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Root morphological and anatomical responses to increasing phosphorus concentration of wheat plants grown under salinity

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ABSTRACT

Understanding the role of nutrients in the alleviation of salt stress effects and the unrevealed significance of root system architecture for plant adaptation is one of the major research areas in the current context of agriculture. Root anatomy is also a valuable parameter to be considered in understanding how the root system counters soil salinity's effect on plant growth. Although Root Phosphorus Acquisition Efficiency (RPAE) under salt stress differs depending on plant species and the severity of salinity in the rhizosphere, optimising phosphorus (P) nutrition seems to bring positive results. This study was planned to investigate the combined effect of salinity and P-availability on root morphology and anatomy as well as nutrient uptake of wheat plants. A pot experiment was performed in open-field conditions using a Moroccan variety of durum wheat. Special emphasis was placed on how orthophosphate and polyphosphate fertilizer forms and phosphorus doses alter the morphology and anatomy of the roots under salt stress. Two soluble fertilizers were used: an orthophosphate (Ortho-A) and a polyphosphate (Poly-B) were applied at four P levels (0, 30, 45 and 60 ppm of P). Our findings showed that salt stress induced, at both anatomical and morphological levels, a series of modifications in the roots of wheat plants. Compared to salt-stressed and unfertilized plants, soluble P-fertilizers significantly increased soil available P, root P- content, RPAE, root length (RL), root surface area (RSA), root volume (RV), root mass density (RMD), root tissue water content (TWC), number of root tips, vascular cylinder diameter and SD/CT ratio. Furthermore, Poly-B showed a positive response in both morphological and anatomical parameters at lower doses while Ortho-A revealed significant results within the increase in P-concentration. The increased root parameters observed under P-treatments could determine the root performance and efficiency to acquire water and P and their transport to the aboveground organs of wheat plants under salinity.

Abbreviations

CT	Cortex thickness
Ortho-A	Orthophosphate A
Poly-B	Polyphosphate B
RC	Root cortex
RD	Root Diameter
RDW	Root dry weight
RE	Root epidermis
RFW	Root fresh weight
RL	Root Length
RM	Root metaxylem
RMD	Root length density
RPAE	Root P acquisition efficiency
RSA	Root Surface Area
RV	Root volume
SD	Stele diameter
SDW	Shoot dry weight
TWC	Tissue Water content
WAS	Weeks after sowing

1. Introduction

Under abiotic stress, plants respond by a multitude of actions to

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encounter the advertised effect of stress, assuring a new state of development. Plants alleviate the negative consequences of abiotic stress by adopting physiological, morphological, and metabolic changes and by developing an adaptative state. The root-soil interface has been subject to many studies on the adaptative processes of plants to different stress conditions (Conde et al., 2011, Wang et al., 2019, Merwad et al., 2020). Root features are known to be influenced by the availability of mineral elements, water, and other physicochemical characteristics of soil and their interactions in the plant rhizosphere (Passioura, 1988, Steudle, 2000).

Root architecture changes depending on the availability of nutrients, and most studies on root morphology and functioning in plant nutrition concern the relationship between root features and P (Khourchi et al., 2022a). The ability of the plant to intercept immobile nutrients such as P by developing new root architecture is considered a plasticity adaptation of the plant to ensure sufficient growth and development (Bodner et al., 2021). Root performance to acquire water and nutrients depends on root features, including the number and diameter of xylem vessels, width of the root cortex, root exodermis, and endodermis (Steudle 2000, Ranathunge et al., 2010). For instance, in salt-stressed plants, roots are the first sensor to detect an excess of Na^+ and Cl^- (Demiral et al., 2017). This salt-stressed condition induced a series of adaptative plant responses in root morphology, anatomy, as well as in root features (Robin et al., 2016).

Root morphology changes in salt-stressed plants have been intensively studied and results are agreed that root morphology re-adapted to ensure efficient water absorption and nutrient uptake and then an efficient water nutrient translocation to leaves (Hermans et al., 2006, Demiral et al., 2017). Disorder nutrient uptake in a plant grown in saline conditions has been investigated in different plant species and salinity degrees, and there is evidence that salt stress leads to nutrient deficiency that influenced spatial root architecture (Robin et al., 2016, Merwad et al., 2020). Root length, surface, diameters, and other root parameters change depending on salinity degree and plant species (Robio et al., 2005, West et al., 2004, Geng et al., 2013, Jiang et al., 2017). Root anatomy is also considered a valuable parameter to be considered in understanding how the root system counter soil salinity effects on plant growth. Root anatomy determines root performance and efficiency to acquire water and nutrients and their transport to the aboveground organs, (Passioura 1988). Furthermore, salt stress induces a series of modifications at the root anatomical level, such as a decrease in cell expansion, perturbed cell division and root elongation, (West et al, 2004, Robin et al. 2016; Jiang et al 2017) as well as a reduction in root meristem size (Geng et al., 2013).

Understanding the role of nutrients in the alleviation of salt stress effects and the unrevealed significance of root system architecture for plant adaptation is one of the major research axes in the actual context of agriculture. To cope with the constraint of the low availability of P and enhance crop productivity, there is an urgent need to focus on the reasonable application of P sources which are more efficient. Polyphosphates have been used in agriculture and are well-known for their continuously and slow release of available P to plants in agricultural soil (Kulakovskaya et al., 2012, McBeath, 2006). These qualities make polyphosphate a sustainable source of P to meet plant needs and reduce phosphorus losses over time in soils. Additionally, it has also been reported that polyphosphate fertilizers differ from orthophosphates by their ability to chelate some micronutrients like manganese, iron, and zinc (Torres-Dorante et al., 2006, Wang et al., 2019, Gao et al., 2020).

Compared to orthophosphates, the plant responses to polyphosphates application under saline conditions is not widely studied. Hence, our study hypothesizes that the use of polyphosphates at different P rates could result in a positive effect on wheat growth and specifically the development of roots, which is crucial for plant nutrient acquisition, especially P. Hence, this study was planned to investigate the effects of salinity stress on root morphology and anatomy as well as nutrient uptake of wheat plants with special emphasis on how polyphosphate and phosphorus doses alter roots' morphology and their anatomy under salt stress.

2. Material and methods

2.1. Plant material, fertilisation, and experimental design

A pot experiment was conducted in a shaded house under open field conditions at the experimental farm of Mohammed VI Polytechnic University (UM6P) in Ben Guerir- Morocco. The temperatures in Ben Guerir during the growth season ranged from 0°C and 45°C, with an average of 19°C. The mean of light intensity per day was around PAR 280 μmol m^{-2} s^{-1}. Karim, a Moroccan variety of durum wheat [*Triticum turgidum* subsp. *durum* (Desf.) Husn.], and one of the most cultivated varieties in Morocco was used in this experiment. The experiment soil was collected from Rass El Ain- Morocco (31°43′55.1"N 7°36′49.9"W). The site was selected for its deficiency in assimilable P (Table 1). Representative soil samples from a 20-cm layer of the chosen soil were analysed to characterize the soil and refine treatments before the experiment. According to standard methods, the physical and chemical characteristics of the soil are summarized in Table 1.

