plastic box filled with distilled water (1.5–2 cm deep). Roots were scanned using an Epson Perfection LA2400 scanner. The obtained root images were analyzed using WinRHIZO™ image analyzing software (Regent Instructions, Quebec, Canada) to determine the total root length (RL), root surface area (RSA), and root crossings defined as the number of visible intersections among roots within the scanned image, serve as an indicator of root system complexity and spatial density. Five independent replicates per treatment were considered.

2.7. Mineral analysis

Elemental concentrations of P, K and Na, were determined on a dry-weight basis of Five independent replicates per treatment, using Inductively Coupled Plasma Optical Emission Spectrometry (Agilent 5110 ICP-OES, USA).

2.8. Statistical analysis

The effects of P-treatment, salinity, and their interaction were evaluated using a two-way analysis of variance (ANOVA). Pairwise comparisons were performed via DUNCAN's multiple range test, executed via the agricolae package in R version 4.4.1. at a 95 % confidence level. Different letters in figures (a, b, c …) express significant differences.

3. Results

3.1. Biomass parameters

A significant reduction in root dry weight (RDW) was observed in plants subjected to salinity stress. The effect of salinity on RDW was more pronounced at S2 (6 dS m^{-1}) in plants grown with Ortho-B fertilizer (Fig. 1A). However, the results showed that plants exhibited a significant difference in RDW between plants grown with both P sources, where Poly-B significantly increased root dry weight by 80 %, 54 %, and 127 %, respectively, at S0, S1 and S2 salinity levels compared to plants grown in Ortho-B (Fig. 1A). In Fig. 1B, the results showed that under all salinity levels, plants grown in both P sources showed significant differences in SDW. However, plants grown in Poly-B showed a significant performance as it increased SDW by 62 %, 508 % and 867 %, respectively, at S0, S1 and S2 salinity levels compared to plants grown in nutrient medium with Ortho-B fertilizer (Fig. 1B). The root-shoot ratio (R/Sh ratio) was calculated, and the results are presented in Fig. 1C. This ratio increased significantly under salt stress, and plants grown in

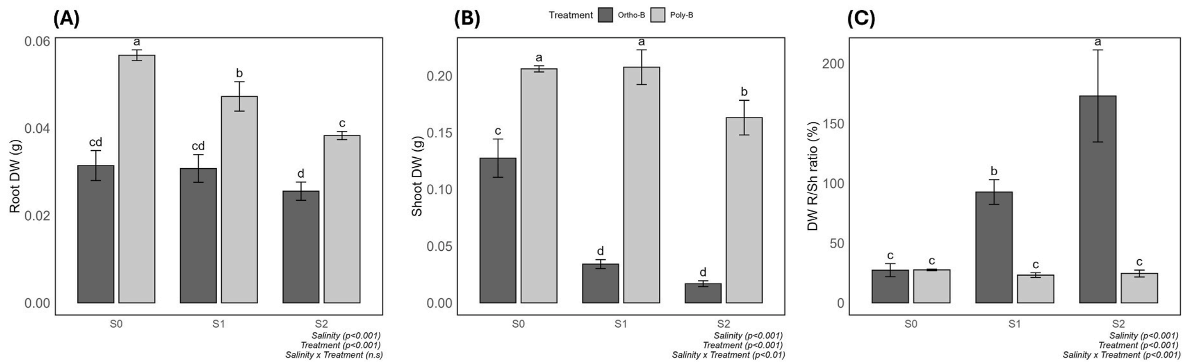

Fig. 1. The interactive effect of Salinity (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) and different soluble P-fertilizers (Poly-B and Ortho-B) on the root dry weight **(A)**, shoot dry weight **(B)** and root shoot ratio (R/Sh ratio) **(C)**. S0: initial electrical conductivity of the nutrient solution (non-saline conditions). Five independent replicates per treatment were considered for the statistical analysis. A two-way analysis of variance (ANOVA) and DUNCAN's multiple range test were performed and executed via the agricolae package in R version 4.4.1. Treatments having a different letter(s) are significantly different at the 5 % level.

medium with Ortho-B showed a significant increase in R/Sh ratio (Fig. 1C).

3.2. Chlorophyll content index

Significant differences in chlorophyll content index (CCI) measurements were observed in salt-stressed plants (Fig. 2). After 35 DAS, plants cultivated with Ortho-B under salinity conditions exhibited significantly lower Chlorophyll Content Index (CCI) values, with reductions of 30 % at S1 and 23 % at S2 compared to the S0 salinity level. However, plants grown in Poly-B medium source showed an increase in CCI by 24 % and 16 % under S1 and S2 conditions, respectively, compared to S0 level. Furthermore, Poly-B fertilizer showed a positive effect compared to Ortho-B fertilizer with an increase in CCI parameter by 55 %, 68 % and 41 % at S0, S1 and S2 levels, respectively.

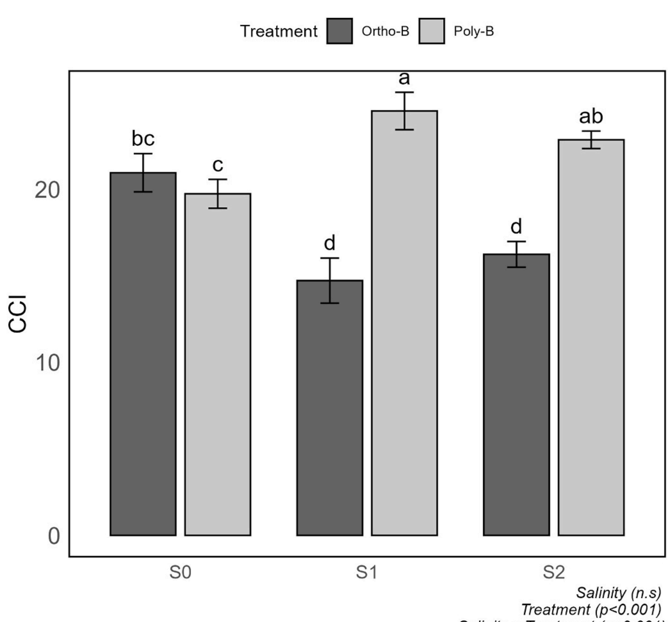

Fig. 2. The interactive effect of Salinity (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) and different soluble P-fertilizers (Poly-B and Ortho-B) on chlorphyll content index. S0: initial electrical conductivity of the nutrient solution (non-saline conditions). 15 measurements were considered for the statistical analysis. A two-way analysis of variance (ANOVA) and DUNCAN's multiple range test were performed and executed via the agricolae package in R version 4.4.1. Treatments having a different letter(s) are significantly different at the 5 % level.

