

## Coupling Effects of Water and Phosphorus on Root Morphology and Phosphorus Uptake in Maize Seedlings (Postprint)

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### Abstract

Water deficit and soil phosphorus deficiency have become the primary limiting factors for maize (*Zea mays* L.) production, yet the mechanisms by which water and phosphorus regulate maize root morphology and phosphorus uptake are not fully understood. This study utilized a pot soil culture experiment, establishing four water gradients [35% of field capacity (W1), 55% (W2), 75% (W3), and 100% (W4)] and two phosphorus treatments [high phosphorus: 205 mg(P) · kg<sup>-1</sup>; low phosphorus: 11 mg(P) · kg<sup>-1</sup>] to investigate the coupling effects of water and phosphorus on root growth and phosphorus uptake in maize seedlings. The results indicated: (1) Regardless of soil phosphorus supply, maize seedling dry weight, root dry weight, total root length, and root surface area exhibited a trend of initial increase followed by subsequent decrease with increasing water supply intensity; soil available phosphorus content displayed a similar pattern; root mass ratio and average root diameter showed a decreasing trend with increasing water supply intensity; while plant phosphorus content and phosphorus accumulation exhibited a consistently increasing trend with increasing water supply intensity. (2) Both water deficit (W1) and excessive supply (W4) were detrimental to maize root growth and dry matter accumulation; water deficit (W1) inhibited maize acquisition of soil phosphorus, whereas excessive water supply (W4) induced luxury absorption of soil phosphorus (W4); mild water stress (W2) promoted maize root growth and dry matter accumulation while reducing luxury absorption of soil phosphorus; adequate water supply (W3) enhanced maize root growth, dry matter accumulation, and soil phosphorus uptake. (3) Phosphorus supply significantly increased maize seedling dry weight, root dry weight (except W4), total root length, root surface area, plant phosphorus content (except W4), and phosphorus accumulation, but decreased root mass ratio. (4) Two-way ANOVA results demonstrated that the relative contributions of water to seedling dry weight, root dry weight, root mass ratio, total root length, root surface area, average root diameter, plant phospho-

rus content, plant phosphorus accumulation, and soil available phosphorus content were 45.94%, 36.71%, 67.95%, 59.63%, 58.34%, 81.86%, 24.75%, 35.66%, and 3.00%, respectively; the corresponding relative contributions of phosphorus were 34.78%, 21.19%, 14.84%, 9.22%, 9.21%, 1.56%, 35.54%, 49.75%, and 94.40%, respectively. These results demonstrate that water is the key factor controlling maize root morphology and dry matter accumulation, whereas phosphorus is the key factor controlling plant phosphorus uptake and soil available phosphorus content. Overall, under low phosphorus conditions, maize root acquisition of soil phosphorus tends toward a morphology-dominated adaptive strategy, while under high phosphorus conditions, it tends toward a physiology-dominated adaptive strategy. Optimal coupling between water and phosphorus can promote maize root growth and dry matter accumulation while reducing luxury consumption of soil phosphorus.

## Full Text

### Coupled Effects of Water and Phosphorus on Root Morphology and Phosphorus Uptake in Maize at the Seedling Stage

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#### Abstract

Water deficit and soil phosphorus (P) deficiency have become major limiting factors in maize (*Zea mays* L.) production, yet the mechanisms by which water and phosphorus regulate maize root morphology and phosphorus uptake remain incompletely understood. This study employed a pot experiment with soil culture to investigate the coupled effects of water and phosphorus on root growth and phosphorus uptake in maize seedlings. Four water gradients [35% (W1), 55% (W2), 75% (W3), and 100% (W4) of field capacity] and two phosphorus treatments [high P: 205 mg(P) · kg<sup>-1</sup>; low P: 11 mg(P) · kg<sup>-1</sup>] were established. The results demonstrated that: (1) Regardless of phosphorus supply, shoot dry weight, root dry weight, total root length, and root surface area initially increased then decreased with increasing water supply intensity, a pattern mirrored by soil available phosphorus content. Root mass ratio and average root diameter declined with increasing water supply, while plant phosphorus content and accumulation increased steadily. (2) Both water deficit (W1) and excess water supply (W4) adversely affected root growth and dry matter accumulation. Water deficit (W1) inhibited soil phosphorus acquisition, whereas excess water supply (W4) induced luxury phosphorus uptake. Mild water stress (W2) promoted root growth and dry matter accumulation while reducing luxury phosphorus uptake, and adequate water supply (W3) enhanced root growth, dry matter accumulation, and soil phosphorus uptake. (3) Phosphorus supply significantly increased shoot dry weight, root dry weight (except under W4),