The soil was air-dried and passed through an 8-mm sieve. Ten healthy seeds were sown into plastic pots containing 10 kg of dried soil. The pots were previously filled with a layer of gravel and drilled to ensure drainage. Only six seedlings were kept after plant emergence (with the same size and appearance). Basal manure consists of four increasing doses (0, 30, 45 and 60 ppm of P) using two hydrosoluble P-fertilizers: Ortho-A and Poly-B. The P doses were chosen following the fertilization recommendation proposed by the COMIFER method (COMIFER, 2009) considering different criteria (requirement of the crop, soil analysis, recent past of P fertilization, and crop residues from the previous one). Accordingly, 30 ppm of P was optimal for wheat growth under normal conditions (without salt stress). Hence, in a preliminary laboratory trial, the chosen doses were tested under different salinity levels and showed positive responses. The use of contrasting forms of P (Ortho-A and Poly-B) aims to examine the eventual contribution of the P fertilizer form to these responses. The Ortho-A fertilizer is a phosphoric acid-based fertilizer with potassium (52% of P2O5 with 100% Orthophosphate) while the Poly-B fertilizer is a linear polyphosphate with a short chain (47% P2O5 with 100% polyphosphate in

Table 1
Physical and chemical analysis of the selected soil.

Soil characteristics			Unit	Analysis method
Texture	Clay	15	%	NFX 31-107
	Slit	26		
	Sand	58		
pH-water		7,893	-	NF ISO 10390
Electrical conductivity (EC) 1/5 at 25°C		1,587	dS/m	NF ISO 11265
Total CaCO3		2,490	%	NF EN ISO 10693
Organic matter (OM)		3,11		NF ISO 14235
Phosphorus Olsen (P2O5)		30,33	mg/Kg	NF ISO 11263
Exchangeable elements	Potassium (K2O)	228,3		NFX 31-108
	Sodium (Na2O)	1546,66		
	Magnesium (MgO)	624		
	Calcium (CaO)	6472		
Trace-elements	Copper (Cu)	0,71		NFX 31-121
	Manganese (Mn)	11,04		
	Iron (Fe)	6,26		
	Zinc (Zn)	0,62		
Ammoniacal nitrogen (N-NH4)		7,893		SKALAR
Nitric nitrogen (N-NO3)		54,017		
Cation Exchange Capacity (CEC)			méq/100g	NFX 31-130

form of tripolyphosphates). The negative control (C-) consisted of unfertilized wheat plants without salinity, while the salt-stressed and unfertilized wheat plants were also used as positive control (C+) to compare the plant responses under both salinity and P deficiency. Wheat crop requirements were calculated according to the amount of nitrogen (N) and potassium (K) provided by the selected soil and P-fertilizers. Ammonium nitrate and potassium sulphate were applied for all treatments to equalize N and K amounts which were adjusted for control as well. The initial electrical conductivity (EC) of the soil was EC= 1,587 dS/m (Table 1). Two weeks after sowing (WAS), the salt stress was applied by the addition of saline water (with definite EC) after the seedlings' establishment. The salinity degree was progressively increased to reach moderate salt stress conditions (EC= 3,003 dS/m). The experiment was arranged in a completely randomized design with ten replicates per treatment. The total N amount was divided, as recommended, into three supplies: at one leaf stage, at tillering, and at the stem elongation stage, respectively. During the experiment, the plants were watered with rap water when soil moisture content fell to 60 % of its initial value. Soil EC monitoring was ensured using the HH2 WET sensor (Delta-T devices) before and after pot irrigation. The samples of plants and soil were taken at 12 WAS, which corresponds to the heading stage according to Zadok's scale (Z68 - Z71).

2.2. Root morphology

At 12 weeks after sowing, the roots of plants grown in all treatments were cut carefully and cleaned from impregnated soil between the roots. By using an Epson Perfection LA2400 scanner, roots were spread over a water-filled plastic box (1,5-2 cm deep) and scanned. The images obtained at 300 dpi resolution were analysed using WinRHIZO™ software (Regent Instructions, Quebec, Canada) to quantitatively measure root morphological characteristics such as root length (RL), root surface area (RSA), root volume (RV) and the number of root tips. All data were digitalized and analysed.

2.3. Root biomass

2.3.1. Root mass density and tissue water content

Roots of all treated plants were dried in an oven at 70°C for 2 days to determine root dry weights (RDW). Root mass density (RMD) was also calculated according to the following formula:

$$RMD = RDW/RV \quad (1)$$

The root volume (RV) was estimated by the WinRHIZO™ image analyzing system. Root Tissue Water Content (TWC) (2) and Root: Shoot ratio (3) were calculated using the following formulas:

$$TWC = (FW - DW)/DW \quad (2)$$

$$Root : Shoot\ ratio = RDW/SDW \quad (3)$$

With:
RFW: Root fresh weight
RDW: Root dry weight
SDW: Shoot dry weight

2.4. Root nutrient analysis

Based on a dry-weight basis, elemental concentrations of P, K and Na were measured and analyzed using Inductively Coupled Plasma Optical Emission Spectrometry (Agilent 5110 ICP-OES, USA).

2.5. Root phosphorus acquisition efficiency

According to Elhaissoufi et al. (2020), the root P acquisition efficiency (RPAE) was calculated by dividing the root P content by the root biomass (mg P g^{-1} RDW). This parameter indicates the root capacity to pick up P from the soil solution.

2.6. Root anatomical analysis

Root samples were collected 12 weeks after sowing and were cut carefully from 2 cm above the root apex, and all the collected materials were immediately fixed in FAA (formalin, acetic acid, ethyl alcohol) for 48 hours and then dehydrated in a graded ethyl alcohol series (10%, 30%, 50%, 70%, 90%, and 95%). The root samples were embedded in histological paraffin and transverse sections (7 μm of thickness) were obtained using an automatic rotary microtome (Thermo Fisher Scientific HM355S, USA), and double-stained with safranin and fast green. Sections were observed under an optical microscope (BB.1153-PLi, Euromex, Netherlands) equipped with a digital camera (CMEX-18PRO, Euromex, Netherlands). For each root sample, root and stele diameter (μm), cortex thickness (μm), central metaxylem vessels area (μm2), central metaxylem, and Protoxylem number were measured using Image Focus software version 1.3.1.4. (Euromex Microscopes Holland, Arnheim, Netherlands).

2.7. Soil nutrient analysis

Soil available P, K, and Na were evaluated by the analysis of these elements in the rhizosphere. This analysis was carried out 12 weeks after sowing.

2.8. Statistical analysis

Analysis of variance (ANOVA, one-way) was performed to reveal the differences in root morphological and anatomical parameters among P-treatments using SPSS statistical software (SPSS version 19.0, IBM SPSS Inc., Chicago, IL, United States). Significant differences among means were separated by the Duncan test at the $p < 0.05$ probability level, and it was reflected by different letters in the figures. Pearson's Correlation coefficients r were calculated to determine the association between Rhizosphere mineral content, biomass, morphological, and anatomical parameters.

