

Leaf gas exchange, phosphorus uptake, growth and yield responses of cotton cultivars to different phosphorus rates

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Abstract

Growth and physiological responses of cotton (*Gossypium hirsutum* L.) cultivars with different phosphorus (P) efficiencies under variable P environment are poorly known. Therefore, this study explored effects of normal P [P⁺, 70 kg(P₂O₅) ha⁻¹] and without P (P⁻, 0 kg ha⁻¹) on yield, growth, and physiology of different P-efficient cultivars [low-efficient Xinluzao 13 (L₁) and Xinluzao 26 (L₂); medium-efficient Xinluzao 10 (M₁) and Xinluzao 24 (M₂); high-efficient Zhongmiansuo 42 (H₁) and Xinluzao19 (H₂)]. Cotton growth and yield was higher in H₁ and H₂ cultivars under P⁺ compare to P⁻. Leaf photosynthesis, intercellular CO₂ concentration, stomatal conductance, and net assimilation rate increased under P⁺ and in high-efficient cultivars. Greater Rubisco activity and higher soluble sugar content further promoted P uptake and utilization efficiency which resulted in a higher yield under normal P⁺ than that at P⁻ treatment. High-P-efficient cultivars have the potential to increase the yield by improving cotton growth and physiological attributes under P⁺.

Additional key words: enzymatic activity; leaf area index; net assimilation rate; photosynthesis; photosynthetic pigments.

Introduction

Cotton production has increased due to the introduction of high-yielding varieties. However, fertility of cotton raising soils has decreased, because of continuous cultivation of arable crops, and inadequate supply of organic and inorganic fertilizers (Jayakumar and Surendran 2017). Nevertheless, to pursuit higher yields in order to meet the demand of fibre and food for the expanding global population with poor management practices, *i.e.*, mismanagement of inputs and imbalanced fertilizers application, has led to depleted soil nutrients and raised concerns about the potential long-term adverse impacts on soil fertility, productivity, and environmental quality (Surendran and Murugappan 2010). Poor and marginal farmers often use suboptimal rates of P fertilizers and choose wrong cultivars due to lack of resources available to them. In future, higher input costs and limited nutrient resources can further worsen this situation resulting in rising fertilizer prices and increases of production costs

(Jayakumar and Surendran 2017). Under such circumstances, it is important to understand the responses of cotton cultivars under various P supply.

Phosphorus is an essential mineral nutrient for normal growth and development of cotton crops and its deficiency or suboptimal supply result in lower photosynthesis and metabolism leading to a substantial yield reduction (Jayakumar and Surendran 2017, MacDonald *et al.* 2011). However, under limited soil P availability, plants often experience morphological and physiological changes, *i.e.*, stunted growth, reduction in a leaf number, leaf area, reduced photosynthesis, increased leaf chlorophyll (Chl) and protein contents (Lauer *et al.* 1989, Rao and Terry 1989, Suriyagoda *et al.* 2014). Depending on root penetration and proliferation, availability of P in the rhizosphere may vary which affects P uptake in cotton plants (Jayakumar and Surendran 2017). Root growth is not restricted under P deficiency as much as the shoot

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Abbreviations: C_i – intercellular CO₂ concentration; Chl – chlorophyll; CGR – crop growth rate; DM – dry mass; FM – fresh mass; g_m – mesophyll conductance; g_s – stomatal conductance; HP – high P efficiency; LAI – leaf area index; LP – low P efficiency; MP – medium P efficiency; NAR – net assimilation rate; P_N – net photosynthetic rate; PP – photosynthetic potential.

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growth. More carbohydrates are distributed to the roots to assist in root exploration of the soil and expansion to acquire more P (Girma *et al.* 2007).

Current agriculture management practices commonly experience low plant nutrient-use efficiency due to natural chemical sorption and transformations. For example, up to 90% of P fertilizer applied to soil is unavailable to plants because it binds to Ca, Al, and Fe-bearing soil mineral surfaces or is lost from the ecosystem through leaching (Randriamanantsoa *et al.* 2013). Low availability of soil P significantly influences root morphological and biochemical processes arresting plant growth and development in cotton. This phenomenon also induces formation and secretion of acid phosphatase and other special enzymes of the root system and upregulation of the gene expression of high-affinity P translocator (Yan *et al.* 1997, 2000; Lefebvre *et al.* 1990, Muchhal and Raghothama 1999). However, optimal P has the potential to enhance plant adaptation to stressful conditions resulting in a higher nutrient uptake; and utilization ultimately increases cotton yields. In contrast, low P hampers plant growth which in turn causes substantial yield loss. Different plant genotypes display genetic diversity in the absorption and utilization ratios of P. Cotton cultivars with high P efficiency may increase plant performance under low P conditions by increasing root activity, water, and P

acquisition (Sharpley *et al.* 2015).