total root length, root surface area, plant phosphorus content (except under W4), and phosphorus accumulation, but decreased root mass ratio. (4) Two-way ANOVA revealed that water contributed 45.94%, 36.71%, 67.95%, 59.63%, 58.34%, 81.86%, 24.75%, 35.66%, and 3.00% to the variance in shoot dry weight, root dry weight, root mass ratio, total root length, root surface area, average root diameter, plant phosphorus content, plant phosphorus accumulation, and soil available phosphorus content, respectively. Corresponding contributions from phosphorus were 34.78%, 21.19%, 14.84%, 9.22%, 9.21%, 1.56%, 35.54%, 49.75%, and 94.40%, respectively. These findings indicate that water is the key factor controlling maize root morphology and dry matter accumulation, while phosphorus is the primary regulator of phosphorus absorption in aerial tissues and soil available phosphorus content. Overall, under low phosphorus conditions, maize root acquisition of soil phosphorus favored a morphology-oriented adaptation strategy, whereas under high phosphorus conditions, it favored a physiology-oriented absorption strategy. Optimal coupling of water and phosphorus promoted root growth and dry matter accumulation while reducing luxury phosphorus uptake.

**Keywords:** Maize; Water supply; Phosphorus supply; Root morphology; Phosphorus uptake

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Phosphorus is a crucial nutrient that participates in numerous physiological and biochemical processes and plays a vital role in plant growth and development. However, due to fixation, adsorption, complexation, and biological transformation in soil, phosphorus bioavailability is typically very low. To acquire sparingly soluble phosphorus, plants enhance soil phosphorus bioavailability through increased root growth, branching, and intensified rhizosphere effects. When plants absorb sufficient phosphorus to maintain adequate shoot phosphorus levels, root proliferation and phosphorus absorption capacity often decrease.

Soil phosphorus bioavailability is closely related to soil moisture content. Water influences phosphorus transport in soil and plant phosphorus absorption, utilization, and allocation, while appropriate phosphorus levels can enhance plant drought adaptation and water use efficiency. Recent studies have documented phosphorus-nutrition and water-regulation interactions in various crops. In wheat (*Triticum aestivum*), insufficient water supply exacerbated the adverse effects of low phosphorus stress on tiller number, leaf relative water content, chlorophyll content, and dry matter accumulation, demonstrating additive stress effects. In moth bean (*Vigna aconitifolius*), phosphorus application significantly alleviated drought-induced reductions in leaf water potential, net photosynthetic rate, chlorophyll content, starch concentration, soluble protein concentration, and nitrate reductase activity. In soybean (*Glycine max*), phosphorus application improved yield and drought resistance by enhancing total root length, root surface area, and phosphorus uptake, though excessive phosphorus provided limited yield benefits and even caused yield reductions. In maize (*Zea mays*), phosphorus application under adequate water conditions in-

duced luxury phosphorus uptake, whereas under water deficit, it reduced soil phosphorus absorption. In *Bauhinia faberi*, phosphorus promoted growth and adaptation under drought stress. These studies collectively show that appropriate phosphorus application can mitigate water deficit effects on plant growth, but excessive phosphorus provides limited relief and may even reduce plant adaptation to water stress.