3. Results

Many studies have described the strong interactions between P-uptake and different root functional parameters linked to P-acquisition efficiency, which may differ significantly within or between plants (Wen et al., 2019, Lyu et al., 2016, Walk et al., 2006, Isaac and Borden, 2019). However, limited information is available on how root parameters cooperate and coordinate to improve P acquisition under salt stress conditions in response to P availability through different types of P inputs notably Polyphosphate and Orthophosphate fertilizers.

3.1. Root biomass

In the present work, shoot and root dry weights (DW) declined significantly in unfertilized plants grown under salinity (C+) compared to fertilized ones (Fig. 1. A). The shoot DW did not show significant differences between P treatments, but the increase reached 157% and 109% in comparison with C+ and C- plants, respectively. The root DW depends both on the P-doses and forms of the P-fertilizers. Ortho-A shows the best performance at 30 and 40 ppm of P with an increase of 99.8% and 93%, respectively compared to C+. For Poly-B, the root DW increased with the increase in P dose from 30 to 45 ppm of P which reached 46% and 87%, respectively compared to C+ (Fig. 1. A). Furthermore, the dose of 60 ppm of P increased this parameter by 67% and 46% for Ortho-A and Poly-B, respectively compared to C+ but it showed a decline in roots DW for both Ortho-A and Poly-B (-38% and -89%, respectively) in comparison with the 45 ppm P-dose. In addition, The Root/Shoot ratio decreased significantly for all P-treatment except

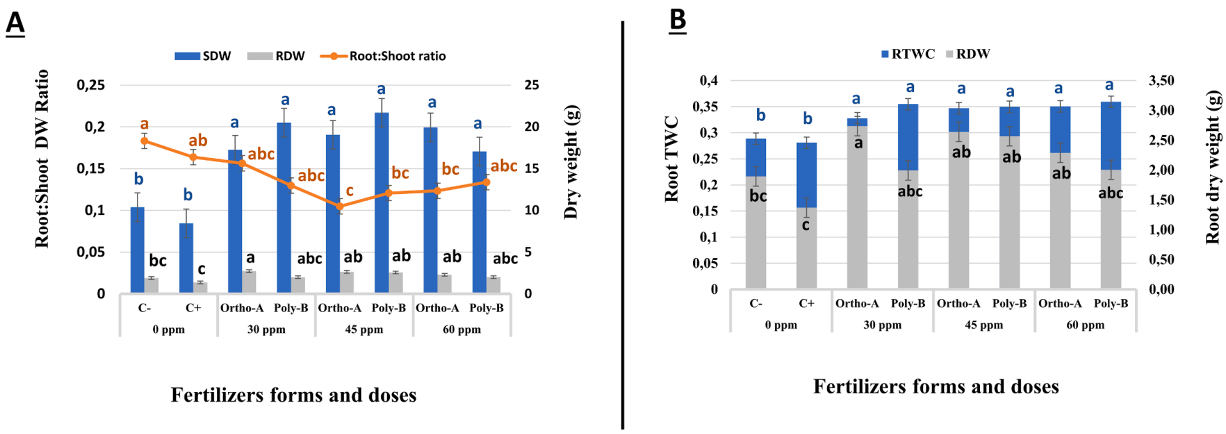

Fig. 1. The interactive effect of P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) on Root Dry weight (RDW) and Shoot Dry weight (SDW), Root/Shoot DW ratio (A), and RDW with Root Tissue Water content (TWC) (B) of wheat plants grown under salt stress conditions, measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants. *Statistical analysis was conducted using one-way ANOVA and SPSS data processing software. Duncan's test was used for the comparison of means. Treatments having a similar letter(s) are not significantly different at the 5% level.*

the Ortho-A 30 treatment, which showed similar results as unfertilized plants under salt stress (C+) or not (C-) (Fig. 1. A). Contradictory reports exist regarding the influence of salinity on the root: shoot biomass ratio. This ratio has been reported to be affected (increased or decease) or unaffected. Biomass allocation to root or shoot depends on the salt degree, time and duration of exposure, plant species, and developmental stage.

A different pattern was observed in another calculated growth parameter: Tissue water content (TWC), which was significantly decreased in control plants compared to fertilized ones under saline conditions with a reduction of 22% (Fig. 1. B).

3.2. Root & rhizosphere mineral content

The available P in the soil and his acquisition by roots significantly increased according to the P-doses (Fig. 2. A and B) which was among the expected results. This tendency was observed in both forms Ortho-A and Poly-B but is strongly expressed at 60 ppm of P. Compared to 30