3.3. Chl a fluorescence curve: OJIP transient

The chlorophyll *a* fluorescence (Chl*a*F) transients recorded from all treatments displayed the characteristic OJIP curve when plotted on a logarithmic timescale. The OJIP transient was divided to two phases: photochemical phase O–J and a thermal phase J–I–P (Strasser et al., 2004). These phases reflect three different reduction processes of the electron transport chain (Schansker et al., 2003; Strasser et al., 2004; Stirbet, 2012; Kalaji et al., 2017). The O-J phase of the curve reflects the reduction of the first electron acceptor, Quinone A (Q_A), while the J-I phase represents the reduction of the plastoquinone pool including plastoquinone, cytochrome, and plastocyanin. The I-P phase shows an increase in Chlorophyll *a* fluorescence (Chl*a*F) that is attributed to the reduction of photosystem I transporters (Schansker et al., 2005). In our experiment, the fluorescence yield, such as J, I and P steps of OJIP transitions measured in plants cultivated in Ortho-B form, was gradually quenched when the level of salinity was increased from 3 to 6 dS m^{-1} compared to control S0 (Fig. 3B). However, no significant effect was observed in plants grown in the medium with Poly-B fertilizer (Fig. 3A). Inhibitory effect of salt stress on PSII photochemistry and electron transport activity observed in plant grown in medium with Ortho-B was significant at S2 condition (Fig. 3B) and the decrease of F_M indicates a block in the electron transport to Q_A- (Krause and Weis, 1991) and a development of non-radiative dissipation of the excited states of PSII antennae chlorophylls.

3.4. Performance Index (PI tot)

The total performance index (PI_{total}), which integrates the overall efficiency of the photosynthetic apparatus including both PSII and PSI electron transport, declined significantly with increasing salinity levels. This reduction was particularly pronounced in plants supplied with Ortho-B, where PI_{total} exhibited a significant decrease of approximately 99 % compared to plants grown under non-saline conditions (Fig. 3C), indicating a severe impairment of the photosynthetic electron transport chain under salinity stress.

3.5. Spectral reflectance curve

Spectral reflectance curves are shown in Fig. 4. The reflectance spectra obtained between 300 and 500 nm did not display any significant differences between the P sources fertilizers. Nonetheless, significant differences were observed among the fertilized plants in the region of 500–600 nm when exposed to increasing salinity levels. Under non-saline conditions (S0), plants treated with Ortho-B exhibited higher reflectance values compared to those receiving Poly-B. This pattern persisted at both moderate (S1) and high (S2) salinity levels, where Poly-

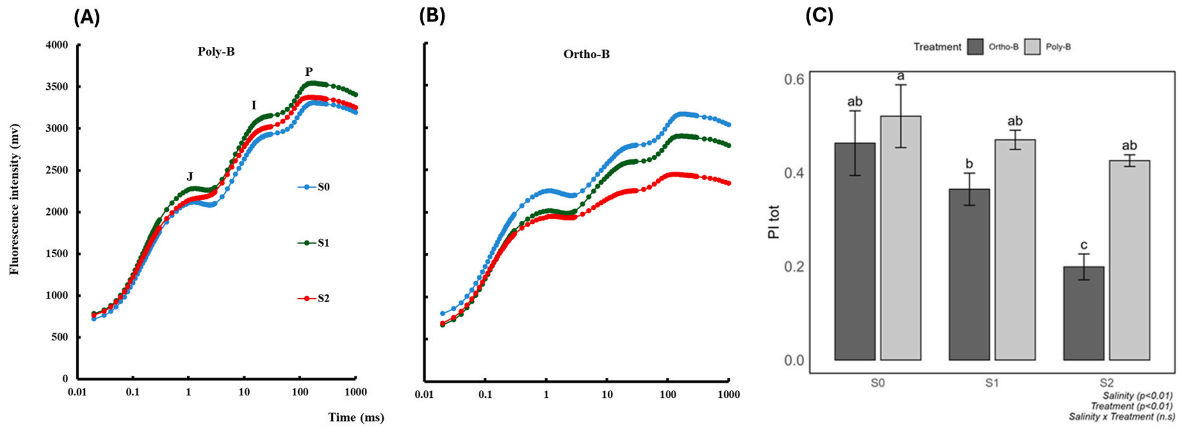

Fig. 3. The effect of different soluble P-fertilizers on the typical Chlorophyll *a* polyphasic fluorescence curve known as OJIP transient, under non-saline conditions (S0), and salt stress level at: S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) for Poly-B **(A)** and Ortho-B **(B)** fertilizers and the parameter photosynthetic performance (PI_{tot}) **(C)**. The transients are graphed on a logarithmic time scale, and the JIP test uses the marked time points to compute structural and functional parameters. The signals used include fluorescence intensity Fo (measured at 20 μs), fluorescence intensities F_J (measured at 2 ms) and F_I (measured at 30 ms), and maximal fluorescence intensity F_M. Each transient on the graph and PI_{tot} represents an average of 15 measurements. Statistical analysis was performed using a two-way analysis of variance (ANOVA) and DUNCAN's multiple range test and executed via the agricolae package in R version 4.4.1Treatments having different letter(s) are significantly different at the 5 % level.