Although numerous studies have addressed water and phosphorus effects on plant growth and phosphorus uptake, focusing primarily on dry matter accumulation, phosphorus absorption, and yield formation, few have examined these interactions from a root perspective. This study investigated the effects of phosphorus and water on maize dry matter accumulation, root morphology, and phosphorus uptake through a pot experiment, providing a scientific basis for improving water and phosphorus use efficiency in maize production.

## Materials and Methods

### Soil Preparation

The experimental soil was collected from farmland in the Baoding suburbs, Hebei Province (depth 2–10 cm), classified as fluvo-aquic soil. Baseline soil fertility parameters were: organic carbon  $8.42 \text{ g} \cdot \text{kg}^{-1}$ , total nitrogen  $0.85 \text{ g} \cdot \text{kg}^{-1}$ , total phosphorus  $0.58 \text{ g} \cdot \text{kg}^{-1}$ , available phosphorus (Olsen-P)  $5.2 \text{ mg} \cdot \text{kg}^{-1}$ , alkaline hydrolyzable nitrogen  $65.74 \text{ mg} \cdot \text{kg}^{-1}$ , pH (in deionized water) 8.57, bulk density  $1.42 \text{ g} \cdot \text{cm}^{-3}$ , and field capacity 35%. After air-drying, the soil was passed through a 2 mm sieve to remove plant residues.

### Experimental Design

The experiment employed a two-factor completely randomized design. Factor A was water supply with four levels: W1 (35% field capacity), W2 (55% field capacity), W3 (75% field capacity), and W4 (100% field capacity). Factor B was phosphorus supply with two levels: high P [ $205 \text{ mg(P)} \cdot \text{kg}^{-1}$ ] and low P [ $11 \text{ mg(P)} \cdot \text{kg}^{-1}$ ], totaling eight treatments with four replicates (32 pots). Commercial plastic pots (upper inner diameter 20 cm, bottom inner diameter 16 cm, height 11 cm) were filled with 3.2 kg air-dried soil per pot. Except for phosphorus, other nutrients were added at the following rates ( $\text{mg} \cdot \text{kg}^{-1}$ ):  $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$  1,686,  $\text{K}_2\text{SO}_4$  133,  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$  43.3, Fe-EDTA 5.5,  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$  2.0,  $\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$  6.6,  $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$  125,  $\text{H}_3\text{BO}_3$  0.67,  $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$  0.12, and  $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$  10. Phosphorus was applied as  $\text{KH}_2\text{PO}_4$  solution: high P at  $878 \text{ mg}(\text{KH}_2\text{PO}_4) \cdot \text{kg}^{-1}$  soil (corresponding to  $199.8 \text{ mg total P} \cdot \text{kg}^{-1}$  soil) and low P at  $25 \text{ mg}(\text{KH}_2\text{PO}_4) \cdot \text{kg}^{-1}$  soil (corresponding to  $5.7 \text{ mg total P} \cdot \text{kg}^{-1}$  soil). Potassium from phosphorus application was supplemented with KCl (analytical grade). After filling, soil moisture was maintained at 75% field capacity using the weighing method.

## Plant Cultivation

The maize cultivar ‘Zhengdan 958’ was used. Seeds were surface-sterilized with 30%  $\text{H}_2\text{O}_2$  for 10 min, then germinated on moist filter paper at 25 °C for 48 h. Uniformly germinated seeds were selected and three seeds were sown per pot, with soil moisture maintained at 75% field capacity. The experiment was conducted in a growth chamber with the following conditions: 16 h light (28 °C) and 8 h dark (25 °C), light intensity  $300 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , and relative humidity 55%. After emergence, weeds were removed promptly and pot positions were randomly changed every 5 days to minimize environmental heterogeneity effects. Seven days after emergence, pots were weighed daily (ignoring plant weight) to calculate soil moisture content. Once the target moisture levels were reached, pots were weighed daily at 9:00 AM to replenish water loss and maintain the designated moisture levels. Plants were harvested after 40 days of growth for determination of biomass, root morphology parameters, plant phosphorus content, and soil available phosphorus content.