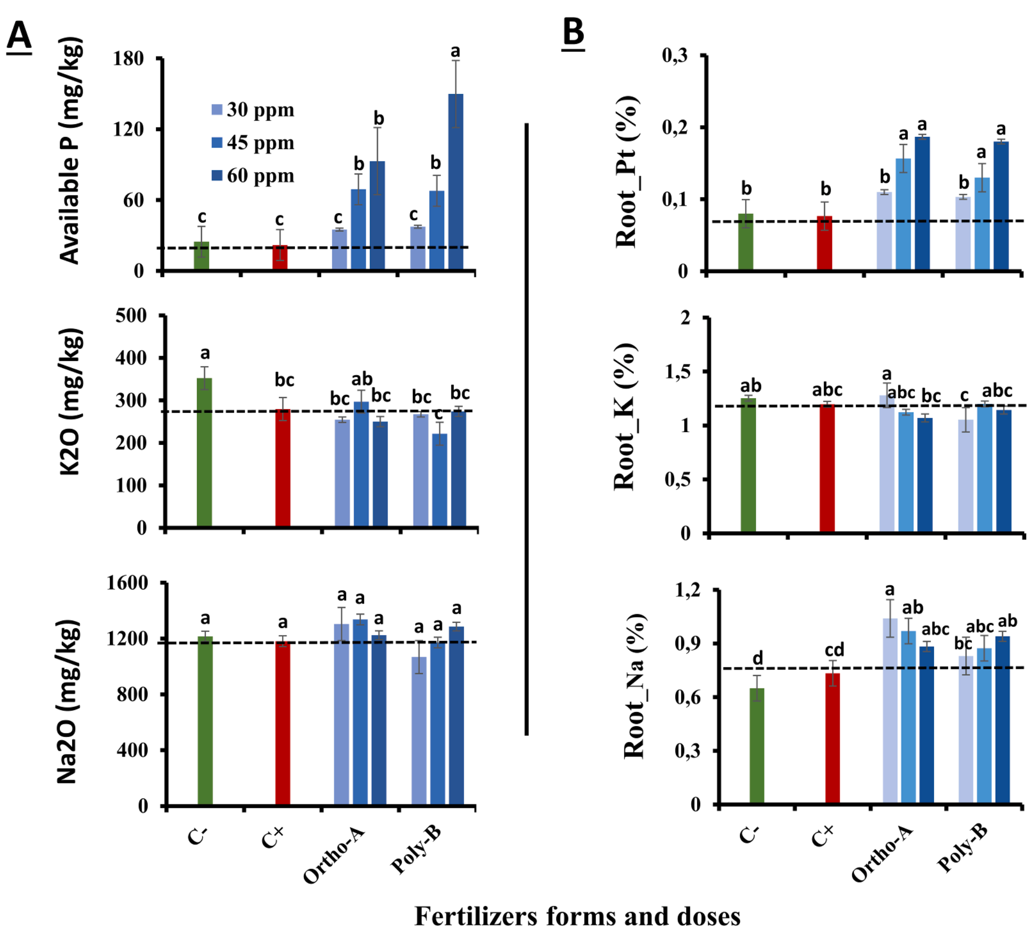

Fig. 2. The interactive effect of P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) on soil available P, K2O and Na2O rhizosphere contents (A), on Root total phosphorus (Pt), Potassium (K) and Sodium (Na) contents (B) of wheat plants grown under salt stress conditions, measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants. *Statistical analysis was conducted using one-way ANOVA and SPSS data processing software. Duncan's test was used for the comparison of means. Treatments having a similar letter(s) are not significantly different at the 5% level.*

ppm of P, the dose 60 ppm of P showed an increase of 166% and 328% in the soil available P for Ortho-A and Poly-B, respectively. The P accumulation also increased by 80% for both fertilizers at 60 ppm of P compared to 30 ppm of P and by 143% compared to C+. The potassium content in the soil was similar for all salt-stressed plants compared to C- plants in which the K content increased by 25%. This similarity seems to be logical as we adapted each treatment according to the amount of K provided by the P-fertilizers, the selected soil, as well as wheat requirements (Fig. 2. A). Accordingly, there is no significant difference in the K content in the roots of unfertilized and fertilized salt-stressed plants except for Poly-B fertilizer at 30 ppm of P which showed a decrease in the potassium accumulation estimated to -14% compared to C+ (Fig. 2. B). As an unexpected result, the sodium content in the root increased in fertilized plants compared to unfertilized ones under salt stress (C+). Using Ortho-A fertilizer, the accumulation was more relevant at 30 ppm of P with an increase of 42% in the sodium content in the roots of wheat plants compared to C+ (Fig. 2. B).

3.3. Root morphology

The scanned root images were obtained by the Epson Perfection scanner and the WinRHIZO image analysing system (Fig. 3). The root system architecture was significantly affected by salinity and P deficiency and revealed negative structural changes in the control and unfertilized and salt-stressed plants. The difference from fertilized plants was significant for both fertilizers at 30 and 45 ppm P. However, a negative effect on root system architecture appears at a high concentration of Poly-B.

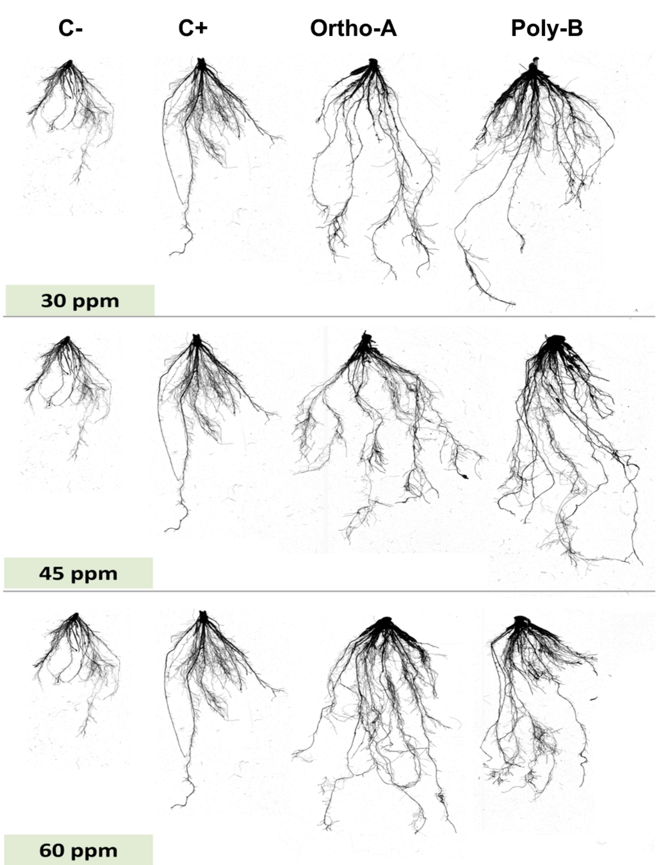

Fig. 3. Scanned root images using Epson Perfection LA2400 scanner and the WinRHIZO image analyzing system of wheat plants grown under the combined effect of salt stress and different P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants.

Fig. 4 shows root length (RL), Root volume (RV), root surface area (RSA), number of root tips and Root mass density (RMD) in salt-stressed plants, unfertilized or fertilized by soluble fertilizers. Fertilized plants presented significant responses compared to control and unfertilized salt-stressed ones. Fertilizer forms and phosphorus dose showed a significant effect on all root morphology parameters. Compared to unfertilized and salt-stressed plants, P-fertilizers significantly increased root length, root surface area, tip number, root volume and other root morphological parameters (Fig. 4). Plants fertilized by Ortho-A at 45 and 60 ppm P, had a higher root volume. Together with Poly-B mainly at 30 ppm P, higher values of tips number, RL, and RSA were shown. The RMD varied depending on applied treatments and P doses. This parameter increased by 28% and 20.9% at 45 and 30 ppm of Ortho-A and Poly-B, respectively compared to salt-stressed and unfertilized plants (C+) (Fig. 4). This means that under salinity, the root morphology of fertilized plants was re-adapted to ensure efficient water absorption and nutrient uptake and then an efficient water nutrient translocation to leaves.

3.4. Root anatomy

Although the two fertilizers didn't show a significant difference between each other at the same P rate for Cortex thickness (CT) and Root diameter (RD), the difference from the positive control was most strongly expressed for the SD and SD/CT ratio (Fig. 5). The SD for Ortho-A 60 ppm increased by 32% in fertilized plants higher than in unfertilized ones (C+), and the same tendency was obtained from Poly-B at 30 ppm, which confirms the results obtained in the anatomical sections (Fig. 6). This implies that P fertilization could enhance salinity tolerance and potentially improve the water uptake capacity by increasing stele diameter, which would promote deeper rooting.

3.5. Root P acquisition efficiency (RPAE)

Fig. 7 shows a significant increase in the Root P acquisition efficiency (RPAE) of fertilized plants compared to unfertilized plants exposed to salinity (C+) or not (C-). The effect was more relevant at 45 and 60 ppm of P for both fertilizers. The form of P-fertilizers has a significant effect but depends on the P dose. At 45 ppm of P, P fertilizers showed similar results with an increase of 26% in RPAE of salt-stressed plants in comparison with C- (Fig. 7. A and B). However, Ortho-A did not show any difference with the C- at 30 ppm of P. The same tendency was observed for the available P in the soil and root P content where the doses 30 and 45 ppm of P did not show a significant difference between P-fertilizer forms (Fig. 2 and Fig. 7). However, compared to unfertilized plants (C- and C+), P-fertilizers showed a significant increase in RPAE at 60 ppm of P which reached 28% and 70% for Ortho-A and 59% and 113 % for Poly-B compared to C+ and C-, respectively (Fig. 7. A and B).

