



Effects of phosphorus supply and salt stress on plant growth, organic acid concentration, and sodium, potassium, calcium, magnesium, and phosphorus utilization in wheat

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Abstract

Nutrient utilization efficiency in wheat could be affected by fertilizer supply and soil properties such as salinity. A greenhouse pot study involving two wheat genotypes (Shavano and AK58), two phosphorus (P) supply levels [imposed by adding 0.5 mM KH_2PO_4 (+P), and 0 mM KH_2PO_4 (–P)], and two salt stress levels [imposed by adding 100 mM NaCl (+S), and 0 mM NaCl (–S)] was undertaken to study the impact of P supply and salt stress on organic exudation, nutrient utilization, and plant growth in wheat. At the seedling stage in the –P–S treatment, the tall genotype (Shavano) had higher succinic, fumaric, malic, and malonic acid concentrations in roots than the dwarf genotype (AK58), suggesting genotypic differences in adapting to unfavorable conditions. Salt stress increased Na and decreased K in roots and shoots (straw). At maturity, the –P treatment increased the total root length (TRL) to aboveground biomass (ABG) ratio relative to the +P treatment, suggesting that –P wheat required more root length to sustain equivalent aboveground biomass than +P wheat. AK58 and Shavano required 8.6–13.8 mg and 31.9–36.1 mg P to achieve 1 g grain across all treatments, respectively. The increased P efficiency of AK58 relative to Shavano was probably due to the increased harvest index conferred by dwarf genes. Wheat coordinated adaptations in root architecture and aboveground plant biomass combined with changes in root exudation and nutrient uptake to deal with P deficiency and salt stress, consequently altering nutrient utilization.

Keywords Salt stress · Phosphorus supply · Root · Organic acid · Plant performance

Introduction

Phosphorus (P) is an essential element for plant growth. P deficiency usually leads to adaptive responses at the physiological and biochemical levels, consequently modifying root morphology/architecture and aboveground plant development to maintain essential P uptake (Lynch 1995; Tshewang et al. 2020).

Plant root exudation interacts with the soil surrounding roots; for instance, low molecular weight organic acids (LMWOAs) can change the redox state and pH of the rhizosphere, facilitating nutrient uptake for plant growth (Wu et al. 2018). Organic acids such as malic, citric, fumaric, succinic, oxalic (OA), and oxalo-acetic acids involved in the Krebs cycle are among the most-studied LMWOAs. A recent study on wheat reported increased soil Olsen-P concentrations, P uptake, and yields after applying LMWOAs, particularly OA and citric acid, combined with soil P fertilizer (Mohankumar et al. 2022). Given

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that genetic and environmental factors govern organic acid exudation, two strategies can be explored to improve crop P economy in agricultural practices: (1) selecting genotypes with an increased ability to exude organic acids and uptake P and (2) manipulating the environment surrounding the root surface to increase P availability.

Salt-affected soils seriously inhibit plant growth, including morphological appearance and biomass accumulation. The reduced growth can be partially attributed to reduced levels of bioactive gibberellins inhibiting the protoxylem cell differentiation process and changes in nutrient uptake (Møller et al. 2009; Zhao et al. 2021; Augstein et al. 2022). In addition, salt-affected soils have limited P availability due to P and Ca fixation. As soil salinity and P deficiency both adversely affect plant growth (Abbas et al. 2018), it is important to determine the interactive effects of P supply and salt stress on plant growth and nutrient utilization. However, these effects are inconsistent in the literature; for example, salinity reduced (Martinez et al. 1996), increased (Martinez & Lauchli 1994), or did not change (Silberbush & Ben-Asher 1989) P uptake, probably due to genetic differences between species and/or within genotypes, sampling growth stages, and growth substrates used (Marschner 1995).

Zribi et al. (2011) reported that salt-treated barley plants under P deficiency had higher salt tolerance than those grown under sufficient P supply, which they attributed to increased root:shoot dry weight ratio, root length, K^+/Na^+ ratio, leaf proline, and soluble sugar concentrations and decreased Na^+ accumulation in upper leaves. In another study, moderate salinity stress alleviated P deficiency effects in *Hordeum maritimum* L. (Zribi et al. 2012).

Mineral concentrations in mature wheat grain rely on root-to-shoot translocation and remobilization during senescence. K and Mg are rapidly translocated after root uptake, while Ca is predominantly retained by mature and senescent organs, with little Ca translocation from leaves to seeds (White and Broadley 2003; Cobalchin et al. 2021). Wheat straw contains higher amounts of K and Mg than grain, while Ca is equally concentrated in straw and grain (Jankowski et al. 2016). Large amounts of Na in saline soils will compete with the Ca and Mg adhering to soil particles; therefore, Ca and Mg uptake in plants under salt stress likely differs those under non-saline conditions.

Macronutrient deprivation can cause large fluctuations in plant elemental compositions and thus imbalance the nutrient environment (Courbet et al. 2021); combined low P availability and salt stress presumably has a similar effect. We hypothesized that an increased organic acids concentrations and an altered root architecture would facilitate nutrient uptake under suboptimal P conditions combined with

salt stress. A pot experiment was therefore conducted to investigate the interactive effects of P supply and salt stress on plant growth, organic acid concentrations, and Na, K, Ca, Mg, and P utilization in wheat.

Materials and methods

Plant material

A dwarf wheat cultivar ‘AK58’ (also known as ‘Bainong Aikang 58’), widely grown in Northern China Plain, and a tall wheat genotype ‘Shavano’ originally from the USA were used in this study.

Greenhouse experiment

Greenhouse experiment was conducted from October 2021 to May 2022 at Binzhou University (Binzhou, Shandong province, China), with light and temperature conditions set to 16 h light at 25 ± 3 °C and 8 h dark at 18 ± 3 °C.

Three factors P supply, salt stress, and genotype were employed in the experiment with three replications. P-added and non-P-added treatments were regarded as two ‘P supply’ levels, while non-salt stress and salt stress were regarded as two ‘salt stress’ levels. ‘AK58’ and ‘Shavano’ were regarded as two levels for factor ‘genotype’. The experiment was designed with intention to examine effects of the treatment factors at two sampling time points, one at six weeks after transplanting and another at maturity. In total, there were forty-eight plastic pots involved in the experiment. Each plastic pot (diameter: 14 cm, height: 18 cm) was filled with 1.3 kg Turface Athletics™ Profile® Porous Ceramic Greens Grade soil amendment as a growth substrate (PROFILE Products LLC, USA; www.profileproducts.com). The Greens Grade had 74% porosity, pH 5.5, 33.6 m Eq/100 g cation exchange capacity, and 5.5 mg/kg $NaHCO_3$ extractable Olsen-P concentration. The pots were irrigated with either 1.2 L of 100 mM NaCl or 1.2 L distilled water to saturation (100% relative water content) and placed in a greenhouse for 10 days to allow the soil moisture to decrease to a relative water content of about 60%. Relative water content was calculated using formula: $\frac{W_x - W_0}{W_s - W_0} \times 100\%$, W_0 represents weight of pot with dry soil amendment and W_s represents saturated pot, while W_x was the weight of tested pot.