## Measurement Methods

**Plant Harvest:** After 40 days of growth, shoots were cut at the stem base and placed in labeled envelopes for biomass and phosphorus content determination. For root harvest, soil was passed through a 2 mm sieve (the sieved soil was collected in plastic bags for soil available phosphorus measurement), roots were collected, washed clean, placed in labeled plastic bags, and stored at -20 °C until scanning analysis.

**Biomass Determination:** Shoots were oven-dried at 105 °C for 30 min, then at 70 °C for 48 h to constant weight before weighing (g). Root dry weight was measured after scanning and oven-drying to constant weight. Root mass ratio (RMR, %) was calculated as [root dry weight/(shoot dry weight + root dry weight)  $\times$  100%].

**Plant Phosphorus Content:** Dried shoots were ground to powder (<0.5 mm) and digested with  $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ . Phosphorus concentration in the digest was determined using the vanadomolybdate yellow method. Plant phosphorus content ( $\text{mg} \cdot \text{g}^{-1}$ ) was expressed as mg phosphorus per g dry weight, and phosphorus accumulation was calculated as phosphorus content ( $\text{mg} \cdot \text{g}^{-1}$ ) multiplied by plant dry weight (g).

**Root Morphology Parameters:** Frozen roots were slowly thawed and scanned using a dual-sided scanner (Epson Expression v750, Japan). Scanned root images were analyzed using WinRHIZO Pro 2009 software to obtain total root length (cm), root surface area ( $\text{cm}^2$ ), and average root diameter (mm).

**Soil Available Phosphorus:** Soil collected after root harvest was extracted with  $\text{NaHCO}_3$  and analyzed using the molybdenum-antimony anti-colorimetric method.

## Data Analysis

Data were analyzed using SPSS 13.0 (SPSS Inc., 2004, USA). Independent samples t-tests assessed differences between the two phosphorus treatments for individual parameters. One-way ANOVA followed by Tukey' s HSD test evaluated differences among water supply treatments. Two-way ANOVA examined the effects of water, phosphorus, and their interactions on dry matter accumulation, root morphology, phosphorus uptake, and soil available phosphorus.

## Results

### Coupled Effects of Water and Phosphorus on Maize Biomass Accumulation and Allocation

As shown in [Figure 1: see original paper], phosphorus supply significantly increased shoot dry weight and root dry weight (except under W4) but decreased root mass ratio ( $P < 0.05$ ). Under low phosphorus, shoot and root dry weight increased with water supply intensity, with W3 producing maximum values, though W4 reduced root dry weight. Under high phosphorus, shoot and root dry weight initially increased then decreased with water supply, with W2 producing maximum values and W4 reducing both parameters. Root mass ratio decreased with increasing water supply. Under low phosphorus, W1 produced the highest root mass ratio, while W2, W3, and W4 showed similar values. Under high phosphorus, W1 again produced the highest root mass ratio, while W3 and W4 produced the lowest values. Two-way ANOVA indicated significant effects of phosphorus and water on shoot dry weight, root dry weight, and root mass ratio, with significant interactions ( $P < 0.05$ , ). Water contributed 45.94%, 36.71%, and 54.89% to the variance in these parameters, while phosphorus contributed 34.78%, 21.19%, and 14.84%, respectively.

### Coupled Effects of Water and Phosphorus on Root Morphology

Phosphorus supply significantly increased total root length and root surface area ( $P < 0.05$ ) but had no significant effect on average root diameter except under W2 ( $P > 0.05$ ). Under low phosphorus, total root length and root surface area initially increased then decreased with water supply, with W2 and W3 producing maximum values and W4 reducing both parameters. Under high phosphorus, total root length and root surface area showed similar trends, with W2 producing maximum values and W3 and W4 reducing both parameters [Figure 2: see original paper]. Average root diameter decreased with increasing water supply. Under low phosphorus, W1 produced the largest average root diameter, while W3 and W4 showed similar values. Under high phosphorus, W1 again produced the largest average root diameter, while W2, W3, and W4 showed similar values. Two-way ANOVA revealed significant water effects on total root length, root surface area, and average root diameter, significant phosphorus effects on total root length and root surface area, and significant interactions for total root length and root surface area ( $P < 0.05$ , ). Water contributed 59.63%, 58.34%,

and 81.86% to the variance in these parameters, while phosphorus contributed 9.22%, 9.21%, and 1.56%, respectively.