4. Discussion

The present study highlights the complex interaction between salinity and P that exists in plants with a focus on parameters associated with root function, P uptake and P use efficiency. Interestingly, our findings reveal a strong correlation between biomass, P uptake and different root anatomical and morphological parameters as well as P sources and rates, which contributes to enriching the existing knowledge on wheat growth and leads to a higher P acquisition efficiency and better use of polyphosphates by durum wheat plants under saline conditions where both applied and fundamental knowledge is still scarce.

According to several studies, it was shown that phosphorus is an important factor in the growth of shoots and roots, and low phosphorus uptake under salinity may reduce biomass development (Demiral 2017; Khan et al., 2018). In the last decades, the root/shoot ratio was adopted for assessing plant growth and was considered a sensitive growth parameter and indicator in plant stress physiology. To minimize the

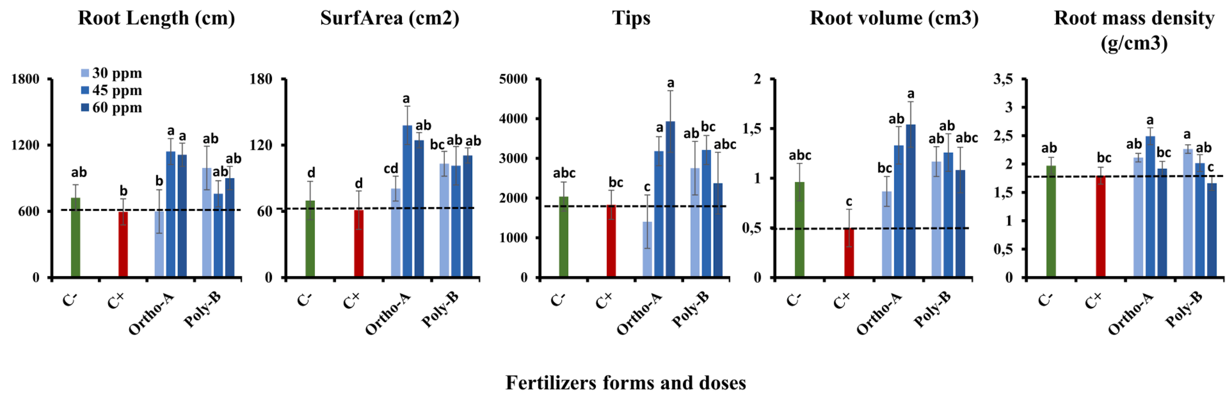

Fig. 4. The interactive effect of P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) on tips number, total root length (cm), Surface Area (cm2), Root volume (cm3) and root mass density (RMD) (g/cm3) of wheat plants grown under salt stress conditions, measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants. *Statistical analysis was conducted using one-way ANOVA and SPSS data processing software. Duncan's test was used for the comparison of means. Treatments having a similar letter(s) are not significantly different at the 5% level.*

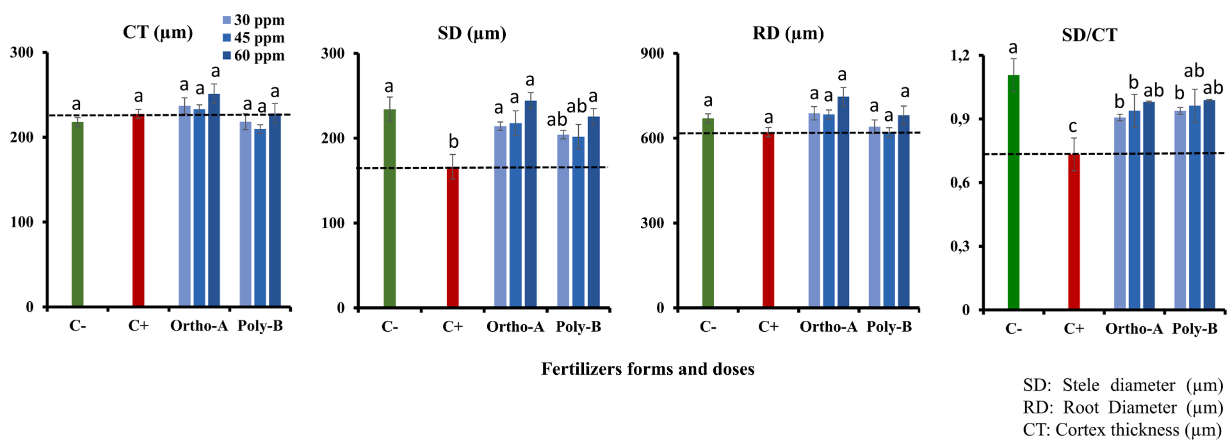

Fig. 5. The interactive effect of P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) on Stele diameter-SD (µm), Root Diameter-RD (µm), Cortex thickness- CT (µm) of wheat plants grown under salt stress conditions, measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants. *Statistical analysis was conducted using one-way ANOVA and SPSS data processing software. Duncan's test was used for the comparison of means. Treatments having a similar letter(s) are not significantly different at the 5% level.*

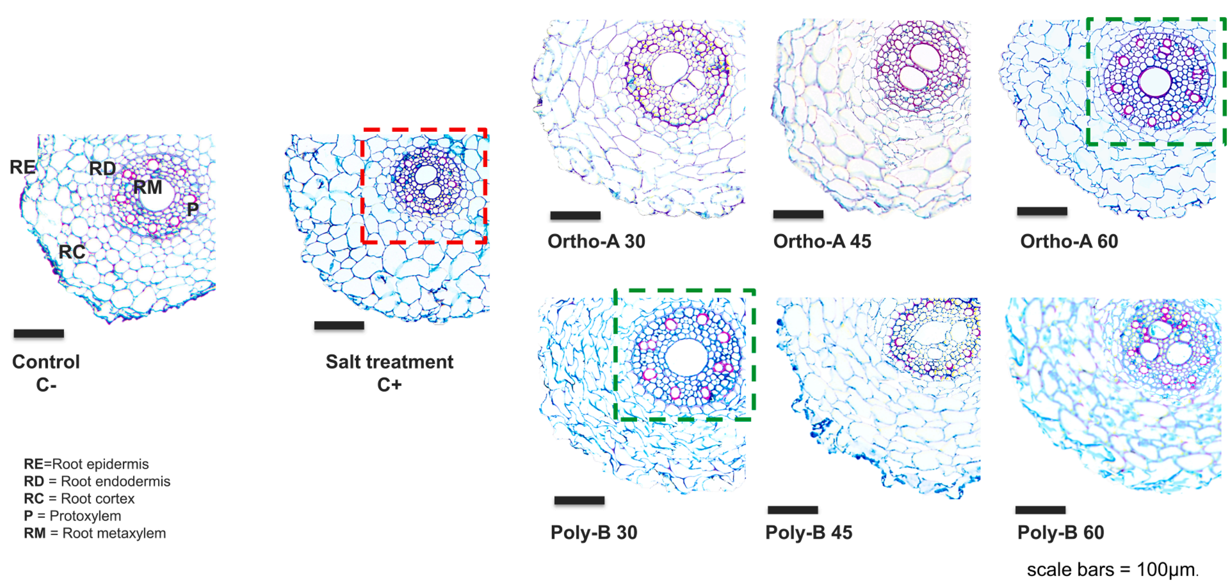

Fig. 6. Cross sections of wheat roots under the combined effect of salt stress and different P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants (scale bars = 100µm).