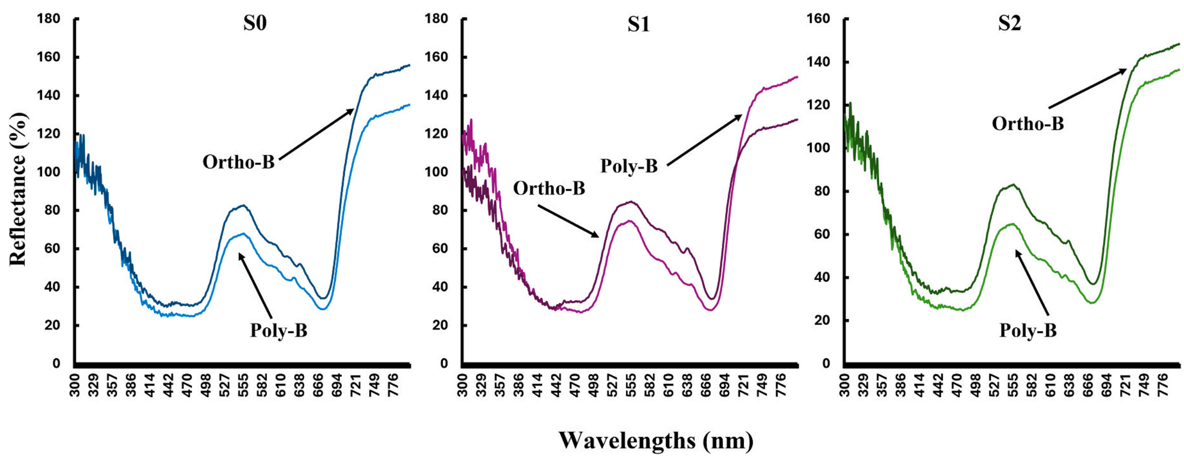

Fig. 4. Effect of different soluble P-fertilizers (Poly-B and Ortho-B) on the Leaf Spectral reflectance within the 300–800 nm wavelength range under non-saline conditions (S0) (A), salt stress levels (S1 = 3 dS m^{-1}, S2 = 6 dS m^{-1}) of wheat plants grown in hydroponic conditions.

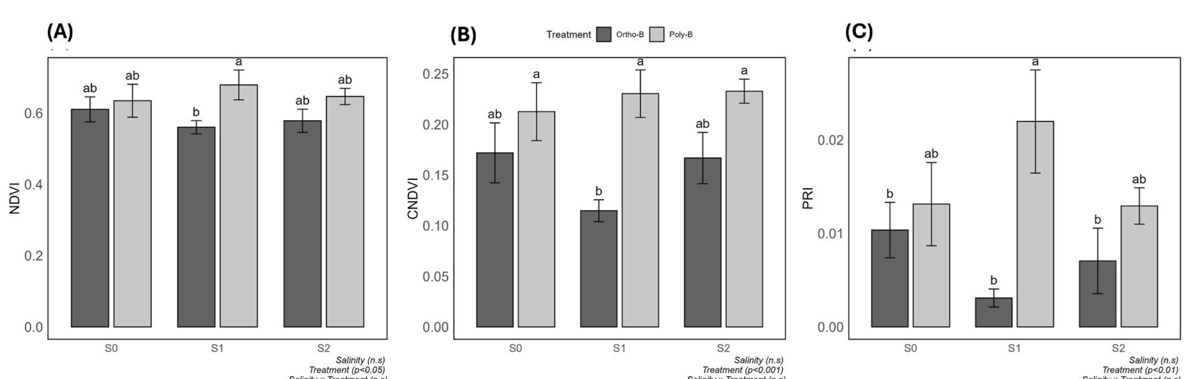

Fig. 5. The interactive effect of Salinity (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) and different soluble P-fertilizers (Poly-B and Ortho-B) on calculated reflectance indices of wheat plants grown under hydroponic conditions: Normalized Difference Vegetation Index (NDVI) **(A)**, Chlorophyll Normalized Difference (CNDVI) **(B)**, and Photochemical Reflection Index (PRI) **(C)**. S0: initial electrical conductivity of the nutrient solution (non-saline conditions). Six independent replicates per treatment were considered for the statistical analysis. A two-way analysis of variance (ANOVA) and DUNCAN's multiple range test were performed and executed via the agricolae package in R version 4.4.1. Treatments having a different letter(s) are significantly different at the 5 % level.

B consistently resulted in the lowest reflectance values within this spectral range (500–600 nm). The same tendency was observed from 600 to 700 nm. In this region, the chlorophyll content of plants determines their reflectance properties (Craigie, 2022). Indeed, the increased chlorophyll content in salt-stressed and fertilized plants resulted in a reduction of reflectance specifically at 600–650 nm, which was more pronounced for Poly-B fertilized plants under S1 and S2 levels. However, in the far-red region (over 700 nm), the difference between the P sources was more important. At non-saline conditions (S0) and high salinity level (S2), higher reflectance values were recorded in plants fertilized with Ortho-B. In contrast, at the moderate salinity level (S1), reflectance significantly increased in plants receiving Poly-B treatment in the far-red region.

3.6. Reflectance indexes

To further analyze and describe the reflectance data, different reflectance indexes were calculated in the region of 300–800 nm (Fig. 5). The NDVI was not affected by salinity treatments or P sources (Fig. 5A). Another calculated index was the Photochemical Reflection Index (PRI) (Fig. 5C). The results revealed significant variations between phosphorus fertilizer forms across the different salinity levels. The PRI was less affected by salinity mainly in plants grown in Poly-B fertilizer medium. The enhancement of the PRI by Poly-B was estimated at 27 %, 498 % and 84 % under S0, S1 and S2 salinity levels compared to plants grown in Ortho-B medium (Fig. 5C). The same tendency was also observed for the CNDVI, a modified NDVI formulation where we replaced the RED waveband with 705 nm and the NIR waveband with 750 nm (Fig. 5B). Poly-B medium significantly enhanced the CNDVI parameter in plants by 24 % under S0, by 101 % under S1 and by 40 % under S2 in comparison with plant grown in Ortho-B medium (Fig. 5B).