### **Coupled Effects of Water and Phosphorus on Plant Phosphorus Content and Accumulation**

As shown in [Figure 3: see original paper], phosphorus supply significantly increased plant phosphorus content (except under W4) and phosphorus accumulation ( $P < 0.05$ ). Under low phosphorus, plant phosphorus content and accumulation initially increased then decreased with water supply, with W1 producing minimum values. Under high phosphorus, plant phosphorus content and accumulation increased with water supply, with W4 producing maximum values. Due to differences in shoot dry weight, W3 and W4 showed similar phosphorus accumulation values [Figure 3: see original paper]. Two-way ANOVA indicated significant effects of phosphorus and water on plant phosphorus content and accumulation, with significant interactions ( $P < 0.05$ , ). Water contributed 24.75% and 35.66% to the variance in these parameters, while phosphorus contributed 35.54% and 49.75%, respectively.

### **Effects of Water and Phosphorus Supply on Soil Available Phosphorus Content**

Soil available phosphorus content depended on both water supply intensity and phosphorus application rate . Under low phosphorus, soil available phosphorus showed an initial increase then decrease with water supply, but differences among the four water treatments were not statistically significant. Under high phosphorus, soil available phosphorus showed a similar trend, with W2 producing the highest content, followed by W3, while W1 and W4 produced the lowest values. Two-way ANOVA revealed significant effects of phosphorus and water on soil available phosphorus content, with significant interactions ( $P < 0.01$ , ). Water contributed 94.4% to the variance in soil available phosphorus, while phosphorus contributed 3.0%.

## **Discussion and Conclusion**

Roots are the primary organs for water and nutrient uptake, playing crucial roles in shoot growth, yield formation, quality development, and nutrient acquisition. During initial stages of water and nutrient deficit, plants often develop deeper, larger root systems with increased root length and dry matter allocation to cope with dual stress, though these adaptive advantages often disappear under prolonged stress. In this study, maize under water deficit (W1) and low phosphorus stress (except W4) showed significant reductions in root dry weight, total root length, and root surface area at later growth stages, while root mass ratio increased significantly, consistent with reports by Hermans et al. and Songsri et al.

The beneficial effects of phosphorus application on maize root growth depended

strongly on water supply. Jin et al. reported that under severe water stress (65–75% field capacity), phosphorus application significantly increased total root length and surface area in soybean cultivar ‘Denglong46’ but had smaller effects on ‘Heisheng101’. Under adequate water supply, phosphorus increased these parameters in both cultivars, demonstrating that soil moisture regulates genotype-specific root responses to phosphorus. In this study, phosphorus application significantly increased total root length and surface area under both severe water stress (W1) and adequate water supply (W3), consistent with Jin et al.’s findings for ‘Denglong46’. Zhao et al. reported that both adequate (75% field capacity) and excess (90% field capacity) water supply increased maize root dry weight. In contrast, this study found that adequate water supply (W3) significantly increased root dry weight, while excess water supply (W4) had no significant effect. This discrepancy may reflect differences in water supply intensity, as Zhao et al. used 90% field capacity for excess water while this study used 100% field capacity. Notably, under mild water stress (W2), phosphorus’s positive effects on total root length and surface area were fully realized, whereas under excess water supply (W4), phosphorus had negative effects on these parameters. These contrasting responses likely relate to soil aeration. Research indicates that root growth ceases when soil oxygen concentration falls below  $10 \text{ mg} \cdot \text{L}^{-1}$ . In this study, the mild water stress treatment (W2) provided good soil aeration and oxygen supply, facilitating root respiration and allowing phosphorus to stimulate root growth significantly. In contrast, excess water supply (W4) saturated soil pores, reducing aeration and likely inhibiting root respiration, causing phosphorus to negatively affect total root length and surface area. In addition to length and surface area, root diameter plays a critical role in phosphorus acquisition, reflecting root fineness and determining water and nutrient absorption capacity. Regardless of phosphorus supply, water deficit (W1) produced the largest average root diameter, indicating thicker roots that reduced phosphorus acquisition but enhanced tolerance to adverse conditions. Thus, soil water supply significantly influenced maize root growth and phosphorus uptake.