Seeds of each genotype were germinated on Petri dishes at room temperature. Three uniformly germinated seeds were selected and transplanted to each pot with substrate pre-irrigated by salt or water. On the day of transplanting, each pot was watered with 400 mL of nutrient solution. The nutrient solution for the P-added (+P) treatment contained

1 mM $\text{Ca}(\text{NO}_3)_2$, 0.5 mM MgSO_4 , 0.5 mM KH_2PO_4 , 1.5 mM KCl , 2.5 mM CaCl_2 , 1 μM H_3BO_3 , 50 nM $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$, 0.5 μM CuSO_4 , 1 μM ZnSO_4 , 1 μM MnSO_4 , 0.1 mM FeNa-EDTA , and the non-P-added (–P) treatment contained 1 mM $\text{Ca}(\text{NO}_3)_2$, 0.5 mM MgSO_4 , 2.0 mM KCl , 2.5 mM CaCl_2 , 1 μM H_3BO_3 , 50 nM $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$, 0.5 μM CuSO_4 , 1 μM ZnSO_4 , 1 μM MnSO_4 , and 0.1 mM FeNa-EDTA .

Thereafter, the pots were irrigated every 10 days, with each pot receiving 200 mL nutrient solution combined with 200 mL of 100 mM NaCl for salt stress treatment (+S) and 200 mL distilled water for non-salt treatment (–S).

Plants were harvested at two time points, six weeks after transplanting and maturity. The harvested seedlings were separated into roots and shoots, while mature plants were separated into roots, straw, and grain; mature roots were rinsed with distilled water to remove residual adhered soil. Plant parts were oven-dried and ground (as per the roots) immediately after harvest.

Evaluation of salinity in the growth substrate

In order to evaluate the salinity that plants had been subjected to during the growth period, electrical conductivity (EC) of the growth substrate at the end of the experiment was measured using a conductivity meter (DDS-307, Shanghai Leici Instrument Co. Ltd, China) as described in Zhao et al. (2022). An equivalent NaCl concentration was then estimated as an index of salinity based on a linear regression equation between NaCl concentration and EC (Supplementary Fig S1): salinity (mM) = $(\text{EC}_{\text{salt treatment}} - \text{EC}_{\text{non-salt treatment}})/0.0813$, wherein $\text{EC}_{\text{salt treatment}}$ was the EC value of growth substrate under salt treatment and $\text{EC}_{\text{non-salt treatment}}$ for that under non-salt treatment, respectively.

Root length measurements

For the first harvest, three seedlings in the pot were harvested six weeks after transplantation by carefully removing the soil particles with tap water, with the washed roots subsequently scanned with an Epson® Expression 10000XL scanner to determine root length. At maturity, the roots were harvested once the soil had nearly dried at room temperature, air-dried, shaken to remove any remaining attached soil particles, and scanned. Total root length (TRL) for each root sample was determined using the WinRHIZO Root Analysis System (Regent Instruments, Canada). Root length per pot was used as an index to be compared between treatments, due to the difficulty in separating root for each plant.

Measurement of organic acid concentrations

Fifty milligrams of root or shoot sample was weighed into a 15 mL tube with 10 mL of 30% methanol aqueous solution (containing 0.1% formic acid). The tube was oscillated 100 times per minute on a shaker for 5 min and then centrifuged at 10,000 rpm for 10 min at 4 °C; the supernatant was subsequently transferred to a detection bottle. Organic acid concentrations were measured using an Acquity UPLC® Beh C18 column (2.1 × 100 mm, 1.7 μm , Waters, USA) set at 40 °C, with mobile phases of (A) water (containing 0.1% formic acid) and (B) methanol water (containing 0.1% formic acid). Gradient elution conditions were 0–3 min at 30% B, 3–5 min at 30–50% B, 5–7 min at 50–90% B, 7–9 min at 90% B, and 9–13 min at 30% B with a 0.4 mL/min flow rate.

The concentration of each organic acid (succinic, fumaric, malic, citric, malonic, and pantothenic) in roots/shoots ($\mu\text{g/g}$) was calculated as:

$$C_{\text{organic acid in roots/shoots}} = (C_{\text{organic acid in supernatant}} \times 10 \text{ mL})/50 \text{ mg.} \quad (1)$$

Elemental measurements

Root, shoot, and grain samples (50 mg each) were digested in 13 mL nitric acid and 2 mL H_2O_2 using a microwave digestion instrument. P, Na, K, Ca, and Mg concentrations were measured using an inductively coupled plasma mass spectrometer (ICP-MS).

Calculation of Na, K, Ca, Mg, and P utilization

At both harvests, aboveground plants and roots were oven-dried at 70 °C and weighed with a digital balance (accuracy 0.1 mg) to obtain aboveground biomass (ABG) and root dry weight.

Na, K, Ca, Mg, and P accumulation in seedlings shoot, root, and whole plant (mg/pot) was calculated as:

$$\begin{aligned} \text{Total accumulation of an individual element in shoot (mg/pot)} \\ = \text{shoot weight} \times C_{\text{shoot}}, \end{aligned}$$

$$\begin{aligned} \text{Total accumulation of an individual element in root (mg/pot)} \\ = \text{root weight} \times C_{\text{root}}, \end{aligned}$$

$$\begin{aligned} \text{Total accumulation of an individual element in whole plant (mg/pot)} \\ = \text{shoot weight} \times C_{\text{shoot}} + \text{root weight} \times C_{\text{root}}, \end{aligned}$$

where C_{shoot} and C_{root} are the concentrations (mg/kg) of each measured element in shoots and roots, respectively.