The effects of sufficient and deficient P supply on cotton photosynthetic characteristics (Jensen *et al.* 2002), soluble protein (Rao and Terry 1989), and Chl content (Rao and Terry 1989, Pan *et al.* 2003), Rubisco activity (Lauer *et al.* 1989), and net photosynthetic rate (P_N) (Jensen *et al.* 2002, Pan *et al.* 2003) have been reported; but data regarding cotton cultivars with different P efficiency under different P rates are lacking. Screening and using P-efficient genotypes and cultivars with efficient uptake and utilization ratios of P can potentially increase P utilization in plants (Yan *et al.* 1997, Wang and Li 2000, Luo *et al.* 2016, Wang *et al.* 2008). Therefore, screening for suitable characteristics of P-efficient cotton cultivars, especially under different P rates under arid climatic conditions, are essential for reaching optimal yield and for future breeding program. Therefore, this study aimed: (1) to explore effects of sufficient and deficient P fertilization on different P-efficient cultivars in their yield, growth, physiological attributes; and (2) to determine physiological mechanisms causing differences in yields and P-utilization efficiencies between low-P-, medium-P-, and high-P-efficiency cultivars. These data can provide a theoretical basis for genetic improvement and breeding for the high-P-efficiency in cotton crops.

Materials and methods

Experimental site: An experiment was carried out at the experimental farm of Xinjiang Agricultural Reclamation Academy of Sciences, in the northwestern China (45°19'N, 74°56'E) during 2014 and 2015 growing season. A composite soil sample was obtained using a soil auger from the experimental area prior to planting of cotton plants. The soil characteristics comprised of 1.14% organic matter, 32.1 mg(alkali-hydrolyzed nitrogen) kg^{-1} , 8.5 mg(available phosphorus, P_2O_5) kg^{-1} , and 128.1 mg(available potassium, K_2O) kg^{-1} .

Experimental design: The experiment was designed in a split plot arrangement with six cotton cultivars of different P efficiencies (Wang *et al.* 2008), *e.g.*, Xinluzao 13 (L_1), Xinluzao 26 (L_2) with low P efficiency (LP); Xinluzao 10 (M_1), Xinluzao 24 (M_2) with medium P efficiency (MP); Zhongmiansuo 42 (H_1), Xinluzao19 (H_2) with high P efficiency (HP) under normal phosphorus [P^+ , 70 $\text{kg}(\text{P}_2\text{O}_5)$ ha^{-1}] and no (P^- , 0 kg ha^{-1}). A split-plot design with four replicates was used to increase the accuracy of comparisons. The experimental plot size was 30 m^2 (6 × 5 m). Prior to sowing, the field was leveled followed by cultivation and planking operations. Seeds of different cotton cultivars were sown on raised bed in respective plots. Seedlings were thinned two weeks after emergence to the desired plant population density. Fertilizer nitrogen at the rate of 150 $\text{kg}(\text{urea}) \text{ha}^{-1}$ with 46% N was supplemented to each plot. Crop management practices, such as

irrigation, weeding, hoeing, and pesticide application, were implemented to reduce competition for nutrients, light, water, and spacing for a better crop stand. Mepiquat chloride (*Kaifeng Lirui Inc.*, China) was applied as a growth regulator in order to reduce vegetative growth.

Cotton leaf gas-exchange attributes: Net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) was measured at different reproductive phases, *e.g.*, squaring, flowering, and boll-setting from top functional leaf on the main stem using *LI-6400* (*LI-COR Inc.*, NE, USA). These measurements were performed on sunny days between 10:00 and 12:00 a.m. in each unit under the following conditions: light intensity of 1800 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$, the ambient CO_2 concentration was 366 $\mu\text{mol mol}^{-1}$, and the vapor pressure was 3.5 kPa at field temperature. Mesophyll conductance (g_m) was assessed according to Xiao *et al.* (1998).

Cotton growth, yield, phosphorus uptake and utilization: Ten successive and uniform plants were tagged after emergence to determine plant growth parameters. Cotton plants were carefully uprooted at different growth stages and separated into vegetative and reproductive structures. Leaf area was determined by measuring subsamples with a *Li-Cor* planimeter (*Model Li-3100*, *Li-COR Inc.*, Lincoln, USA). Seed cotton yield (g per plant) was calculated by hand-picking all open bolls from each

subplot. The plants were dried in an electric fan-assisted oven at 105°C for 30 min to stop consumption by respiration and then dried at 80°C for 48 h until a constant mass was obtained. Leaf area index (LAI), crop growth rate, and net assimilation were assessed using the following formula:

$$\text{Leaf area index} = \frac{\text{Leaf area per plant}}{\text{Land area occupied by the plant (cm)}} \quad (1)$$

$$\text{Crop growth rate (CGR)} = \frac{W_2 - W_1}{A (t_2 - t_1)} \quad (2)$$

$$\begin{aligned} \text{Net assimilation rate (NAR)} &= \\ &= \frac{(W_2 - W_1) (\text{Ln}S_2 - \text{Ln}S_1)}{(S_2 - S_1) (t_2 - t_1)} \quad (3) \end{aligned}$$

where W_1 and W_2 are crop dry mass (DM, g m⁻²) at initial (t_1) and final times (t_2), respectively. Photosynthetic potential (PP) was determined as a product of the leaf area during different growth period and the duration of the growth period. Oven-dried plant organs were analyzed for P uptake and utilization. The samples were digested according micro-Kjeldahl method (Bremer and Mulvaney 1982). Concentrations of P were expressed on a DM basis and P uptake was determined as the product of concentration and DM. Cotton plant P efficiency was assessed by obtaining the ratio of DM to single-plant P uptake.

Chl, soluble protein and Rubisco, Ca²⁺-ATPase and Mg²⁺-ATPase activities: Chl contents were determined according to the method of He *et al.* (2002). Briefly, 0.25 g of fresh leaves was placed in a 100-ml test tube. Plant tissues were homogenized with a polytron homogenizer after addition of 10–15 ml of pure methanol. The homogenate was then filtered and made up to 100 ml with pure methanol. The Chl concentration was calculated using spectrophotometer (UV-2401, Shimadzu Corporation, Japan) determined at 652 and 665 nm. Leaf samples (0.5 g) were homogenized at 4°C in 5 ml of cold water and centrifuged at 800 × g for 5 min. The supernatant was stored on ice and the pellet was re-suspended in 3 ml of

cold water prior to re-centrifugation (800 × g) for another 5 min. The supernatants were pooled centrifuged and stored on ice. The pellet was re-suspended in 2 ml of cold water and centrifuged at 800 × g and the supernatant was pooled for analysis of soluble protein content by the *Coomassie Blue* dye-binding assay of Bradford (1976). The absorbance readings were converted using BSA as standard curve.

The Rubisco activity was assessed according to Dong *et al.* (1996). The reaction solution composed of 1 mol(Tris-HCl) L⁻¹ (pH 8.0), 1 mmol(EDTA) L⁻¹, 100 mmol(MgCl₂) L⁻¹, 50 mmol(ATP) L⁻¹, 2 mmol(NaHCO₃) L⁻¹, mmol L⁻¹ RuBP (ribulose-1,5-bisphosphate), 15 units of phosphoglyceric acid kinase, 15 units of glyceraldehyde phosphate dehydrogenase, and 0.1 mL of crude enzyme extract, with a total volume of 3.0 mL. Prior to adding RuBP, solution was placed at 30°C in water bath for 10 min. After that, the solution was exposed to colorimetric determination using an spectrophotometer (UV-2401, Shimadzu Corporation, Japan) immediately after the substrate was added. Ca²⁺-ATPase and Mg²⁺-ATPase activities were measured according to Huang (1985). Assays were carried out at 30°C for 30 min in 0.5 mL reaction volume containing 1 mmol(Tris-ATP) L⁻¹, 1 mM mol(MgSO₄) L⁻¹ or 2 mmol(CaSO₄) L⁻¹, 40 mmol(Tris-MES) L⁻¹ (pH variable), 0.02% (w/v) *Triton X-100*, with or without 25 mM K₂SO₄. The reaction was initiated by addition of the enzyme and terminated by adding 1 mL of color development solution, containing 0.75% (w/v) (NH₄)₆Mo₇O₂₄, 0.375 M H₂SO₄, 3% (w/v) FeSO₄, and 0.75 (w/v) SDS. After 10 min, 0.5 mL 7% (w/v) sodium citrate was added to prevent further color development due to non-enzymatic hydrolysis of ATP. The activities of nitrate reductase (NR) were determined with commercially available kits (*COMIN, Suzhou, China*).

Statistical analysis: Analysis of variance (*ANOVA*) was performed with *SPSS version 11.5*. Means were separated using *Duncan's* multiple range test at $P < 0.05$. The figures were plotted using *Sigma Plot version 10.0*. The data are presented as mean ± standard error (SE).

Results

Leaf gas-exchange parameters and Chl content: Cotton leaf gas-exchange attributes and Chl content of different cultivars was significantly influenced by sufficient (P⁺) and no (P⁻) P conditions at different growth stages (Table 1). Leaf Chl contents were at peak for HP cultivars compared with MP and LP cultivars at the squaring, flowering, and boll-setting stage under both conditions. However, the contents were significantly higher under P⁺ compared to P⁻ conditions.