3.7. Mineral analysis

The shoot phosphorus content varied significantly among the different treatments in this experiment (Fig. 6). The results showed that plants exhibited a significant increase in this parameter using Poly-B fertilizer medium where the shoot P content rose by 7 %, 34 % and 20 % at S0, S1 and S2 salinity levels, respectively, in comparison with plants grown in Ortho-B medium (Fig. 6D). For shoot K content, the results showed that under non-saline conditions (S0), plants exhibited a significant difference between P fertilizers P where Poly-B increased shoot K content by 40 % in comparison with Ortho-B (Fig. 6E). However, this parameter decreased significantly with the increase of salinity levels for both fertilizers. The effect was more significant at S2 with Poly-B (−56 %) followed by Ortho-B (−27 %), respectively in comparison with fertilized and non-salt-stressed plants (S0) (Fig. 6E). Compared to Poly-B, Ortho-B showed the best K content in the roots of non-salt-stressed plants (S0) and plants under the S2 salinity level (Fig. 6B).

The sodium (Na) content in the shoots and roots of fertilized plants increased significantly with the increase of salinity levels (Fig. 6C–F). However, this parameter was significantly impacted by the form of P fertilizers only under the S2 salinity level where Ortho-B exhibited the higher significant root accumulation of Na (Fig. 6C). The same tendency was observed for shoot Na accumulation (Fig. 6F).

3.8. Roots morphological parameters

Results showed that root length (RL), root surface area (RSA), root volume and crossings were significantly affected in plants grown in Ortho-B under saline condition (Fig. 7). However, Poly-B fertilizer showed a significant improvement in these root morphological parameters under saline and non-saline conditions (S0). For instance, the RL increased in Poly-B fertilizer medium by 58 %, 90 % and 104 % respectively at S0, S1 and S2 salinity levels compared to plants grown in

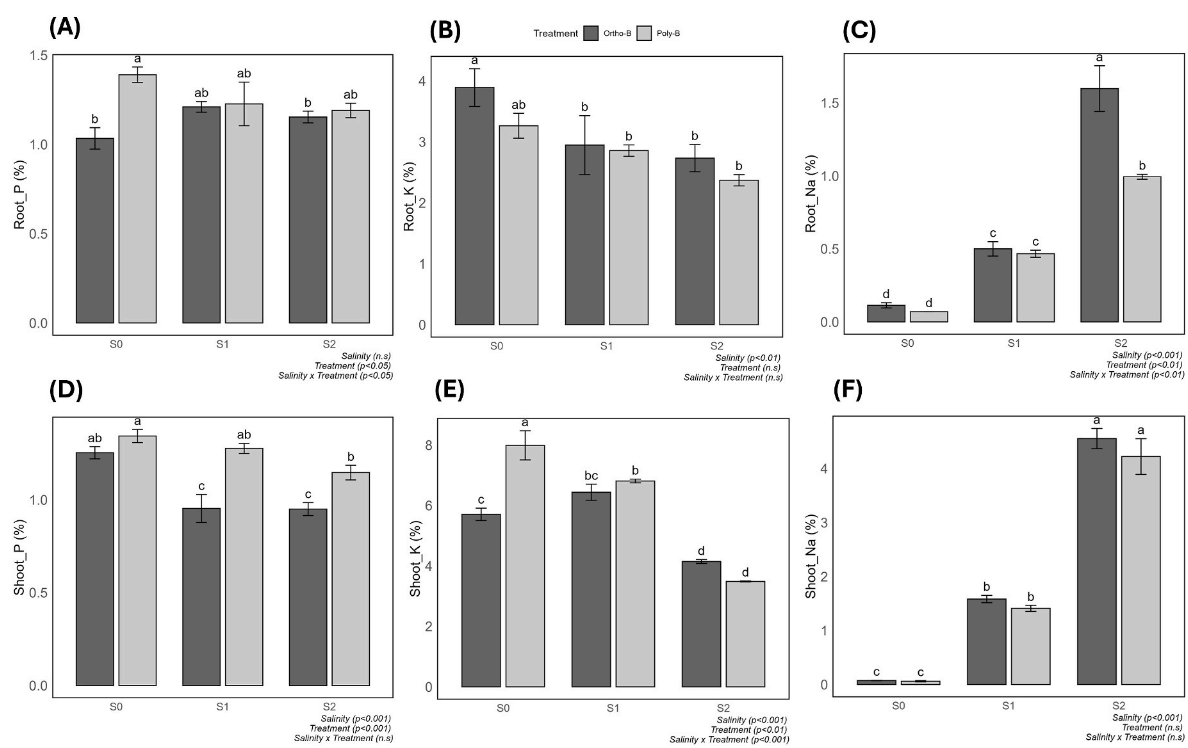

Fig. 6. The interactive effect of Salinity (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) and different soluble P-fertilizers (Poly-B and Ortho-B) on the accumulation of Phosphorus (P) **(A, D)**, Potassium (K) **(B, E)**, and Sodium (Na) **(C, F)**, in shoots and roots of wheat plants grown under hydroponic conditions. S0: initial electrical conductivity of the nutrient solution (non-saline conditions). Five independent replicates per treatment were considered for the statistical analysis. A two-way analysis of variance (ANOVA) and DUNCAN's multiple range test were performed and executed via the agricolae package in R version 4.4.1. Treatments having a different letter(s) are significantly different at the 5 % level.