Total Na, K, Ca, Mg, and P accumulation in mature grain, straw, root, and whole plant (mg/pot) was calculated as:

Total accumulation of an individual element in grain (mg/pot)

$$= \text{grain weight} \times C_{\text{grain}}$$

Total accumulation of an individual element in straw (mg/pot)

$$= \text{straw weight} \times C_{\text{straw}}$$

Total accumulation of an individual element in root (mg/pot)

$$= \text{root weight} \times C_{\text{root}}$$

Total accumulation of an individual element in whole plant (mg/pot)

$$= \text{grain weight} \times C_{\text{grain concentration}} + \text{straw weight} \times C_{\text{straw}} + \text{root weight} \times C_{\text{root}}$$

where C_{grain} , C_{straw} , and C_{root} are the concentrations (mg/kg) of each measured element in grain, straw, and roots, respectively.

For crop P economy, the P requirement (expressed per g of grain yield) was calculated as:

$$\text{P requirement} = \text{Total P accumulation (mg)} / \text{grain weight (g)}$$

Statistical analysis

Statistical analysis was conducted using SPSS software (version 16.0, Chicago, SPSS Inc.). For plant growth parameters, i.e., plant height (cm), grain weight (g/pot), aboveground biomass (g/pot), root weight (g/pot), and total root length (m/pot), analysis of variance (ANOVA) was used to test significance of the effect of three factors (salt stress, P supply, genotype) and their interactions. For other parameters, organic acid concentrations, elemental concentrations, and total elemental accumulation, analysis of variance (ANOVA) was used to test the significance of effect of four factors (salt stress, P supply, genotype, and organ) and their interactions. Multiple comparisons (Duncan's) for a given genotype were conducted after ANOVA to compare the significance between values in different treatments, following the suggestion that combined stresses should be regarded as a new state of abiotic stress (Mittler 2006).

Results

Root development and plant growth as affected by P supply and salt stress

The average electrical conductivity (EC) of growth substrate under salt stress treatments at the end of experiment was

16.8 dS/m, while the value under non-salt treatment was 3.2 dS/m. Compared with the 100 mM NaCl solution which had an EC of 9.8 dS/m, it was therefore reasonable to deduce that the plants grown in the growth substrate under salt stress had been subjected to a gradually increased salinity from 100 mM NaCl to a salinity equivalent of 167 mM NaCl at the late growth stage.

Aboveground biomass measured at six weeks post-transplanting was significantly affected by salt stress ($P < 0.01$) and P supply ($P < 0.01$) but not by genotype or their interactions (Supplementary Table S1). In contrast, root dry weight measured at six weeks post-transplanting was significantly affected by genotype ($P < 0.01$), salt stress ($P < 0.01$), and P supply ($P < 0.05$) but not by their interactions (Supplementary Table S2). Aboveground biomass and root dry weight of both genotypes (AK58 and Shavano) decreased with -P supply compared with +P supply (Fig. 1A, B). Lateral root length and TRL were significantly affected by genotype and salt stress but not P

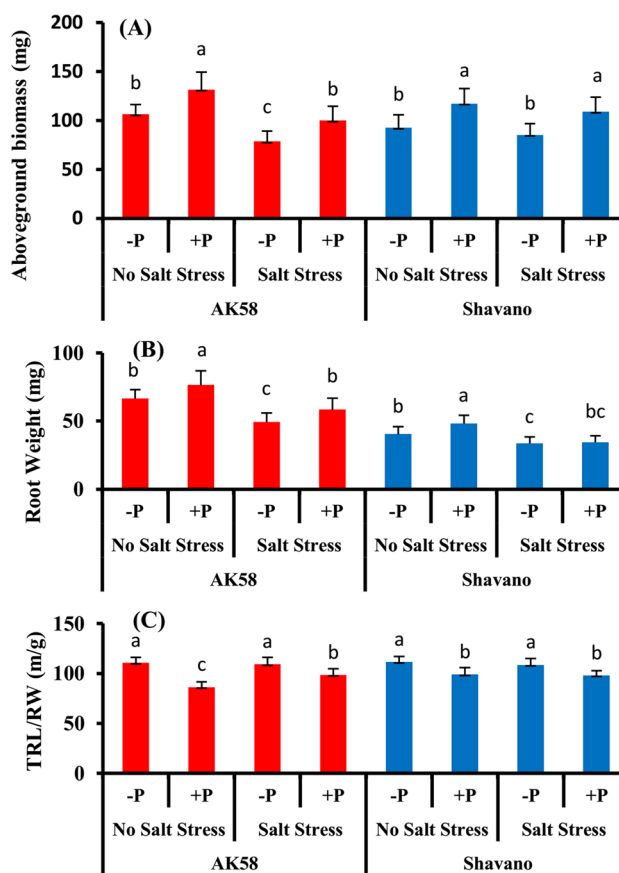


Fig. 1 Aboveground biomass **A**, root dry weight **B**, and TRL/RW ratio **C** at six weeks post-transplanting of two wheat genotypes [dwarf AK58 (red) and tall Shavano (blue)] grown under two P supply levels [no P (-P), P added (+P)] and two salt stress levels [no salt stress (-S), salt stress (+S)]. Different letters within the same genotype indicate significant differences ($P < 0.05$) between treatments

Table 1 Growth parameters at maturity of two wheat genotypes (AK58 and Shavano) grown under two P supply levels [no P (–P), P added (+P)] and two salt stress levels [no salt stress (–S), salt stress (+S)]

Genotype	Treatment	Plant height (cm)	Grain weight (g/pot)	Aboveground biomass (g/pot)	Root weight (g/pot)	Total root length (m/pot)
AK58	–S–P	49.3±3.3 bc	1.8±0.15 b	3.6±0.32 c	1.4±0.12 b	79.2±10.20 b
	–S+P	57.8±1.0 a	2.2±0.14 a	6.1±0.27 a	2.5±0.15 a	111.2±11.89 a
	+S–P	47.0±4.9 c	1.2±0.07 d	5.1±0.20 b	1.2±0.09 b	67.8±9.93 b
	+S+P	50.0±2.6 b	1.5±0.14 c	5.6±0.48 a	1.4±0.13 b	69.9±12.66 b
Shavano	–S–P	69.7±5.6 b	0.6±0.03 b	3.5±0.14 b	2.0±0.10 b	109.1±13.43 b
	–S+P	79.0±5.3 a	0.8±0.06 a	5.1±0.28 a	3.3±0.18 a	138.4±12.55 a
	+S–P	65.3±5.0 b	0.5±0.03 c	3.4±0.11 b	1.9±0.13 b	108.2±13.61 b
	+S+P	73.7±2.5 ab	0.7±0.04 ab	4.5±0.15 a	2.0±0.16 b	95.8±14.19 b

Different letters within the same genotype indicate significant differences ($P < 0.05$)