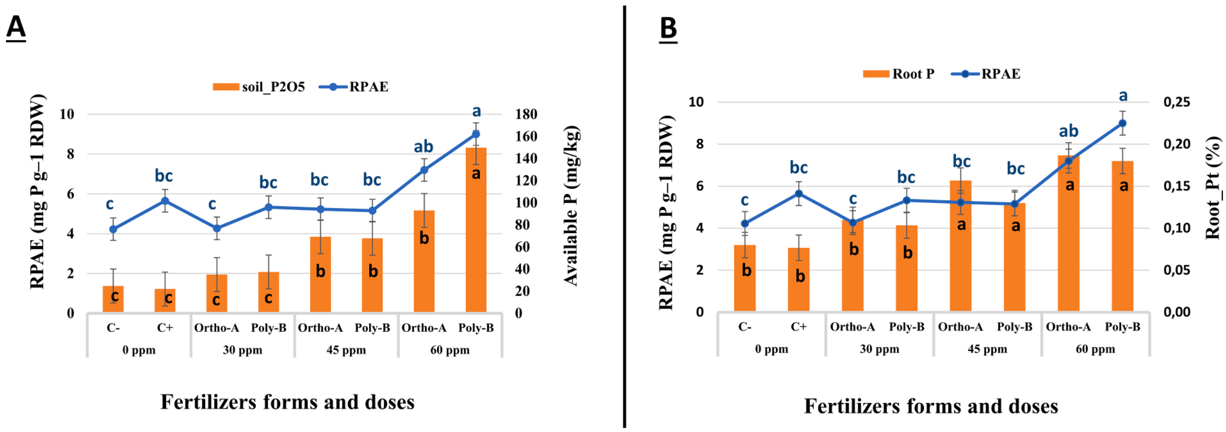

Fig. 7. The interactive effect of P-fertilizer forms (Ortho-A and Poly-B) and doses (0, 30 and 45 ppm) on Root P acquisition efficiency (RPAE) and soil available P content (A), and RPAE with Root Pt content (B) of wheat plants grown under salt stress conditions, measured 12 Weeks After Sowing (WAS). C-: unfertilized plants without salt application, C+ salt-stressed and unfertilized plants. *Statistical analysis was conducted using one-way ANOVA and SPSS data processing software. Duncan's test was used for the comparison of means. Treatments having a similar letter(s) are not significantly different at the 5% level.*

negative effect of salt stress, the plant developed phenotypic plasticity (Bodner et al., 2021). Contrary to what has been reported in previous studies, the root/shoot ratio rose in stress conditions, in our investigation, this ratio declined (Fig. 1. A). This means that biomass was allocated in shoots rather than in roots. Hence, biomass partitioning might be considered a process for the optimisation of growth. Balanced growth of both shoots and roots could be a strategy to enhance plant productivity in soil under salinity, which results in an optimal allocation (Hermans et al., 2006) and improves both water acquisition and P-uptake (Maggio et al., 2007). In this regard, our results show a significant increase at 60 ppm P of RPAE by 28% and 59% under salinity using Ortho-A and Poly-B, respectively, compared to salt-stressed and unfertilized plants (C+) and by 70% and 113 % for Ortho-A and Poly-B, respectively compared to C- plants (Fig. 7).

These findings indicate that under salt stress, P-fertilizers promote investment in root biomass. This has also been confirmed recently by Gao et al. (2020), who reported that the application of polyphosphates significantly increased the P uptake (60 kg P ha^{-1}) in shoots and roots of maize. Thus, the enhancement of P uptake in maize plants by the application of polyphosphate may result in the progressive enhancement of the available P in soil using polyphosphate fertilizers (Torres et al., 2006, Gao et al., 2020) (Fig. 7. A). For instance, Poly-B application improved root dry weight (RDW) under salinity compared to Ortho-A fertilizer or unfertilized and control plants (Fig. 1). This agreed with results obtained by Gao et al. (2020) using maize plants fertilized with polyphosphates improved root dry biomass. In addition, the same study found a significant correlation between the total dry biomass of maize plants and P uptake under polyphosphate supply ($r = 0.91$). This was in line with our findings that P- fertilization of Ortho-A and Poly-B enhanced root parameters such as RSA (improved by 55.7 and 44.8% at 45 and 30 ppm of P, respectively, compared to salt-stressed and unfertilized plants (C+) and RMD (increased by 28.1 and 20.9% at 45 and 30 ppm of Ortho-A and Poly-B, respectively compared to C+) (Fig. 4), which are considered an important trait facilitating a large surface area exploration mainly when the investment in root biomass is relatively small. Indeed, significant correlations between P acquisition efficiency and root parameters (Table 2) may explain wheat growth enhancement under salinity using soluble P-fertilizers notably polyphosphates.

Correspondingly, Honvault et al. (2021) showed that P concentration in shoots was negatively correlated with root surface area ($r = -0.30$). This same study suggested that this correlation can be explained by the carbon cost to plants of different root parameters implicated in P acquisition as well as the variation of P availability in the environment surrounding roots. Hence, the expression of root traits depends on their carbon cost for plants and the status of P availability in the rhizosphere (Wen et al., 2019, Lyu et al., 2016, Pearse et al., 2006, Giovannetti et al., 2019). In relation to nutrient root uptake efficiency, higher RSA, RMD and RV are known as acquisitive root parameters which are closely related to improved P-acquisition efficiency in different crops under contrasting rates and sources of P (Wen et al., 2019, Fort et al., 2015). Similar responses were found by Wang et al. (2016) in a hydroponic experiment using different wheat genotypes. The plants under the P-application of 200 µmol/L KH_2PO_4 exhibited high root length (RL) and root surface area (RSA) in comparison with plants treated with low P concentration.