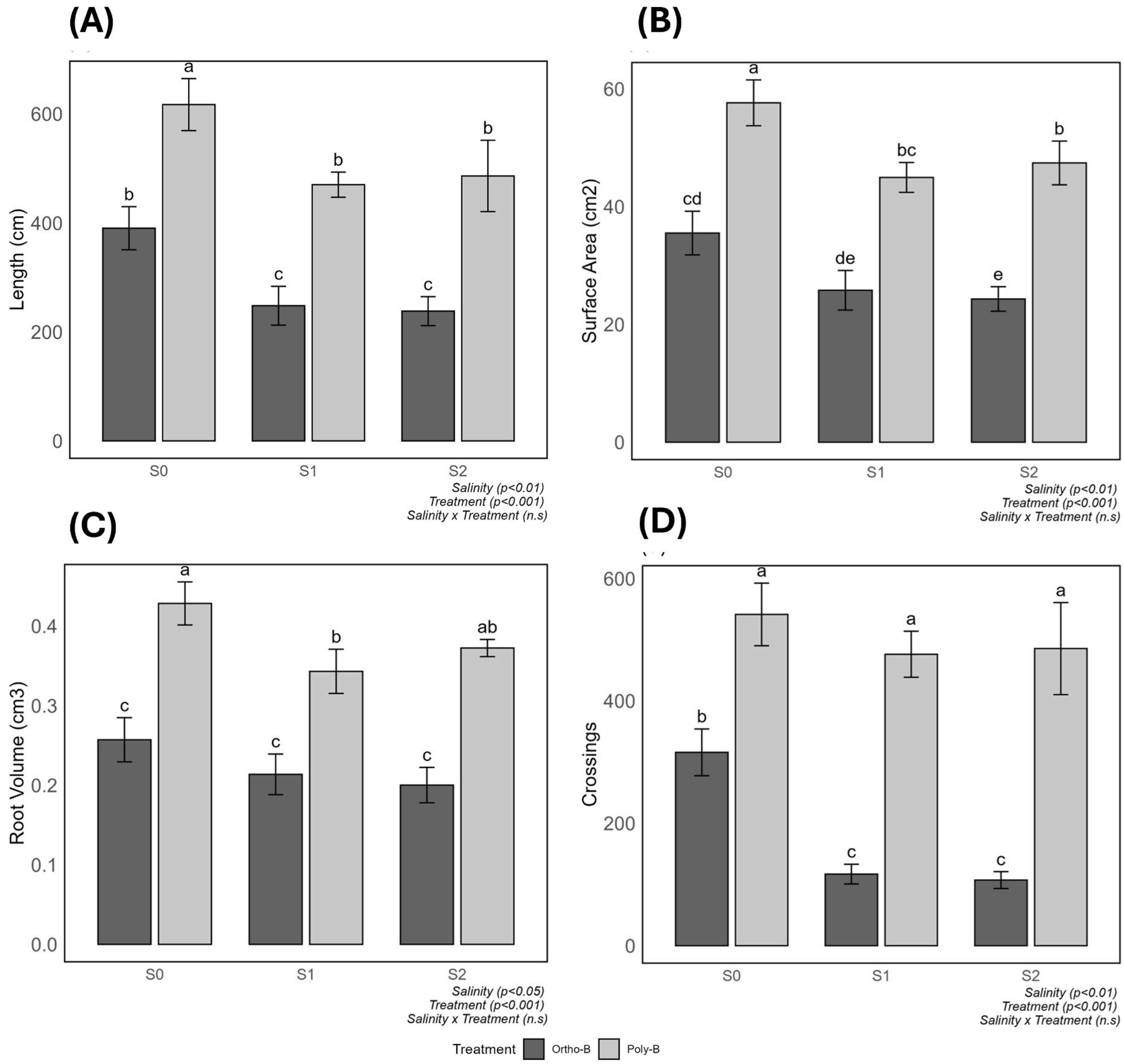

Fig. 7. The interactive effect of salinity (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) and different soluble P-fertilizers (Poly-B and Ortho-B) on root length **(A)**, root surface area **(B)**, root volume **(C)**, and crossing number **(D)** of wheat plants grown under hydroponic conditions. S0: initial electrical conductivity of the nutrient solution (non-saline conditions). Five independent replicates per treatment were considered for the statistical analysis. A two-way analysis of variance (ANOVA) and DUNCAN's multiple range test were performed and executed via the agricolae package in R version 4.4.1. Treatments having a different letter(s) are significantly different at the 5 % level.

Ortho-B medium (Fig. 7A). Similarly, Poly-B medium significantly increased the RSA by 62 %, 74 % and 95 % at S0, S1 and S2 salinity levels compared to plants grown Ortho-B medium (Fig. 7B). The root crossing number showed a significant difference between P sources and salt treatments (Fig. 7D). This metric reflects the degree of root branching or overlap, which enhances soil exploration capacity, especially under nutrient-limited conditions like phosphorus deficiency, offering valuable insight into the root system's capacity for functional adaptation. In our experimental conditions, this parameter was not significantly affected by salt stress in Poly-B fertilized plants, which showed a higher significant number of root crossings. Compared to Ortho-B medium, the improvement of the crossing number by Poly-B reached 71 %, 307 % and 353 % at S0, S1 and S2 salinity levels, respectively (Fig. 7D). Here, the response was form-dependent.

All these findings of studied root morphological parameters were confirmed by the observation of the WinRHIZO root scanned images shown in Fig. 8.

4. Discussion

Our findings showed that both shoot and root dry weights significantly decreased under salinity, with the effect being more pronounced in plants grown with Ortho-B fertilizer, showing a significant decrease under S1 and S2 compared to non-salt-stressed plants, which is consistent with previous reports (Zribi et al., 2021). This decrease in dry biomass observed in our study was likely caused by a reduction in chlorophyll content (Nemeskéri et al., 2019). In this regard, previous studies on maize, quinoa, and pepper have shown that it positively correlates with photosynthetic capacity and biomass production under salinity stress (Altuntas et al., 2018; Hessini et al., 2019; Manaa et al., 2019). The decrease in dry biomass could be a survival strategy for the plant, which invests more energy in defense mechanisms rather than biomass production. Additionally, our results suggest that the source of fertilizers has a significant effect on dry weight. Indeed, Poly-B fertilizer significantly increased the shoot DW in salt-stressed plant in comparison with plant grown with Ortho-B fertilizer. The observed effect may be due to the improved availability of P in the nutrient solution, as PolyP has