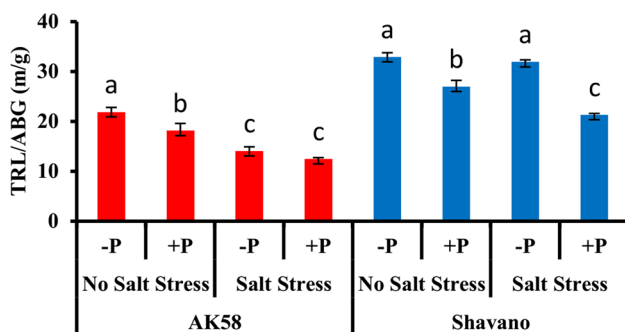


Fig. 2 TRL/ABG ratio of mature plants of two wheat genotypes [dwarf AK58 (red) and tall Shavano (blue)] grown under two P supply levels [no P (–P), P added (+P)] and two salt stress levels [no salt stress (–S), salt stress (+S)]. Different letters within the same genotype indicate significant differences ($P < 0.05$) between treatments

supply (Supplementary Tables S3 and S4). P supply significantly affected the TRL/ABG ratio ($P < 0.01$) (Supplementary Table S5, Fig. 1C), generally increasing under –P supply relative to +P supply.

At maturity, –P supply inhibited the growth of AK58 and Shavano in terms of plant height, aboveground biomass, grain weight/pot, and root weight/pot, compared with +P supply (Table 1). The TRL/ABG ratio for all treatments ranged from 12.5 to 21.9 m/g for AK58 and 21.3–32.9 m/g for Shavano (Fig. 2). Both genotypes under –P supply had higher TRL/ABG ratios than +P supply regardless of salt treatment.

For AK58, the –P treatment had 44% and 14.3% less root weight/pot than the +P treatment under –S and +S supply, respectively. The corresponding reductions for Shavano were 39.4% and 5%. Both genotypes had a greater root weight/aboveground biomass ratio under –P supply than +P supply regardless of salt treatment.

Organic acid concentrations in roots and aboveground plants as affected by P supply and salt stress

Genotype, salt stress, P supply, organ, and their interactions affected succinic, fumaric, malic, citric, malonic, and pantothenic acid concentrations (Supplementary Tables S6–S11). Significant effects occurred for salt stress on the concentrations of all six measured organic acids, genotype on succinic, malic, malonic, and pantothenic acid concentrations, and P supply on succinic, fumaric, malic, and pantothenic acid concentrations.

Organic acid concentrations differed between roots and shoots (Supplementary Tables S6–S11), concentrations of succinic, fumaric, malic, citric, malonic, and pantothenic acid in the shoots were higher than roots (Table 2). Salt stress significantly reduced succinic, fumaric, malic, citric, and pantothenic acid concentrations in the roots of both genotypes.

Due to the interactive effects between salt stress and P supply, salt stress significantly affected organic acid concentrations in response to P supply. For example, in AK58, –P supply without salt stress decreased fumaric, malic, citric, and malonic acid concentrations in roots, while –P supply with salt stress increased succinic, fumaric, malic, and citric acid concentrations in roots (Table 2). Organic acid concentrations also significantly differed between genotypes in response to salt stress and P supply. For Shavano, –P supply without salt stress increased succinic, citric, malonic, and pantothenic acid concentrations in roots, and –P supply with salt stress increased succinic, malic, citric, and pantothenic acid concentrations in roots (Table 2); for AK 58, –P supply without salt stress increased pantothenic acid concentrations in roots, and –P supply with salt stress increased, though not significantly, the concentrations of succinic, fumaric, malic, citric, and pantothenic acid in roots.

Table 2 Root and shoot organic acid concentrations at six weeks post-transplanting of two wheat genotypes (AK58 and Shavano) grown under two P supply levels [no P (–P), P added (+P)] and two salt stress levels [no salt stress (–S), salt stress (+S)]

Genotype	Organ	Treatment	Organic acid concentration (ug/g)					
			Succinic acid	Fumaric acid	Malic acid	Citric acid	Malonic acid	Pantothenic acid
AK58	Root	–S–P	4.6±0.65 b	1.6±0.24 b	127.0±23.03 b	117.7±42.40 b	1.2±0.25 c	23.6±2.45 a
		–S+P	5.7±0.52 a	2.5±0.90 a	328.8±28.48 a	213.2±28.44 a	2.6±0.28 a	10.0±3.01 b
		+S–P	3.3±0.70 c	0.5±0.04 c	36.9±3.66 c	59.7±5.47 c	1.2±0.04 c	3.7±1.01 c
		+S+P	2.9±0.33 c	0.4±0.08 c	15.5±2.39 c	38.0±4.59 c	1.7±0.12 b	3.6±0.31 c
	Shoot	–S–P	13.9±2.3 b	1.5±0.43 b	288.0±9.80 b	774.6±40.80 b	46.3±5.45 a	282.2±9.88 a
		–S+P	16.3±4.0 b	2.1±0.25 a	411.2±48.61 a	879.6±57.06 a	54.4±5.59 a	102.1±12.91 b
		+S–P	23.3±1.3 a	1.2±0.14 bc	270.0±40.05 bc	437.0±50.32 c	31.1±3.47 b	81.8±5.11 c
		+S+P	24.1±4.4 a	0.9±0.24 c	213.4±6.33 c	285.8±10.08 d	20.1±3.93 c	59.0±12.44 d
Shavano	Root	–S–P	5.5±0.63 a	1.8±0.11 a	168.6±25.81 a	116.4±12.92 a	2.3±0.11 a	7.5±0.29 a
		–S+P	4.3±0.23 a	2.0±0.17 a	195.6±23.62 a	104.9±13.97 a	1.5±0.09 b	6.5±0.69 a
		+S–P	2.8±0.68 b	0.3±0.03 b	37.8±14.74 b	48.7±16.13 b	1.0±0.32 b	4.0±1.91 b
		+S+P	2.0±0.86 b	0.4±0.16 b	15.2±7.94 b	31.2±12.65 b	1.3±0.59 b	3.7±1.64 b
	Shoot	–S–P	22.4±2.27 b	1.7±0.20 ab	440.0±20.59 a	590.3±45.91 b	34.3±4.72 a	94.4±8.56 bc
		–S+P	29.3±5.62 ab	1.9±0.26 a	461.1±36.30 a	756.8±22.55 a	34.4±5.06 a	121.6±10.30 a
		+S–P	24.2±1.30 b	1.2±0.06 c	358.4±65.37 b	527.9±45.85 b	28.4±5.80 ab	106.0±10.23 ab
		+S+P	37.7±6.57 a	1.5±0.08 bc	307.5±16.58 b	391.0±52.11 c	21.4±3.91 b	82.0±10.54 c