In the present work, Root tissue water content (TWC) was significantly reduced in salt-stressed and unfertilized plants (C+) in comparison with fertilized plants under saline conditions (Fig. 1. B). In line with this, a significant positive correlation was observed between root TWC and root P content (r=0.616**), RPAE (r=0.470*) and soil available P (r=0549**) (Table 2). These findings support the previous work of Li et al. (2010), who found that P shortage altered root hydraulic conductance and lowered plant water potential, by reducing the water channel proteins activity, the aquaporins. Furthermore, the decrease in growth under salinity might be attributed to a nutritional imbalance and excessive sodium acquisition (Isayenkov and Maathuis 2019). In our study, the K content was similar in the roots of fertilized and unfertilized salt-stressed plants (Fig. 2). Remarkably, it has been found that salt stress caused sodium injury, which impacts potassium uptake by root cells (Conde et al., 2011). Furthermore, it is worth noting that potassium (K) and sodium (Na) might exist in competition and induce $K+$ deficiency in the rhizosphere, and depolarization of the plasma membrane also stimulates the $K+$ outward rectifying channels to mediate the efflux of $K+$ and the influx of $Na+$ (Behdad et al., 2021). Our findings are in line with previous works in the literature. Nevertheless, it is interesting to mention that the reduction in both phosphorus and potassium concentration under high salinity is accompanied by a significant increase in sodium content in roots (Fig. 2. B) and shoots (Demiral 2017; Loudari et al.,2020). Besides, Rubio et al. (2005) found in the leaf and root cells of *Zostera marina L*, a Na-dependent high-affinity phosphate transporter in their plasma membrane. Indeed, the increase in P-content in fertilized wheat plants under salinity (Fig. 2. B) could be attributed to a synergistic effect of Na, which is implicated in P acquisition and/or transportation to the aerial part of plants (Grattan and Grieve, 1992). Correspondingly, a significant positive correlation ($r = 0.581^{**}$) was observed between root P content and root Na content (Table 2). However, high external phosphorus enhanced sodium acquisition and reduced the soybean tolerance to salinity (Phang et al., 2009).

Anatomical modifications represent an important strategy in plant survival under salinity. Based on different studies conducted on root

Table 2
Pearson's correlation between biomass, root, and rhizosphere mineral content, measured and calculated anatomical and morphological root parameters of wheat plants grown under salinity using different forms (Ortho-A and Poly B) and doses (30, 45 and 60 ppm P) of soluble P-fertilizers at 12 Weeks After Sowing (WAS) (n = 24). *(Asterisks indicate significant correlation at *p < 0.05, **p < 0.01).*

Pearson's correlation coefficients

	Root_ Pt	Root_ K	Root_ Na	Length	Surf Area	Tips	Root Volume	Soil_ P2O5	Soil_ K2O	Soil_ Na2O	CT (µm)	SD (µm)	RD (µm)	SD/CT	Root Mass Density	Root DW	Root TWC	RPAE
Root_Pt	1	-0,189	0,581**	0,410*	0,694**	0,400	0,437*	0,843**	-0,331	0,126	0,174	0,351	0,251	0,151	-0,373	0,020	0,616**	0,791**
Root_K	-0,189	1	0,277	-0,359	-0,350	-0,549**	-0,522**	-0,227	0,088	0,100	-0,194	-0,250	-0,231	-0,074	0,383	-0,094	-0,386	-0,193
Root_Na	0,581**	0,277	1	0,248	0,471*	0,112	0,057	0,369	-0,422*	0,274	0,197	0,134	0,192	-0,141	0,109	0,303	0,466*	0,251
Length	0,410*	-0,359	0,248	1	0,709**	0,797**	0,568**	0,264	-0,180	0,177	0,112	0,323	0,196	0,289	-0,513*	-0,038	0,535**	0,420*
SurfArea	0,694**	-0,350	0,471*	0,709**	1	0,649**	0,682**	0,479*	-0,312	0,211	0,099	0,274	0,169	0,167	-0,456*	0,244	0,717**	0,423*
Tips	0,400	-0,549**	0,112	0,797**	0,649**	1	0,492*	0,268	-0,039	0,049	0,364	0,445*	0,425*	0,097	-0,470*	-0,054	0,357	0,371
Root Volume	0,437*	-0,522**	0,057	0,568**	0,682**	0,492*	1	0,235	-0,266	0,182	-0,040	0,319	0,082	0,448*	-0,694**	0,119	0,619**	0,327
Soil_P2O5	0,843**	-0,227	0,369	0,264	0,479*	0,268	0,235	1	-0,120	0,106	0,043	0,289	0,133	0,228	-0,311	-0,126	0,549**	0,810**
Soil_K2O	-0,331	0,088	-0,422*	-0,180	-0,312	-0,039	-0,266	-0,120	1	0,293	-0,051	0,097	-0,004	0,219	0,052	-0,152	-0,422*	-0,160
Soil_Na2O	0,126	0,100	0,274	0,177	0,211	0,049	0,182	0,106	0,293	1	0,212	0,188	0,222	0,010	-0,039	0,145	0,127	0,078
CT (µm)	0,174	-0,194	0,197	0,112	0,099	0,364	-0,040	0,043	-0,051	0,212	1	0,644**	0,964**	-0,439*	0,023	-0,008	-0,062	0,146
SD (µm)	0,351	-0,250	0,134	0,323	0,274	0,445*	0,319	0,289	0,097	0,188	0,644**	1	0,825**	0,382	-0,401	-0,201	0,225	0,435*
RD (µm)	0,251	-0,231	0,192	0,196	0,169	0,425*	0,082	0,133	-0,004	0,222	0,964**	0,825**	1	-0,191	-0,123	-0,077	0,033	0,260
SD/CT	0,151	-0,074	-0,141	0,289	0,167	0,097	0,448*	0,228	0,219	0,010	-0,439*	0,382	-0,191	1	-0,564**	-0,282	0,272	0,324
Root Mass Density	-0,373	0,383	0,109	-0,513*	-0,456*	-0,470*	-0,694**	-0,311	0,052	-0,039	0,023	-0,401	-0,123	-0,564**	1	0,561**	-0,386	-0,632**
Root DW	0,020	-0,094	0,303	-0,038	0,244	-0,054	0,119	-0,126	-0,152	0,145	-0,008	-0,201	-0,077	-0,282	0,561**	1	0,137	-0,542**
Root TWC	0,616**	-0,386	0,466*	0,535**	0,717**	0,357	0,619**	0,549**	-0,422*	0,127	-0,062	0,225	0,033	0,272	-0,386	0,137	1	0,470*
RPAE	0,791**	-0,193	0,251	0,420*	0,423*	0,371	0,327	0,810**	-0,160	0,078	0,146	0,435*	0,260	0,324	-0,632**	-0,542**	0,470*	1