Cotton plant g_s , g_m , and P_N increased with the plant development. Compared to LP and MP cultivars, the g_s , g_m , and P_N increased for HP cultivars at the squaring and flowering stage, although g_s , g_m , and P_N decreased at the

boll-setting stage under both P conditions. However, C_i increased under P⁻ for LP and MP cultivars at various growth stages compared to others. Compared to P⁻, leaf gas-exchange parameters and g_m conductance were higher at different growth phases under P⁺.

Cotton plant growth characteristics: Cotton growth characteristics, *i.e.*, LAI, CGR, NAR, and PP were significantly impacted by variable P environment at different reproductive stages. As the plants grew, LAI of different cultivars increased under both conditions. The LAI of all cultivars was the highest at the boll-setting stage under P⁺ compared to P⁻ (Fig. 1). Compared to other

cultivars, HP cultivars had higher LAI during the boll-setting phase under P⁺ conditions. However, the no significant differences were found between MP varieties and LP cultivars during the flowering stage. Furthermore, at the full flowering stage, the difference between HP cultivars and MP cultivars was not significant.

Data regarding CGR, NAR, and PP of different cultivars under the influence of variable P environments

are presented (Fig. 2). HP cultivars performed better in terms of greater CGR under both conditions. CGR was significantly reduced for P⁻ compared to P⁺ for all cultivars. Nitrate reductase activity and photosynthetic capacity for high P-efficient cultivars were increased for P⁺ treatment but reduced under P⁻ conditions. The HP cultivars were efficient in terms of greater CGR, NAR, and PP under P⁻.

Table 1. Cotton leaf chlorophyll (Chl) content and leaf gas-exchange parameters as influenced by phosphorus and cultivars at various reproductive stages. L, M, and H indicate the average values of L₁–L₃, M₁–M₃, and H₁–H₃, respectively. Data represent the mean ± standard error (*n* = 4). Means within a column followed by the same letters are not significantly different at *P* < 0.05 according to Duncan's multiple range test.

	Cultivar	Squaring		Flowering		Boll setting	
		P ⁺	P ⁻	P ⁺	P ⁻	P ⁺	P ⁻
Chl	L	5.48 ± 0.14 ^a	5.07 ± 0.34 ^a	6.24 ± 0.21 ^a	5.24 ± 0.28 ^a	5.15 ± 0.12 ^a	4.21 ± 0.37 ^a
[mg g ⁻¹ (FM)]	M	5.84 ± 0.24 ^a	5.29 ± 0.25 ^a	6.54 ± 0.31 ^a	5.47 ± 0.24 ^a	5.14 ± 0.42 ^a	4.34 ± 0.36 ^a
	H	5.63 ± 0.35 ^a	5.37 ± 0.41 ^a	6.87 ± 0.42 ^a	5.64 ± 0.23 ^a	4.84 ± 0.23 ^a	4.52 ± 0.35 ^a
g _s	L	0.65 ± 0.02 ^{ab}	0.42 ± 0.02 ^c	0.88 ± 0.04 ^a	0.59 ± 0.03 ^c	0.53 ± 0.04 ^b	0.30 ± 0.01 ^c
[mol(H ₂ O) m ⁻² s ⁻¹]	M	0.62 ± 0.03 ^b	0.51 ± 0.03 ^b	0.93 ± 0.04 ^a	0.63 ± 0.03 ^b	0.51 ± 0.03 ^b	0.34 ± 0.01 ^b
	H	0.68 ± 0.04 ^a	0.60 ± 0.02 ^a	0.90 ± 0.03 ^a	0.73 ± 0.02 ^a	0.57 ± 0.04 ^a	0.41 ± 0.02 ^a
g _m	L	0.52 ± 0.03 ^b	0.34 ± 0.04 ^c	0.75 ± 0.04 ^a	0.44 ± 0.02 ^c	0.46 ± 0.03 ^b	0.20 ± 0.01 ^c
[mol(H ₂ O) m ⁻² s ⁻¹]	M	0.53 ± 0.02 ^b	0.40 ± 0.02 ^b	0.74 ± 0.05 ^a	0.52 ± 0.02 ^b	0.48 ± 0.03 ^b	0.26 ± 0.01 ^b
	H	0.58 ± 0.04 ^a	0.45 ± 0.03 ^a	0.77 ± 0.04 ^a	0.57 ± 0.04 ^a	0.52 ± 0.04 ^a	0.32 ± 0.02 ^a
P _N	L	26.3 ± 2.2 ^b	22.2 ± 2.0 ^b	35.4 ± 1.6 ^b	27.6 ± 2.0 ^c	22.0 ± 1.5 ^b	15.3 ± 0.8 ^c
[μmol(CO ₂) m ⁻² s ⁻¹]	M	27.5 ± 2.8 ^{ab}	23.9 ± 2.4 ^{ab}	36.8 ± 2.1 ^{ab}	30.0 ± 1.1 ^b	23.9 ± 1.4 ^{ab}	19.6 ± 0.8 ^b
	H	29.4 ± 2.9 ^a	25.0 ± 1.2 ^a	38.4 ± 2.8 ^a	33.0 ± 2.2 ^a	24.3 ± 2.0 ^a	23.8 ± 1.2 ^a
C _i	L	276 ± 18 ^a	301 ± 17 ^a	207 ± 15 ^a	255 ± 14 ^a	307 ± 19 ^a	324 ± 14 ^a
[μmol(CO ₂) mol ⁻¹]	M	265 ± 13 ^{ab}	284 ± 14 ^b	201 ± 14 ^{ab}	220 ± 12 ^b	294 ± 15 ^a	301 ± 12 ^b
	H	244 ± 16 ^b	259 ± 11 ^c	162 ± 17 ^b	189 ± 14 ^c	261 ± 12 ^b	272 ± 11 ^c