Water affects root development both directly and indirectly by influencing soil available phosphorus content and phosphorus forms. Previous research demonstrated that water supply significantly increased available phosphorus and aluminum-phosphate (Al-P) concentrations in red paddy soil but did not affect organic phosphorus, iron-phosphate (Fe-P), calcium-phosphate (Ca-P), or occluded phosphorus (O-P). Flooded conditions (100% field capacity) produced significantly higher available phosphorus than aerobic conditions (60% field capacity), with differences increasing with phosphorus supply. In this study, high phosphorus conditions showed an initial increase then decrease in soil available phosphorus with water supply intensity, with W2 producing the highest content. Low phosphorus conditions showed a similar but non-significant trend, possibly due to soil type and crop species differences. At W2, maize exhibited greater root length and surface area, increasing phosphorus capture opportunities and enabling root exudates to mobilize sparingly soluble phosphorus and mineralize organic phosphorus through acid phosphatase

activity, thereby increasing soil available phosphorus. He et al. reported that increasing water supply increased soil available phosphorus without changing organic phosphorus content, suggesting that the increase at W2 resulted more from root exudate-mediated phosphorus mobilization than from organic phosphorus mineralization. In this study, the trend of soil available phosphorus with water supply matched that of root length and surface area but differed from plant phosphorus content and accumulation patterns, suggesting that increased soil available phosphorus stimulated root growth (particularly under high phosphorus), while water supply directly promoted shoot phosphorus absorption.

Previous research on water and phosphorus interactions has focused on wheat, moth bean, soybean, and maize, but rarely quantified the relative importance of these factors. To address this, we calculated the relative contributions of water and phosphorus to root morphology parameters based on two-way ANOVA results. Water contributed 36.71%, 59.63%, 58.34%, and 81.86% to the variance in root dry weight, total root length, root surface area, and average root diameter, respectively, while phosphorus contributed 21.19%, 9.22%, 9.21%, and 1.56%. These results confirm that water is the primary factor controlling maize root growth, with phosphorus playing a secondary role, consistent with findings by Jin et al. and Zhao et al. These quantitative relationships provide a scientific basis for optimizing water and phosphorus management.

Due to poor mobility and low diffusion rates in soil, phosphorus acquisition depends heavily on root morphological changes. Relatively long, large-surface-area, highly branched root systems can occupy more soil volume and increase phosphorus contact area, providing clear advantages for phosphorus acquisition. In this study, maize employed two distinct strategies for soil phosphorus acquisition depending on phosphorus and water supply. Under low phosphorus conditions, plants with greater root dry weight, total root length, and surface area acquired more soil phosphorus regardless of water supply, indicating that root morphological changes were critical and that a morphology-oriented adaptation strategy predominated. Under high phosphorus conditions, plant phosphorus content and accumulation increased steadily with water supply intensity regardless of root morphology, indicating that water was crucial and that a physiology-oriented absorption strategy dominated. Under high phosphorus with mild water stress (W2), maize exhibited maximum root dry weight, total root length, and surface area but lower phosphorus acquisition than plants under adequate or excess water supply, likely due to greater carbon allocation to roots at the expense of physiological phosphorus absorption capacity. Under high phosphorus with excess water supply (W4), despite poor soil aeration and smaller root dry weight, total root length, and surface area, strong physiological phosphorus absorption enabled greater phosphorus acquisition.

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