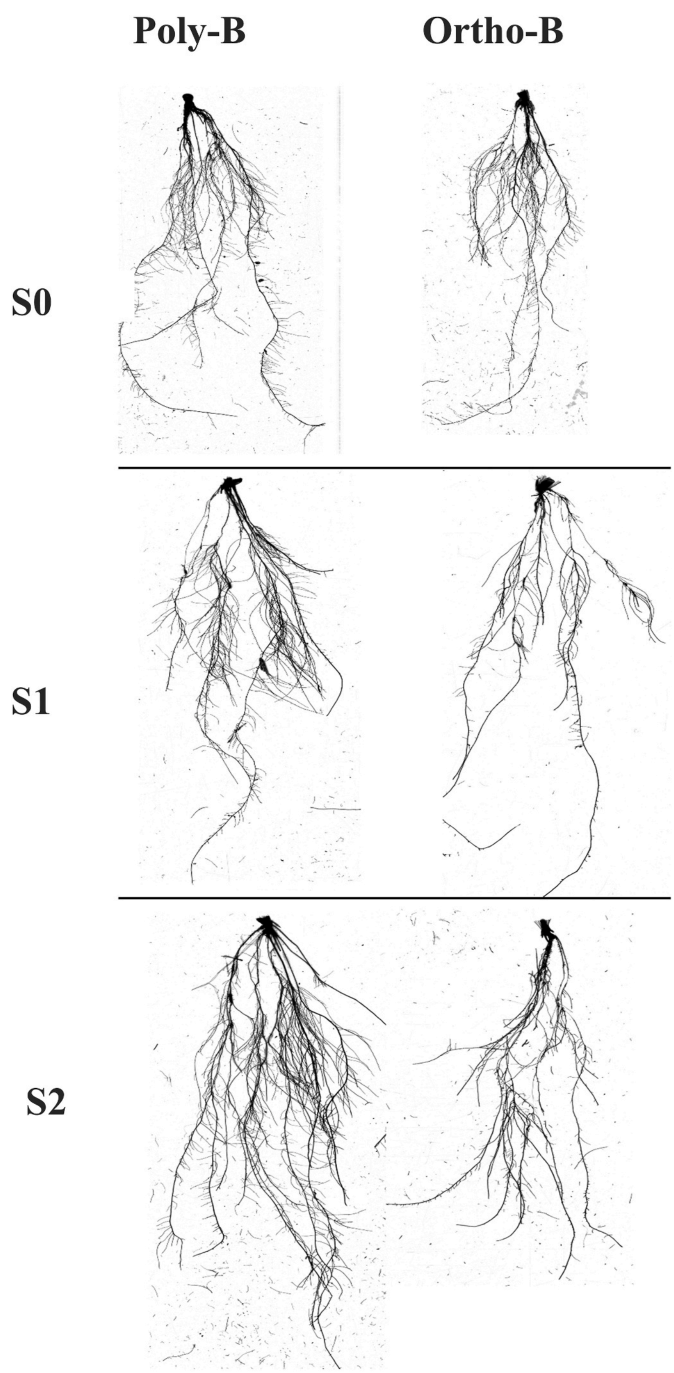

Fig. 8. Scanned root images obtained using the Epson Perfection LA2400 scanner and the WinRHIZO™ image analyzing system of wheat plants grown under the interactive effect of Salinity (S1 = 3 dS m^{-1} and S2 = 6 dS m^{-1}) and different soluble P-fertilizers (Poly-B and Ortho-B). S0: initial electrical conductivity of the nutrient solution (non-saline conditions).

slowed and continuous release properties (Khourchi et al., 2023). The allocation of biomass can be considered a process of optimizing growth (Hermans et al., 2006). The root-to-shoot ratio has been used to evaluate plant growth in recent decades and is considered a sensitive growth parameter and an indicator of plant stress physiology. Previous studies have indicated that the root/shoot ratio increases under stressful conditions, which was consistent with our findings using Ortho-B fertilizer. The root/shoot ratio increased significantly in salt-stressed plant grown in nutrient medium with Ortho-B fertilizer compared to the S0 level. This suggests that biomass was allocated more to roots than to shoots. However, this ratio was unaffected in plants fertilized with Poly-B and subjected to salt stress. Balanced growth of both roots and shoots could be a strategy to improve plant productivity in salty conditions. This promotes a more efficient allocation of resources, thereby improving phosphorus uptake and enhancing the plant's ability to acquire water under stress conditions (Meng et al., 2021). These results suggest that Poly-B fertilizer is beneficial for both root and shoot growth under salt stress. This is supported by a recent study by Gao et al. (2020) which found that PolyP fertilizers increased P uptake in maize shoots and roots, likely due to the gradual release of P in the soil and therefore the increase of its availability.

Our study showed that wheat leaves exposed to salt stress had a lower chlorophyll content, which has been reported in many other studies investigating the impact of salinity on plants (Usman et al., 2023; Tabassum et al., 2023). After 35 DAS the CCI increased by Poly-B by 24 % and 16 % under S1 and S2, respectively, compared to the S0 level. Hence, previous studies have emphasized the importance of adequate phosphate nutrition for efficient ion compartmentalization in salt-stressed wheat, as it contributes to the effective partitioning of carbon and the use of photo-assimilates (Khan et al., 2018). The reduction in chlorophyll content observed in salt-stressed wheat could be due to either a limitation in chlorophyll biosynthesis or the degradation of existing chlorophyll (Shoukat et al., 2019), which can lead to structural changes in the light-harvesting complex, disrupt the ability to capture light, and reduce photosynthetic efficiency (Meng et al., 2021). Conversely, higher levels of chlorophyll in P-fertilized plants promote photosynthetic activity, vigorous growth, and increased biomass yield (Mohamed et al., 2021). This statement confirms our findings in plants treated with Poly-B fertilizer in comparison with Ortho-B fertilizer with an increase in CCI estimated by 55 %, 68 % and 41 % at S0, S1 and S2, respectively.

The concentration of Na significantly increased in the roots and shoots of salt-stressed plants, with higher root accumulation observed in plants fertilized with Ortho-B. This observation aligns with our results, which showed a significantly higher accumulation of Na^+ in the roots than in the shoots of salt-stressed plants supplemented with phosphorus fertilizers. Moreover, previous studies have suggested that the reduction in plant growth under salinity could be caused by a nutritional imbalance and an excessive uptake of Na (Mirrani et al., 2024; Waqas et al., 2024). High Na concentrations can severely inhibit numerous enzymes, including photosynthetic enzymes, when above 100 mM (Shabala and Munns, 2017). Phosphorus and potassium have also been reported to play a role in mitigating salt stress in most crops (Chakraborty et al., 2021). In line with this, the observed increase in shoot K content under Poly-B application may be attributed to several interconnected mechanisms. Firstly, phosphorus is essential for ATP synthesis, which fuels H^+-ATPases in root cells, creating electrochemical gradients that facilitate K^+ uptake through HAK and KUP-type transporters (Wang & Wu, 2021). Additionally, Poly-B provide a more sustained release of P, which may enhance this energy-driven uptake mechanism more efficiently than orthophosphates (Khourchi et al., 2023).