Ca²⁺-ATPase and Mg²⁺-ATPase activities: Data regarding Ca²⁺-ATPase and Mg²⁺-ATPase activities under the influence of variable P environment are shown in Fig. 3. Mg²⁺-ATPase and Ca²⁺-ATPase activity were higher during the full squaring stage, but decreased in the flowering and boll-setting stages at P⁺ and P⁻. Among the cultivars, HP cultivars were the most efficient in terms of higher Mg²⁺-ATPase and Ca²⁺-ATPase activity under both P conditions during the full budding stage followed by full flowering and boll-setting stage. However, the Mg²⁺-ATPase and Ca²⁺-ATPase activities significantly declined under P⁻ during all growth stages.

Soluble protein content and Rubisco activity: Both P⁺ and P⁻ significantly influenced leaf soluble protein content and Rubisco activity at various reproductive phases (Fig. 4). Compared to LP and MP, HP cultivars showed the highest soluble protein content at the full flowering stage under both conditions. A substantial reduction in soluble protein content was observed during the squaring stage.

Discussion

Phosphorus is multifunctional plant macronutrient used to maximize plant growth and yield. Therefore, reductions in

Rubisco activity was maximum during the full flowering stage for HP cultivars but it was reduced at the boll-setting stage under both P⁺ and P⁻ conditions. Compared to P⁺ conditions, a substantial reduction in protein contents and Rubisco activity was noted under P⁻.

Cotton yield, phosphorus uptake and utilization efficiency: Cotton yield, P uptake, and utilization efficiency of cotton cultivars under P⁺ and P⁻ are presented in Fig. 5. HP cultivars (H₁–H₃) produced a higher seed yield than other cultivars under P⁺ conditions. Similar trend was also observed under P⁻ conditions. A substantial reduction in cotton yield was noted under P⁻ conditions compared to P⁺ (Fig. 5). Significant reductions in P accumulations were noticed for cotton cultivars under P⁻ conditions. HP cultivars resulted in higher P accumulation compared to MP and LP cultivars under P⁺. MP (M₁–M₃) cultivars had high P-use efficiency compared to other cultivars. However, the P-use efficiency was higher under P⁻ conditions relative to P⁺ for MP cultivars.

the supply of P fertilizers could severely diminish crop yields (Yan *et al.* 1997, 2000). It is the major component

of nucleic acids, phosphatides (components of cell membrane), ATP, and photosynthetic parameters of cotton crops (Schachtman *et al.* 1998, Raines 2011, Luo *et al.* 2016). One solution for mitigating the threat of this diminishing resource is to develop sustainable technologies to improve P-use efficiency for plant uptake. Crop management practices, *i.e.*, selection of cultivars and P fertilization are the most important factors for maximizing cotton yield.

In this study, leaf Chl content and gas-exchange parameters were impacted by P supply and different cultivars. We found significant correlations between P_N and g_s at the growth stages as well as between P_N and the nonstomatal conductance of cultivars with different P efficiencies. These data indicate that the P_N improvement of HP cultivars without P application can be ascribed to the improvement of transport capacity for CO_2 toward photosynthetic carboxylation sites. The CO_2 in the liquid phase was separated by the carbonic anhydrase