Different letters within the same organ and genotype indicate significant differences ($P < 0.05$)

Table 3 Root and shoot Na, K, Ca, Mg, and P concentrations at six weeks post-transplanting of two wheat genotypes (AK58 and Shavano) grown under two P supply levels [no P (–P), P added (+P)] and two salt stress levels [no salt stress (–S), salt stress (+S)]

Genotype	Organ	Treatment	Elemental concentration (g/kg)				
			Na	K	Ca	Mg	P
AK58	Root	–S–P	2.1±0.14 c	37.5±1.3 b	2.6±0.11 a	2.0±0.07 d	3.7±0.17 b
		–S+P	2.1±0.20 c	37.4±2.2 b	2.2±0.23 b	2.3±0.19 c	4.0±0.21 b
		+S–P	13.1±1.10 b	41.2±3.3 b	1.9±0.09 b	2.8±0.09 b	4.0±0.31 b
		+S+P	20.8±1.39 a	45.0±3.3 a	2.7±0.25 a	4.4±0.11 a	5.9±0.05 a
	Shoot	–S–P	0.9±0.07 c	81.7±4.5 a	6.2±0.33 a	6.2±0.35 a	10.7±0.57 b
		–S+P	0.6±0.01 c	76.2±1.3 a	3.7±0.23 c	3.6±0.36 c	12.7±0.98 a
		+S–P	3.1±0.35 b	73.7±13.0 a	4.9±0.37 b	5.0±0.72 b	12.8±0.65 a
		+S+P	5.9±0.23 a	76.8±11.6 a	5.4±0.53 b	5.9±0.25 a	11.2±0.32 b
Shavano	Root	–S–P	2.8±0.32 c	41.0±4.1 a	2.1±0.20 c	2.6±0.22 c	4.3±0.27 a
		–S+P	1.8±0.12 d	31.4±2.6 b	2.3±0.11 c	2.0±0.09 d	3.3±0.27 bc
		+S–P	9.4±0.60 b	30.5±1.9 b	3.7±0.13 a	3.2±0.26 b	2.9±0.23 c
		+S+P	12.2±0.64 a	33.6±2.9 b	2.7±0.17 b	5.5±0.43 a	3.6±0.31 b
	Shoot	–S–P	0.6±0.10 c	68.1±10.2 a	7.3±0.85 a	5.4±0.25 b	15.0±1.53 a
		–S+P	0.5±0.06 c	67.2±3.2 a	5.6±0.60 b	4.5±0.21 c	14.3±1.82 a
		+S–P	10.2±1.63 a	73.7±13.6 a	7.1±0.50 a	7.2±0.56 a	13.2±0.33 a
		+S+P	4.5±0.20 b	60.9±5.2 a	5.1±0.26 b	5.4±0.33 b	13.5±0.62 a

Different letters within the same organ and genotype indicate significant differences ($P < 0.05$)

Na, K, Ca, Mg, and P utilization as affected by P supply and salt stress

Genotype, salt stress, P supply, and organ significantly affected Na concentration at the seedling stage and maturity

(Supplementary Tables S12 and S13). Salt stress increased shoot and root Na concentrations at the seedling stage and maturity relative to no salt stress (Tables 3 and 4). Salt stress increased grain Na concentration (except AK58 under –P supply) relative to no salt stress.

Table 4 Root, straw, and grain Na, K, Ca, Mg, and P concentrations at maturity of two wheat genotypes (AK58 and Shavano) grown under two P supply levels [no P (–P), P added (+P)] and two salt stress levels [no salt stress (–S), salt stress (+S)]

Genotype	Organ	Treatment	Elemental concentration (g/kg)				
			Na	K	Ca	Mg	P
AK58	Root	–S–P	3.4±0.27 c	15.4±2.05 a	4.9±0.27 a	4.9±0.46 a	1.1±0.09 ab
		–S+P	1.5±0.03 c	11.2±0.89 b	4.2±0.19 b	3.6±0.22 b	1.0±0.08 ab
		+S–P	20.1±1.72 a	8.1±0.24 c	3.0±0.23 c	2.6±0.17 c	0.9±0.06 b
		+S+P	17.2±1.95 b	10.8±0.79 b	4.4±0.26 b	4.6±0.34 a	1.1±0.08 a
	Straw	–S–P	0.2±0.02 c	28.1±2.89 a	1.5±0.11 d	1.8±0.04 c	3.6±0.23 a
		–S+P	0.2±0.02 c	30.5±2.23 a	3.4±0.15 c	3.6±0.29 b	2.7±0.03 c
		+S–P	34.2±2.06 a	17.3±0.97 b	13.1±0.69 a	12.3±0.65 a	2.8±0.16 b
		+S+P	12.5±0.49 b	18.0±1.16 b	8.8±0.39 b	12.6±0.71 a	3.0±0.28 b
	Grain	–S–P	7.7×10 ⁻² ±5.6×10 ⁻³ b	5.0±0.11 ab	0.6±0.04 a	2.3±0.03 a	4.2±0.33 ab
		–S+P	5.9×10 ⁻² ±4.6×10 ⁻³ c	4.9±0.44 b	0.3±0.02 d	1.9±0.18 b	3.8±0.15 b
		+S–P	7.8×10 ⁻² ±3.6×10 ⁻³ b	5.1±0.23 ab	0.4±0.03 c	2.0±0.13 b	3.8±0.19 b
		+S+P	0.1±9.5×10 ⁻³ a	5.5±0.35 a	0.5±0.02 b	2.1±0.09 ab	4.4±0.14 a
Shavano	Root	–S–P	2.0±0.14 d	14.4±0.75 a	6.2±0.44 b	4.5±0.31 ab	1.3±0.12 b
		–S+P	5.1±0.45 c	12.0±0.82 b	7.2±0.74 ab	6.1±1.96 a	1.6±0.09 a
		+S–P	19.7±0.90 a	6.3±0.34 d	8.2±0.52 a	3.3±0.23 b	1.2±0.10 b
		+S+P	17.2±0.24 b	9.3±0.46 c	6.8±0.59 b	3.4±0.24 b	1.3±0.11 b
	Straw	–S–P	0.7±0.03 c	42.8±2.87 a	2.2±0.12 b	2.9±0.33 a	4.8±0.31 a
		–S+P	0.8±0.07 c	41.3±2.71 ab	1.5±0.13 c	1.3±0.11 b	3.8±0.29 b
		+S–P	14.5±1.17 b	36.8±2.82 b	2.2±0.19 b	3.0±0.07 a	5.1±0.60 a
		+S+P	16.4±1.28 a	39.3±2.75 ab	2.8±0.13 a	3.1±0.32 a	4.6±0.14 a
	Grain	–S–P	0.1±5.4×10 c	7.7±0.07 b	0.5±0.03 b	2.6±0.06 ab	4.5±0.30 b
		–S+P	9.0×10 ⁻² ±9.4×10 ⁻³ c	8.6±0.30 ab	0.6±0.05 a	2.7±0.03 ab	4.8±0.54 b
		+S–P	0.2±0.01 b	8.7±0.76 a	0.5±0.05 bc	2.8±0.31 a	5.6±0.39 a
		+S+P	0.4±0.03 a	7.8±0.39 b	0.4±0.03 c	2.3±0.23 b	4.7±0.36 b