anatomy under salt stress, it has been clearly reported that root structures are modified depending on the intensity of salinity and the exposure time (Demiral et al., 2017, Isayenkov and Maathuis, 2019). Therefore, mild or moderate salinity stresses the root cells of the epidermis and endoderm. Similarly, root vessel elements thicken to prevent the accumulation of Na+ in roots (Choat et al.,2010). Under severe salt stress conditions, deleterious effects take place due to the excess Na+, which affects cell enlargement as well as cell wall integrity (Sellami et al.,2019). In line with that, our results indicate that roots exhibited negative structural changes, which increased with the addition of Na+ compared to the control plants (Fig. 3). These results were clearly linked to the addition of Na+ in the medium, which causes plasmolysis and reductions in the protective tissues (Choat et al., 2010). In this context, the cortex, epidermis and endodermis are considered as mechanical barriers in the water and ions radial transport such as Na+. These elements also prevent and limit the solutes reflux to protect vascular tissues (Doblas et al., 2017). According to many studies, it was reported that the stele: root ratio significantly increased with the reduction of water availability, notably in response to water stress (Steudle, 2000, Bodner et al., 2021) (Fig. 5). In line with that, it is known that the metaxylem and the vascular cylinder contribute to the transport of water to the shoots and affect Na+ efflux through conduction cells (Rubio et al., 2005). The irregularities observed in the root cross-sections under salt stress for both unfertilized and fertilized plants (Fig. 6) reveal disturbances in components production, mainly those of the secondary wall, which leads to modifications in their mechanical characteristics and thus makes them sensitive to negative pressures (Bensussan et al., 2015). Nevertheless, the number and diameter of xylem vessels were neither significantly affected by P dose nor by the form of P-fertilizers (Fig. 6). Hence, variations and changes in these traits could affect the acquisition efficiency of both water and P.

Additionally, the root diameter (RD) is the result of different anatomical root variables, i.e., SD, cortical cell size and cortex cell file number, which could have an opposite effect on RD. Our results indicate that the RD responses of fertilized plants compared to unfertilized ones and control under salinity were perceived to be relatively small in absolute terms for all doses (compared with the SD) (Fig. 5). In this regard, significant positive correlations were observed between RD and CT (r =0.964**) and SD (r =0.825**) (Table 2). Furthermore, many cereals like maize, wheat, etc., are known for a smaller root diameter than legumes (i.e., faba bean, chickpea, etc.), given its role in P acquisition allowing high absorptive capacity (Shen et al., 2018, Lyu et al., 2016) mainly under salt stress. Our results are consistent with other studies on variations in root diameter as an important trait of root morphology implicated in RPAE (Wen et al., 2019, Lyu et al., 2016, Rose et al., 2009, Li et al., 2014, Shen et al., 2018).

In relation to the acquisition of P, it is worth noting that the available P in soil was responsive to the increase of P dose for both fertilizers compared to unfertilized plants under salinity (C+) or not (C-) (Fig. 2. A), especially for Poly-B at 60 ppm of P. Similarly, Root Pt content and RPAE also increased with enhancing P rate under salt stress for Ortho-A and Poly-B P fertilizers (Fig. 7. B).

According to Chimungu et al., 2015, the SD was observed to increase with the improvement of P availability, which is in line with our findings (Figs. 5 and 6). Similarly, a significant positive correlation was found between SD and RPAE (r=0.435*) (Table 2). This could presumably be due to the increased biomass production under the high availability of P in the medium, revealed by significant increases in RDW for salt-stressed and fertilized plants, compared to unfertilized ones and control (Fig. 1). Indeed, the observed improvement in the stele diameter (SD) (Fig. 6) under the combined effect of salt stress and phosphorus application mainly for Poly-B at low rates and Ortho-A within the increase of P dose, suggests one of the plant strategies to enhance water use efficiency, nutrient acquisition efficiency and sodium exclusion in the aerial part via Na+ partition assimilation (Prince et al., 2017). This implies that P-fertilizers could improve salinity tolerance when applied at an adequate dose and eventually improve water acquisition capacity by improving SD. Hence, the enhanced SD may directly impact the crop's ability to tolerate salinity by enhancing resource acquisition and penetration capacity, which indirectly affect P uptake and internal P efficiency by altering the patterns of root distribution (promoting deeper versus shallow rooting) (De Bauw et al., 2019) and by affecting the stele: cortex ratio (Fig. 5). These correlations likely reflect that the root parameter interactions implicated in P acquisition were variously influenced according to the P-fertilizer type. Therefore, these contrasting responses seem to be P-form dependent. Our results suggest that the P-fertilizers used in our experiment can influence differently the relation between root anatomical and morphological characteristics associated with P acquisition efficiency. Besides, there was a significant correlation between RPAE and RL ($r = 0.420^*$), RSA ($r = 0.423^*$), SD ($r = 0.435^*$), Root TWC ($r = 0.470^*$) and RMD ($r = -0.632^{**}$) (Table 2). These findings are in line with several studies showing that P-acquisition efficiency can be reached via various interactions (revealed by negative or positive correlations) between anatomical and morphological root traits (Wen et al., 2017 & 2019, Lyu et al., 2016).

The application of Ortho-A at a high P dose (45 to 60 ppm P) and Poly-B at low doses (30 and 45 ppm P) could be considered the appropriate P sources and doses for durum wheat growth under salinity given suitable root growth performance revealed during the experiment. Compared to orthophosphates, polyphosphates enriched soil with high quantities of available P in the rhizosphere, which positively impacts the P acquisition in the root of plants grown under salt-stress conditions. Furthermore, the improved P uptake under Poly-B could be related to its progressive hydrolysis through acidification of the rhizosphere and secretion of enzymes that hydrolase P, assuming that both mechanisms are implicated in the hydrolysis of polyphosphates (Dick and Tabatabai, 1986, Ahmad et al., 2001, Wang et al., 2019, Khourchi et al., 2022a). However, these interactions are not well understood to date due to the diversity of quantitative root parameters involved in P acquisition by plants (Wen et al., 2017, Walk et al., 2006, Isaac and Borden, 2019).

5. Conclusion

In this study, we focused on different root responses of wheat plants grown under the combined effect of salinity and P availability using different doses and forms of P-fertilizers. Our findings showed that salt stress induced, at both, anatomical and morphological levels, a series of modifications in the roots of wheat plants. Indeed, Compared to salt-stressed and unfertilized plants (C+), soluble P-fertilizers significantly increased soil available P, Root P-content, Root P Acquisition efficiency (RPAE), Root Length (RL), Root surface area (RSA), Root volume (RV), root mass density (RMD), Root Tissue water content (TWC), root tip number, vascular cylinder diameter and SD/CT ratio. The increased anatomical and morphological root parameters observed under P-treatments could determine the root performance and efficiency to acquire water and P and their transport to the aboveground organs of wheat plants under salinity. Furthermore, Poly-B showed the best performance in both morphological and anatomical parameters at lower doses while Ortho-A revealed significant positive responses within the increase in P concentration. Indeed, for appropriate management of P fertilization under salt stress, polyphosphates could be a promising alternative to reduce phosphorus losses over time in soils due to the slow and progressive release of available P in the rhizosphere and their property of chelating micronutrients that can positively affect the yield while reducing the frequency of fertilizer application

Authors contribution

A.L., and A.O conceptualized and designed the experiment and lab studies; A.L and A.M performed the studies, A.L, and R.N analysed the samples and data; A.L., Y.Z., G.C and A.O., wrote the paper. All authors discussed the results and approved the final draft.

Disclosure statement

The authors declare that the research was performed in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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

Data availability

Data will be made available on request.

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