of HCO_3^- to enhance the transportation of CO_2 in cotton leaf physiognomy by transporting CO_2 at an ionic state into liquid phase (Raines 2011). This phenomenon might be an important internal reason for the increase of the g_m in HP cultivars under P^- condition in order to relieve the stomatal limitation of photosynthesis. The increment in leaf photosynthetic capacity might be associated with greater P uptake and utilization efficiency with improved leaf photosynthetic rate. This indicates that sufficient P has the potential to improve cotton leaf photosynthetic capacity. In the present study, intercellular CO_2 concentration of LP cultivars increased under both P rates. The CO_2 concentration is essential to maximize photosynthesis but depends on crop species and environmental conditions (Ku *et al.* 1977). Stomatal conductance may respond to changes in photosynthetic rate to maintain C_i near saturation. Physiologists generally believe that stomata function to prevent desiccation while still allowing the passage of CO_2 . Stomata impose a large limitation on the rate of CO_2 assimilation as well as limit CO_2 assimilation of C_4 plants more compared to C_3 plants. The stomatal limitation of photosynthesis is often thought of as the contribution of stomatal resistance to some total "resistance" to CO_2 uptake. Stomatal limitation decreased despite a decrease in C_i (Farquhar *et al.* 1982). Increment in leaf conductance of CO_2 did not contribute to P_N although external CO_2 concentration did not increase P_N even though C_i increased (Perry *et al.* 1983).

Cotton growth and leaf enzymatic activity was significantly influenced by both factors. HP cotton cultivars exhibited relatively higher NAR under P^- conditions. This data indicates that these cultivars possess high leaf photosynthetic efficiency. Furthermore, the high PP of HP cultivars was closely related to the high LAI at full flowering and boll-setting stages. In this research, High-P efficiency varieties resulted in higher P_N , NAR, and PP during yield formation under P^- conditions. This further led to high CGR and more seed cotton yield during boll opening stage. Leaf enzymatic activity, *i.e.*, Ca^{2+} -ATPase and Mg^{2+} -ATPase activities increased under rich supply of P. This might be due to higher photosystem PSII activity of HP, P acquisition and utilization efficiency. The reductions in the supply of P fertilizers severely diminish cotton growth (Baas *et al.* 2016).

Soluble protein content and Rubisco activity significantly increased under P^+ . Rubisco influences the dark-reaction efficiency of photosynthesis (Xiao *et al.* 1998). Hence, high soluble protein content is the physiological foundation for highly efficient metabolism of the plant (Friedrich and Huffaker 1980). Rubisco activity directly influences photosynthetic dark reaction efficiency. Increasing the supply of inorganic P in the chloroplasts can improve the carboxylation efficiency of Rubisco, the key enzyme of photosynthesis (Mächler 1984). Deficient P supply decreases leaf Chl and soluble protein content (Pan *et al.* 2003). Pan *et al.* (2003) found that the soluble protein, RuBP content, and activity in rice leaves

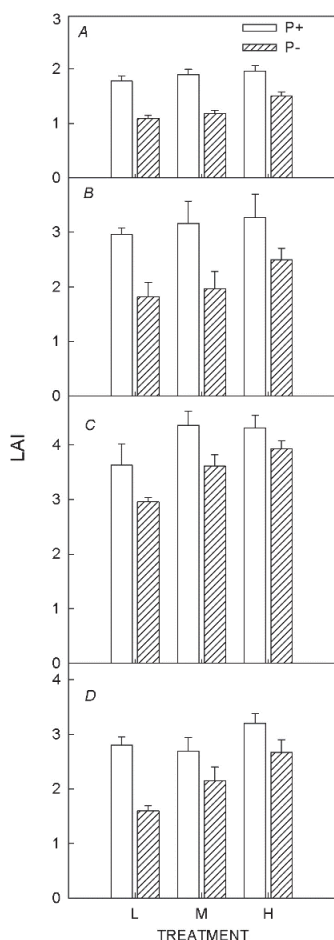


Fig. 1. Values of LAI at the full budding stage (A), full flowering stage (B), full bolling stage (C), and later full bolling stage (D) in cultivars with different P efficiencies. P^+ (70 kg ha^{-1}) P^- (0 kg ha^{-1}), L, M, and H represent low-efficient, medium-, and high-P-efficient cultivars, respectively. Data represent the mean \pm standard error ($n = 4$).

decreased under low P condition compared to adequate P supply. In the present study, the Rubisco activity at the yield-formation stage increased as the P efficiency of cotton cultivars increased. Rubisco activity and P_N during the test period had a significant positive correlation.

Cotton yield, P-uptake and use efficiency was higher under P^+ compared to P^- conditions. The increment in the cotton yield was mainly associated with higher P uptake which further promoted leaf photosynthetic capacity. Soils with a large capacity to bind P are especially because of P delivery to plants requires more inputs relative to the P

outputs in harvested crops (MacDonald *et al.* 2011), resulting in extremely low agricultural P-use efficiency. Soil bacteria can strongly influence the amount of soil P which is plant-available by solubilizing the mineral-associated P (Osorio and Habte 2014), and increasing plant P uptake by stimulating plant root growth (Bal *et al.* 2013). This is achieved by releasing metabolites including organic acids and high-affinity iron chelating (siderophores which solubilize mineral-bound P Shropshire and Bordenstein 2016) and by exuding plant hormones such as auxin (Spaepen 2015).