Different letters within the same organ and genotype indicate significant differences ($P < 0.05$)

At the seedling stage, salt stress and P supply had no significant effects on K concentrations, while genotype and organ had significant effects (Supplementary S14). In contrast, all four factors significantly affected K concentrations at maturity (Supplementary S15). Salt stress sharply increased root and shoot Na/K ratios at the seedling stage relative to no salt stress, on average, by 5.5 (Shavano) to 7.0 (AK58) times in roots and 8.0 (Shavano) to 14.0 (AK58) times in shoots. At maturity, salt stress had significantly decreased shoot and root K concentrations in both genotypes relative to no salt stress (Table 4).

Ca concentrations at the seedling stage were significantly affected by genotype ($P < 0.01$), P supply ($P < 0.01$), organ ($P < 0.01$), and some interactions among factors (Supplementary S16). Mg concentrations at the seedling stage were significantly affected by genotype ($P < 0.01$), salt stress ($P < 0.01$), and organ ($P < 0.01$) (Supplementary S18). P concentrations at the seedling stage were significantly

affected by genotype ($P < 0.01$) and organ ($P < 0.01$) (Supplementary S20). In contrast, at maturity, Ca, Mg, and P concentrations were significantly affected by all four factors, genotype ($P < 0.01$), salt stress ($P < 0.01$), P supply ($P < 0.01$), organ ($P < 0.01$), and all interactions among factors (Supplementary Tables S17, S19, and S21).

Salt stress increased root and shoot (straw) Na accumulation in both genotypes at the seedling stage and maturity relative to no salt stress (Tables 5 and 6) but decreased root and straw K accumulation at maturity (Table 6). Straw had higher K concentrations and total accumulation than roots and grain in both genotypes across all treatments. Ca, Mg, and P accumulation significantly differed between +P and –P supply. For example, AK58 grown under salt stress with +P supply increased root Ca, Mg, and P and shoot Ca and Mg concentrations and total accumulation at the seedling stage relative to –P supply.

The P requirement (expressed as P per g of grain yield), a critical index for evaluating crop P economy, differed

Table 5 Total root and shoot Na, K, Ca, Mg, and P accumulation at six weeks post-transplanting of two wheat genotypes (AK58 and Shavano) grown under two P supply levels [no P (–P), P added (+P)] and two salt stress levels [no salt stress (–S), salt stress (+S)]

Genotype	Organ	Treatment	Total elemental accumulation (g/pot)				
			Na	K	Ca	Mg	P
AK58	Root	–S–P	0.14±0.02 c	2.50±0.32 a	0.18±0.02 a	0.13±0.02 b	0.25±0.03 ab
		–S+P	0.16±0.03 c	2.83±0.50 a	0.16±0.03 a	0.17±0.03 b	0.31±0.04 a
		+S–P	0.64±0.05 b	1.94±0.14 b	0.09±0.01 b	0.14±0.01 b	0.19±0.02 b
		+S+P	1.20±0.16 a	2.64±0.30 a	0.15±0.02 a	0.25±0.03 a	0.35±0.05 a
	Shoot	–S–P	0.10±0.02 c	8.86±1.31 ab	0.66±0.10 a	0.66±0.10 a	1.13±0.17 b
		–S+P	0.07±0.01 c	10.17±1.41 a	0.49±0.08 ab	0.48±0.08 b	1.67±0.27 a
		+S–P	0.24±0.02 b	5.57±0.36 b	0.38±0.02 b	0.39±0.01 b	1.00±0.09 b
		+S+P	0.59±0.07 a	7.81±1.03 b	0.53±0.04 a	0.59±0.08 a	1.11±0.14 b
Shavano	Root	–S–P	0.11±0.03 b	1.76±0.39 a	0.09±0.02 b	0.10±0.02 b	0.18±0.03 a
		–S+P	0.08±0.01 b	1.55±0.07 a	0.11±0.01 ab	0.10±0.01 b	0.16±0.01 ab
		+S–P	0.32±0.04 a	0.97±0.13 b	0.13±0.02 a	0.11±0.01 b	0.10±0.01 b
		+S+P	0.42±0.08 a	1.16±0.25 b	0.09±0.02 b	0.19±0.04 a	0.13±0.03 b
	Shoot	–S–P	0.06±0.02 c	6.48±1.78 b	0.68±0.16 a	0.51±0.09 a	1.40±0.32 ab
		–S+P	0.06±0.01 c	7.54±0.60 a	0.65±0.05 a	0.53±0.05 a	1.65±0.07 a
		+S–P	0.86±0.11 a	6.33±0.88 b	0.60±0.06 ab	0.61±0.05 a	1.12±0.13 b
		+S+P	0.49±0.04 b	7.44±0.44 a	0.55±0.05 b	0.58±0.05 a	1.47±0.13 a

Different letters within the same organ and genotype indicate significant differences ($P < 0.05$)

between dwarf genotype AK58 (8.6–13.8 mg) and tall genotype Shavano (31.9–36.1 mg). The P requirement increased under salt stress with –P and +P supply for AK58 and increased under –P supply and decreased under +P supply for Shavano.

Discussion

Roots usually change at the morphological and architectural level under P deficiency and salt stress. Indeed, increased lateral root length under P deficiency may offer more opportunities for wheat plants to absorb P (Zhao et al. 2018). Similarly, the TRL/ABG ratio at maturity increased under –P supply relative to +P supply, indicating that plants under –P supply require more root length to sustain equivalent aboveground biomass as +P supply. Therefore, an unfavorable P supply would increase the total root length/aboveground biomass ratio of wheat. Salt stress also inhibited the growth of both genotypes relative to no salt stress in terms of root weight, aboveground biomass, and harvest index.