In this regard, improved phosphorus nutrition has been linked to enhanced Na^+ exclusion and K^+ retention, partly through modulation of transporters like SOS1 and NHX1 (Shabala and Pottosin, 2014). While our study did not evaluate the expression of these specific ion transporters, the observed reduction in Na^+ accumulation under Poly-B treatment may be attributed to improved K^+/Na^+ homeostasis mediated by enhanced phosphorus nutrition. Although no specific studies to date have demonstrated that Poly-B directly regulates these genes, the improved ionic balance and reduced Na^+ accumulation observed in polyphosphate-fed plants (Loudari et al., 2023) suggest a potential indirect effect via enhanced energy status and membrane stability under salt stress. Further molecular studies are needed to clarify these potential mechanisms. Furthermore, Zribi et al. (2021) reported that P availability disrupted the transport of Na to shoots, which is consistent with our findings regarding the response of Poly-B fertilizer to Na accumulation in shoots and roots compared to Ortho-B fertilizer. Indeed, the response of P fertilizers on the total P content in the root of salt-stressed plants was similar, and the same trend was observed for shoot-Pt content.

Compared to plant grown in medium with Ortho-B, Poly-B fertilizer significantly improved studied root morphological parameters under salt stress. These morphological traits are important for root growth and exploration of a large surface area, particularly when there is a relatively small investment in root biomass. Previous studies have shown that acquisitive root parameters such as higher root surface area (RSA), root mass density, and root volume can improve P-acquisition efficiency in various crops with different rates and sources of P (Wen et al., 2019). The enhanced shoot P content observed under Poly-B treatment is likely the result of a dual mechanism. First, polyphosphate forms have been shown to stimulate root development, including greater root surface area and branching, which enhances nutrient acquisition under stress conditions (Khourchi et al., 2022a; Loudari et al., 2022a; Liu et al., 2023). Our study also observed increased root crossings and root volume in plants treated with Poly-B, which is consistent with improved P uptake via architectural adaptation. Wang et al. (2016) also found similar results in a hydroponic experiment using different wheat genotypes where plants treated with a high concentration of 200 μM/L KH_2PO_4 showed increased root lenght (RL), and root surface area (RSA) compared to those treated with low P concentration. Second, polyphosphates possess chelating properties that reduce the precipitation of phosphorus with calcium and magnesium, particularly in alkaline or saline conditions (Gao et al., 2020; Chtouki et al., 2022). This improves P solubility and availability in the root zone. Unlike orthophosphates, polyphosphates delay fixation in the solution and release phosphate ions gradually, thereby maintaining a more sustained supply of available P (Wang et al., 2019; Khourchi et al., 2023). These findings suggest that the superior performance of Poly-B in terms of shoot P content is a result of both physiological changes in the root system and favourable chemical interactions in the rhizosphere. Our study also found that root responses to P fertilizer were significantly affected by P sources. Poly-B fertilizer significantly increased RL and RSA. The RL increased by Poly-B +58 %, +90 % and +104 % under S0, S1 and S2 salinity levels compared to root plant grown in nutrient medium with Ortho-B fertilizer.

Salt stress can impact photosynthesis in several ways, including limiting the diffusion of CO_2 into chloroplasts, reducing stomatal opening, and affecting CO_2 transport in mesophyll cells (Kalaji et al., 2018). It can also lead to significant alterations in leaf photochemistry and carbon metabolism and can cause oxidative stress as a secondary effect (Kalaji et al., 2017). This can have a serious impact on the photosynthetic machinery of leaves (Muhammad et al., 2021). In our work, *ChlaF* measurement was used to assess the impact of increasing salinity levels on electron flow through PSII and PSI in plants treated with Ortho-B and Poly-B fertilizers. It has been previously reported that Na accumulation can inactivate photosynthetic and respiratory electron transport (Stirbet, 2012; Kalaji et al., 2017). Our results showed a significant reduction in PI_{tot} and I-P phase (loss of PSI reaction centers) in salt-stressed plants, which confirms the previous findings. The relative stability of the I–P phase observed in Poly B-treated plants under salinity stress suggests a protective effect on PSI activity. This phase reflects the reduction of end electron acceptors at the PSI acceptor side, which is frequently compromised by salt-induced oxidative stress (Kalaji et al., 2018). The improved phosphorus nutrition under Poly-B fertilization appears to facilitate ATP synthesis and sustain cyclic electron flow around PSI, mechanisms that collectively contribute to mitigating the over-reduction of the photosynthetic electron transport chain (Loudari et al., 2022b). In a preview study, we also demonstrated that polyphosphate fertilization under salinity significantly boosts enzymatic and non-enzymatic antioxidant defenses in the wheat plants, helping mitigate ROS-induced damage to PSI components (Loudari et al., 2023). Additionally, El-Mejjaouy et al. (2022) specifically linked improved P nutrition via Poly-B fertilizer in hydroponic conditions to the stabilization of the I–P rise in chlorophyll fluorescence, further confirming its role in sustaining PSI function under our saline conditions.

The J-I-P fluorescence yield was also reduced in ortho-B fertilized plants under salt stress. In our study, plants grown in medium with Ortho-B showed significant differences at this phase, with a relevant decrease in fluorescence yield while Poly-B treatment, on the other hand, stimulated intersystem electron transport regulation between PSII and PSI in salt-stressed wheat leaves, which could be a cellular adaptation to alleviate the harmful effects of salt stress and ensure photosynthetic electron transport equilibrium (Muhammad et al., 2021; Loudari et al., 2022b). Accordingly, the improved PSI and PSII efficiency under salinity could be achieved due to the better P availability ensured by Poly-B, which is critical for maintaining ATP and NADPH production—key molecules in the photosynthetic electron transport chain (Kalaji et al., 2018). Under salinity stress, adequate P supports thylakoid membrane integrity and stabilizes photosystem proteins, thereby reducing the over-reduction of the electron transport chain and photoinhibition (Altuntas et al., 2018; Loudari et al., 2022b). Thus, Poly-B mitigates the negative effects of salinity by maintaining efficient light reactions and overall energy metabolism.