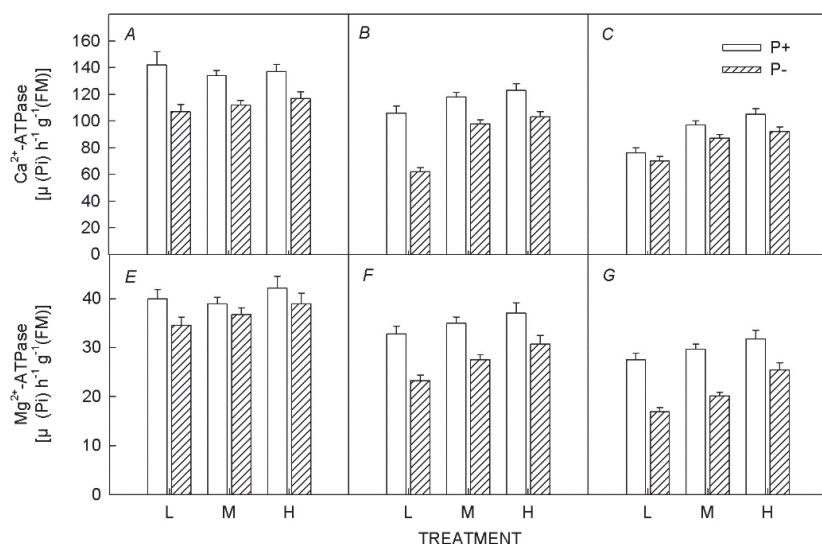


Fig. 2. Values of population growth parameters (CGR, A; NAR, B; PP, C) during the full squaring and boll setting stages in cultivars with different P efficiencies. P^+ (70 kg ha^{-1}) P^- (0 kg ha^{-1}), L, M, H represent low-efficient, medium-, and high-P-efficient cultivars, respectively. Data represent the mean \pm standard error ($n = 4$).

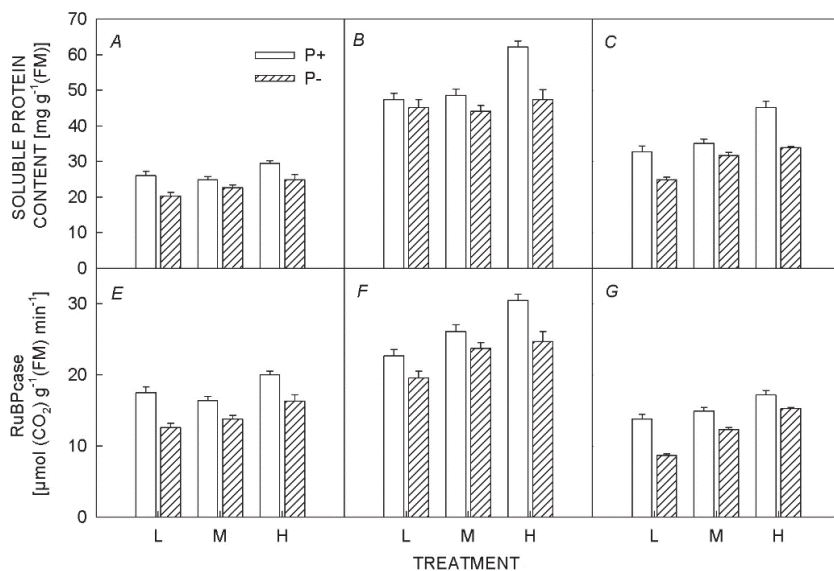


Fig. 3. Cotton cultivars leaf Ca^{2+} -ATPase and Mg^{2+} -ATPase activities during full squaring (A,E), full flowering (B,F), and boll setting stage (C,G) as influenced by P^+ and P^- . P^+ (70 kg ha^{-1}) P^- (0 kg ha^{-1}), L, M, H represent low-efficient, medium-, and high-P-efficient cultivars, respectively. Data represent the mean \pm standard error ($n = 4$).