The link between organic acid concentration and P uptake, particularly under P deficiency, is well documented. Thus, an increased organic acid concentration was assumed to facilitate P uptake suboptimal P conditions. However, changes in organic acid concentrations

under –P supply relative to +P supply were far more complex than anticipated. For example, in AK58, –P supply decreased organic acid concentrations in roots relative to +P supply under no salt stress. However, it increased organic acid concentrations (except malonic acid) under salt stress, suggesting an interactive effect of salt stress and P supply in controlling organic acid metabolism.

McGrail et al. (2021) showed that root tips of wild-type wheat varieties contained more organic acids than modern dwarf genotypes under P stress. Similarly, the tall genotype Shavano had higher succinic, fumaric, malic, and malonic acid concentrations in roots in the –P–S treatment than the dwarf genotype AK58, suggesting different adaptive mechanisms to unfavorable soil conditions.

Consistent with our hypothesis, salt stress and low P supply altered the pattern of nutrient utilization in terms of elemental concentration and total accumulation. For example, salt stress increased Na and decreased K in roots and shoots. In one study, wheat straw had higher K and Mg concentrations than wheat grain but similar Ca concentrations (Jankowski et al. 2016); however, our data showed AK58 and Shavano had higher K and Ca concentrations and total accumulation in straw than grain, while these two genotypes had higher Mg accumulations in straw than grain under salt stress. The discrepancy

Table 6 Total root, shoot, and grain Na, K, Ca, Mg, and P accumulation at maturity of two wheat genotypes (AK58 and Shavano) grown under two P supply levels [no P (-P), P added (+P)] and two salt stress levels [no salt stress (-S), salt stress (+S)]

Genotype	Organ	Treatments	Total elemental accumulation (g/pot)				
			Na	K	Ca	Mg	P
AK58	Root	-S-P	6.04±0.49 b	27.22±3.24 a	8.86±0.49 a	8.73±0.82 a	1.96±0.16 a
		-S+P	2.65±0.06 b	20.11±1.60 a	7.61±0.33 a	6.48±0.39 b	1.85±0.15 a
		+S-P	36.04±3.09 a	14.60±0.43 b	5.39±0.41 b	4.66±0.31 b	1.68±0.10 b
		+S+P	30.83±3.50 a	19.30±1.42 b	7.95±0.46 a	8.24±0.61 a	2.03±0.14 a
	Straw	-S-P	0.38±0.03 c	50.32±5.18 a	2.73±0.20 b	3.20±0.06 b	6.38±0.42 a
		-S+P	0.40±0.03 c	54.68±4.00 a	6.09±0.27 b	6.39±0.51 b	4.86±0.05 b
		+S-P	61.35±3.70 a	31.11±1.74 b	23.51±1.23 a	22.06±1.17 a	5.10±0.30 b
		+S+P	22.36±0.88 b	32.28±2.08 b	15.71±0.71 a	22.58±1.28 a	5.34±0.51 ab
	Grain	-S-P	0.14±0.01 a	8.90±0.20 ab	1.05±0.07 a	4.09±0.05 a	7.48±0.60 a
		-S+P	0.11±0.01 b	8.72±0.79 b	0.49±0.04 b	3.37±0.32 b	6.89±0.26 b
		+S-P	0.14±0.01 a	9.10±0.42 a	0.71±0.06 ab	3.50±0.24 b	6.76±0.34 b
		+S+P	0.19±0.02 a	9.94±0.62 a	0.90±0.03 a	3.71±0.16 ab	7.81±0.24 a
Shavano	Root	-S-P	3.50±0.26 b	25.78±1.35 a	11.13±0.79 b	8.03±0.56 b	2.39±0.22 a
		-S+P	9.19±0.80 b	21.48±1.48 a	30.77±1.33 a	11.81±2.52 a	2.78±0.16 a
		+S-P	35.39±1.61 a	11.36±0.61 b	14.62±0.94 b	5.93±0.42 c	2.08±0.18 b
		+S+P	30.81±0.44 a	16.65±0.82 b	12.17±1.05 b	6.04±0.45 bc	2.28±0.20 ab
	Straw	-S-P	1.24±0.06 b	76.75±5.15 a	3.89±0.22 ab	5.13±0.60 a	8.55±0.56 a
		-S+P	1.39±0.12 b	74.12±4.86 a	2.70±0.24 b	2.41±0.20 b	6.89±0.51 b
		+S-P	26.07±2.10 a	66.05±5.05 b	4.00±0.35 a	5.40±0.13 a	9.17±1.07 a
		+S+P	29.37±2.30 a	70.51±4.94 ab	4.96±0.23 a	5.53±0.57 a	8.23±0.24 a
	Grain	-S-P	0.18±0.01 b	13.83±0.13 b	0.87±0.05 ab	4.58±0.11 b	8.05±0.55 b
		-S+P	0.16±0.02 b	15.35±0.54 a	1.09±0.09 a	4.82±0.05 ab	8.65±0.98 b
		+S-P	0.35±0.03 a	15.63±1.37 a	0.91±0.08 a	5.10±0.55 a	10.12±0.70 a
		+S+P	0.66±0.05 a	13.97±0.70 b	0.77±0.06 b	4.21±0.41 b	8.42±0.65 b

Different letters within the same organ and genotype indicate significant differences ($P < 0.05$)

between this study and Jankowski et al. (2016) could be attributed to differences in soil properties and genotypes.

Wheat production requires substantial P fertilizer inputs; the P requirement (expressed as P amount per g of grain yield) differs between growing conditions, ranging from 1.4 to 6.4 mg (Obaid-ur-Reham et al. 2007), 3.8–4.5 mg (Teng et al. 2013), 1.9–5.3 mg (Jones et al. 1992), and 4.2–4.7 mg (Zhan et al. 2015) in the field conditions. In contrast, the greenhouse conditions in the current study had much lower P efficiencies than field studies, with P requirements ranging from 8.6 to 13.8 mg for dwarf genotype AK58 and 31.9–36.1 mg for tall genotype Shavano. The higher P economy of AK58 is likely due to the increased harvest index conferred by dwarf genes.