In line with that, the combined effect of different types of P fertilizers and salinity levels had a significant impact on the photosynthetic performance PI_{tot}. The decrease in PI_{tot} indicates that the plant's vitality was partially inhibited under our salinity conditions. Poly-B fertilizer showed positive results in the PI_{tot} parameter, with increases of 12 %, 29 %, and 114 % under S0, S1, and S2, respectively, compared to plant grown in medium with Ortho-B fertilizer.

When plants are subjected to environmental stresses, such as salinity, they can exhibit a physiological response that alters their spectral reflectance curve (Craigie, 2022). In our study, significant differences were found in the 500–600 nm region due to higher absorption and lower reflectance in the green region that may be caused by higher anthocyanin content in stressed plants (Prabhakar et al., 2012). Under salt stress, phosphorus fertilization increased chlorophyll content, as shown by higher CCI values. This increase reduced leaf reflectance in the 600–650 nm range, a pattern especially evident in plants treated with Poly-B at both S1 and S2 salinity levels, reflecting improved pigment retention and photochemical efficiency. Between 600 and 700 nm, the reflective characteristics of plants are largely determined by the chlorophyll content (Craigie, 2022), which is a reliable indicator of plant degradation caused by stress (Sims and Gamon, 2002). The impact of stress on plants was reflected in lower reflectance in the 600–650 nm range, which is the result of higher chlorophyll content in stressed plants. In salt-stressed and fertilized plants, the increased chlorophyll content resulted in a reduction of reflectance specifically at 600–650 nm which was more pronounced for Poly-B fertilized plants under S1 and S2 levels.

Normalized Difference Vegetation Index (NDVI) is widely used as a non-destructive proxy for canopy vigor, biomass, and nutrient status in crops (Tucker, 1979). It also provides information about both the structural properties and the level of chlorophyll absorption in a leaf (Prabhakar et al., 2012). Plants that are under stress or have suffered damage tend to reflect more near-infrared light due to changes in the internal scattering of NIR caused by alterations in the structural properties of a leaf, primarily through the air/cell interfaces of the spongy mesophyll, as well as lower chlorophyll content resulting in reduced absorption of red wavelengths (Liew et al., 2008). In our experiment, Poly-B fertilizer showed the best values of the NDVI compared to Ortho-B fertilizer, with an increase of 21 % and 12 % under S1 and S2, respectively. To detect salt stress, the NDVI values were found to be closer to 1, indicating an increase in chemical substances that contribute to green coloration, such as chlorophyll molecules (Jensen, 2000). The reflectance in visible and NIR regions can also be affected by macronutrient deficiencies, increasing NDVI values (Stamford, 2020). Therefore, despite its apparent simplicity, the NDVI can have different levels of response and sensitivity. Recent studies confirm its utility for phosphorus monitoring: for example, Silva et al. (2022) reported a strong positive correlation ($r^2 \approx 0.70$) between NDVI and both shoot biomass and phosphorus uptake in soybean during early growth stages. Additionally, Farias et al. (2023) demonstrated that NDVI captures soybean biomass and nutrient dynamics in response to fertilization. In our study, the elevated NDVI values under Poly-B treatment corresponded with significantly higher biomass and chlorophyll content, which we attribute to enhanced phosphorus uptake. These findings support the application of NDVI as a reliable indicator of both structural (biomass) and functional (nutrient acquisition) improvements under salinity and phosphorus management.

The positive results of the NDVI parameter obtained by Poly-B fertilizer were confirmed for another related parameter, CNDVI which was significantly enhanced under S0 (24 % and 26 %), under S1 (101 %), and under S2 (40 %), respectively using Poly-B fertilizer in comparison with Ortho-B fertilizer. The photochemical reflectance index (PRI) is a measure of the level of de-epoxidation in the xanthophyll cycle, a part of non-photochemical quenching (NPQ) that helps in dissipating heat caused by excess absorbed light energy (Baker, 2008). Salinity often increases NPQ by stimulating the de-epoxidation of violaxanthin to zeaxanthin, lowering PRI values and reflecting enhanced photoprotective activity (Demmig-Adams and Adams, 1996; Sims and Gamon, 2002). This parameter has the potential to be utilized as an indicator of variations in physiological parameters like photosynthetic rate, stomatal conductance, and the operational efficiency of photosystem II (PSII) and NPQ. In our investigation, the PRI was less affected by salinity mainly for Poly-B fertilizer where the PRI increased by 27 %, 498 % and 84 % S0, S1 and S2 salinity levels compared to Ortho-B fertilizer. The higher PRI values observed in Poly-B-treated plants under salt stress may suggest a more balanced photoprotective response, possibly due to improved phosphorus status that stabilizes photosynthetic efficiency and reduces the need for excessive energy dissipation.

5. Conclusion

This study demonstrated the short-term beneficial effects of Poly-B and Ortho-B phosphorus fertilizers in mitigating salinity stress in durum wheat under controlled hydroponic conditions. Poly-B showed a promising potential to enhance physiological traits and nutrient uptake compared to Ortho-B. These findings could enhance the current understanding of the use of PolyP as a sustainable and effective source of P for crop growth in saline conditions. However, to fully validate the practical applicability of these findings, long-term field experiments are necessary. Such studies should consider soil chemistry, microbial interactions, and environmental variability to assess the sustained effectiveness, cost-efficiency, and environmental impact of these fertilizers. Ultimately, integrating Poly-B into field fertilization practices could contribute to improving durum wheat productivity and resilience in saline and phosphorus-deficient soils, particularly in arid and semi-arid regions.

CRediT authorship contribution statement

Aicha Loudari: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Houssameddine Mansouri:** Writing – review & editing, Formal analysis, Data curation. **Gilles Colinet:** Writing – review & editing, Validation. **Abdallah Oukarroum:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2025.110509.

Data availability

Data will be made available on request.

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