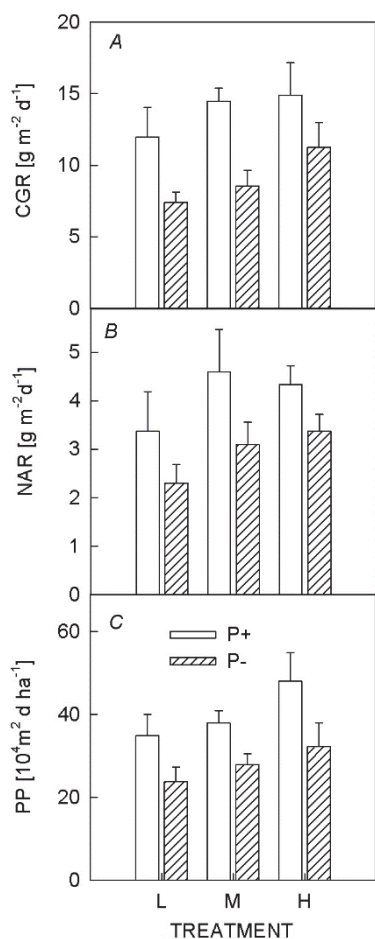


Fig. 4. Soluble protein contents and Rubisco activities of cotton leaves at full squaring (A,E), full flowering (B,F), and full boll setting stage (C,G) as influenced by variable P environments. P⁺ (70 kg ha⁻¹) P⁻ (0 kg ha⁻¹), L, M, H represent low-efficient, medium-, and high-P-efficient cultivars, respectively. Data represent the mean ± standard error ($n = 4$).

Conclusion: In this study, P⁺ and P⁻ significantly influenced cotton growth, yield, and physiology. Under P⁺ supply increased crop growth, soluble protein content, and leaf gas-exchange parameters might be associated with higher P acquisition and utilization efficiency. P⁻ significantly hampered cotton growth and physiological activity. The increment in cotton yield under P⁺ with high-

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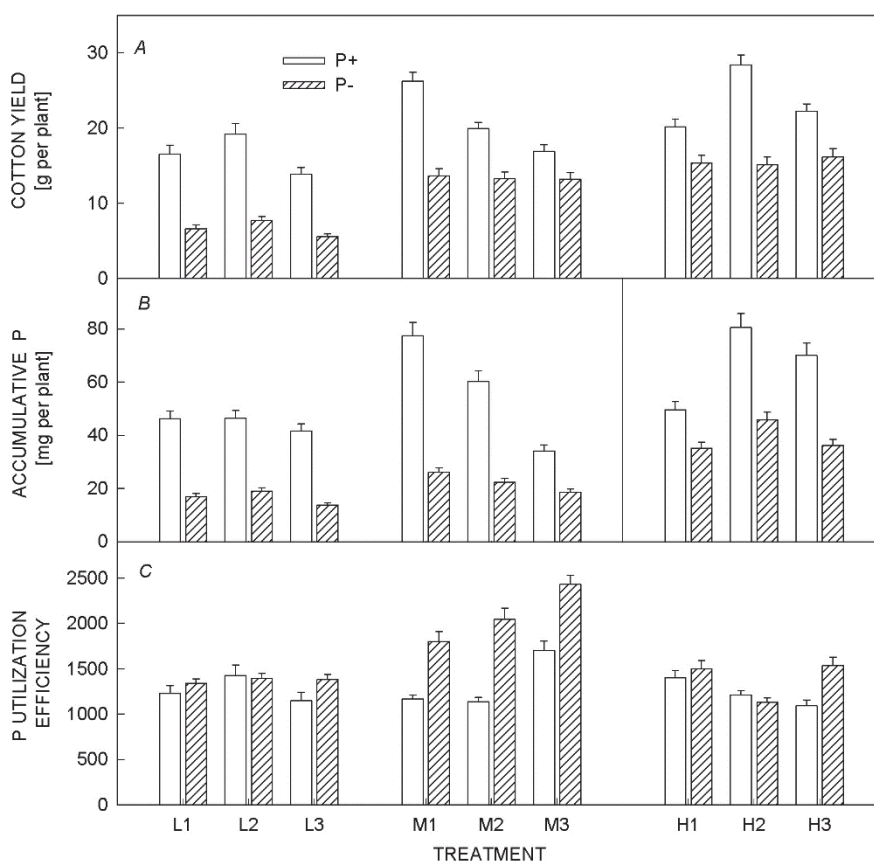


Fig. 5. Cotton yields per plant (A), P uptake per plant (B), and P-utilization efficiency (C) in varieties with different P efficiencies under variable P environments. P⁺ (70 kg ha⁻¹) P⁻ (0 kg ha⁻¹), L, M, H represent low-efficient, medium-, and high-P-efficient cultivars, respectively. Data represent the mean ± standard error ($n = 4$).

P cultivars was associated with greater enzymatic activity and more P uptake during the reproductive phase, resulting in higher leaf photosynthetic capacity. These data can be used to develop a crop management strategy for improving cotton growth and yield in arid region of Xinjiang China and globally.

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