Conclusions

Combined salt stress and P deficiency (+S-P) seemed to have impacted plant growth more severely compared with a single stress either salt stress (+S) or P deficiency (-P). Changes of growth parameters and total mineral accumulation of AK58 and Shavano plants at maturity grown under (-S-P), (+S+P), and (+S-P) relative to that under (-S+P) are shown in Figs. 3 and 4. The increased TRL/ABG ratio with -P supply suggests that plants under -P supply require more root length to sustain equivalent aboveground biomass as +P supply. The higher P economy of dwarf genotype AK58 relative to tall genotype Shavano is likely due to the increased harvest index conferred by dwarf genes. In general, P supply and salt stress significantly affected wheat growth (roots and aboveground

Fig. 3 Changes of growth parameters and total mineral accumulation of AK58 plants at maturity grown under (–S–P), (+S+P), and (+S–P) relative to that under (–S+P). Abbreviations: PH, Plant Height; GW, Grain Weight; ABG, Aboveground Biomass; RW, Root Weight; TRL, Total Root Length

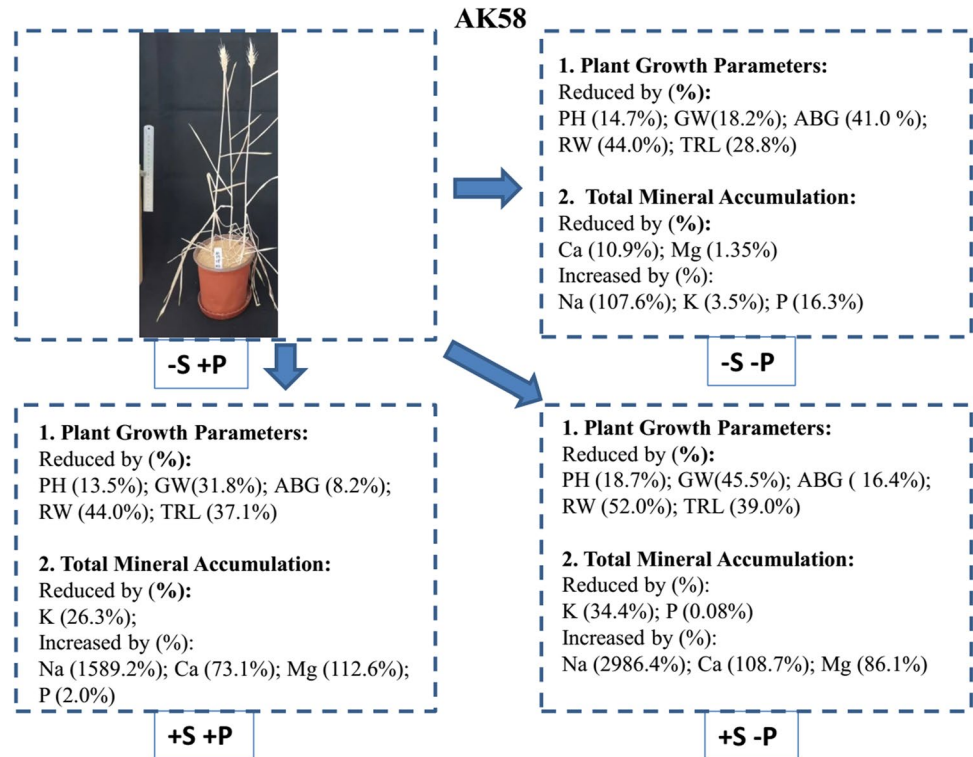
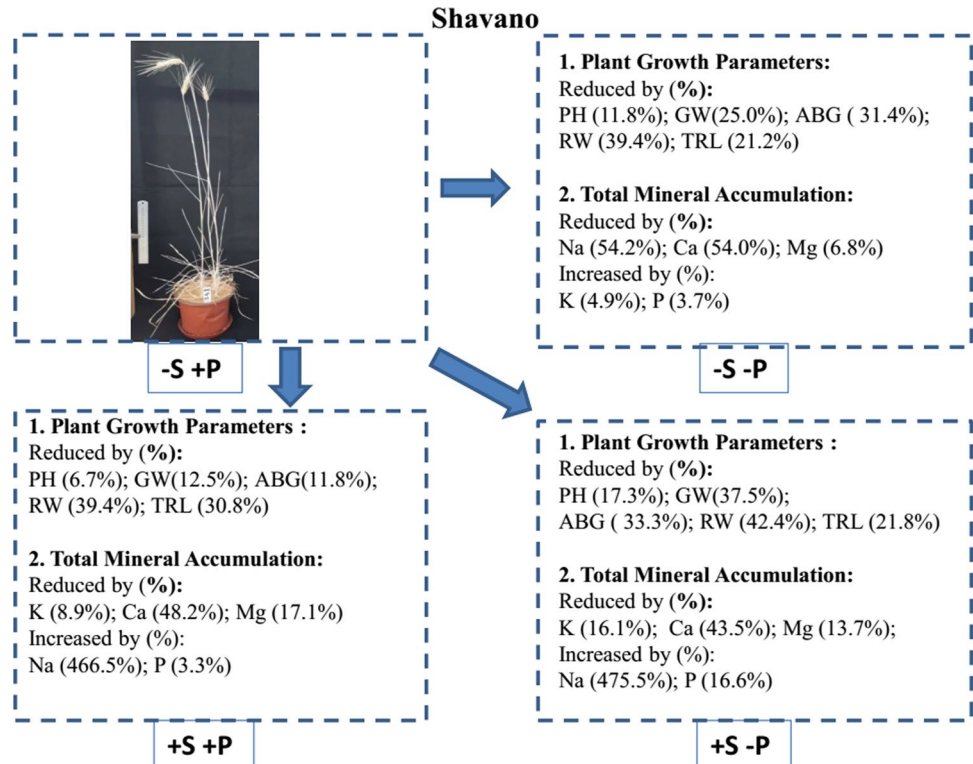


Fig. 4 Changes of growth parameters and total mineral accumulation of Shavano plants at maturity grown under (–S–P), (+S+P), and (+S–P) relative to that under (–S+P). Abbreviations: PH, Plant Height; GW, Grain Weight; ABG, Aboveground Biomass; RW, Root Weight; TRL, Total Root Length



biomass), requiring biochemical and morphological/architectural changes to adapt to salt stress and/or P deficiency, resulting in altered elemental compositions.

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Author contribution DYZ contributed to conceptualization; DYZ and ZWZ contributed to methodology; GLL, SPZ, XLZ, and WFZ contributed to investigation; DYZ contributed to writing; DYZ and KHMS contributed to writing—review and editing.

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Declarations

Conflict of interest The authors declare no competing interests.

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