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Cotton leaf photosynthetic characteristics, biomass production, and their correlation analysis under different irrigation and phosphorus application

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Abstract

Water and fertilizer application are the yield improvement approaches in cotton production, especially in arid regions. We hypothesized that irrigation and phosphorus fertilization regimes would enhance cotton leaf photosynthesis capacity. We examined two irrigation levels, *i.e.*, normal irrigation (W_1: 3,750 $m^3\ hm^{-2}$) and limited irrigation (W_2: 2,500 $m^3\ hm^{-2}$), combined with no phosphorus (P_0) and P application (P_1: applying P_2O_5 with the ratio of the fertilizer to dry soil being 0.15 g kg^{-1}). Leaf area (LA), net photosynthetic rate (P_N), transpiration rate (E), and quantum efficiency of PSII (Y_{II}) of cotton under P_1 were higher than that under P_0. Under P_1 conditions, the increasing rate of fruiting branches LA with W_2 was 12.6% higher than that of W_1 after 69 d (DAE). P_N and E were 9.8 and 6.3% higher, respectively; Y_{II} was 38.0% higher at 69 DAE. The total and reproductive organs dry mass (DM) were in the following pattern: $W_1P_1 > W_1P_0 > W_2P_1 > W_2P_0$. After 69 DAE, there was a highly significant correlation between the fruit-branch LA and Y_{II}, between the fruit-branch LA and P_N, and between P_N and reproductive organs DM and total DM. Therefore, application of P can enlarge leaf area and slow down chlorophyll degradation, thus promoting accumulation of photosynthetic products in reproductive organs, especially under drought conditions.

Additional key words: chlorophyll fluorescence; drip irrigation; gas exchange; *Gossypium hirsutum*; water stress.

Introduction

Cotton is an important fiber crop and is mainly cultivated in semiarid and arid regions worldwide. Water scarcity is the main constraining factor for cotton yield, while the utilization of fertilizers exerts a positive effect on cotton yield (Sahito *et al*. 2015, Chen *et al*. 2017). The synergy of water and fertilizer or the coupling mode of both is an important measure to save water in agriculture (Cabello *et al*. 2009, Patanè 2011). It is important to explore possible approaches to enhance drought resistance capacity of cotton and improve the lint yield. Application of water combined with fertilizer can induce drought tolerance and sustain cotton lint yield under water-saving technology, which is of great importance for the sustainable development of cotton.

Photosynthesis is an important physiological process for plant material production and yield formation (Chaves *et al*. 2009). Improving photosynthetic performance is the basis for the increase of dry matter and crop yield. Soil water and nutrients can play an important role in sustaining crop photosynthetic rate (Shangguan *et al*. 2000, Li *et al*. 2016, Khan *et al*. 2017). Drought triggers closure of stomata, affects electron transport rate, aggravates photoinhibition induced by excess light, and lowers rates of CO_2 assimilation, net photosynthesis, electron transport, as well as reduces the quantity of photosynthetic pigments. All these changes could further lead to a reduction in crop yield and affect crop growth (Chaves 1991, Mittler and Zilinskas 1994, Chen *et al*. 2017).

As one of the necessary nutrients for crops, phosphorus has been commonly recognized as an important environmental factor in crop growth and production (Yang *et al*. 2005, Yan *et al*. 2015). A shortage of phosphorus in soil

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Abbreviations: Chl – chlorophyll; C_i – intercellular CO_2 concentration; DAE – days after emergence; DM – dry mass; E – transpiration rate; F_v/F_m – maximum quantum efficiency of PSII photochemistry; g_s – stomatal conductance; LA – leaf area; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; Y_{II} – quantum efficiency of PSII; Y_{NPQ} – quantum yield of regulated energy dissipation of PSII.

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can restrict a stretching of cotton branches and leaves and inhibit photosynthetic activities as well as the accumulation and distribution of photosynthetic products, leading to yield reduction (Rodríguez *et al.* 2000, Singh *et al*. 2013, Wang *et al*. 2018). Moreover, it can also inhibit PSII by increasing the initial fluorescence (F_0) and decreasing both the maximal fluorescence (F_m) and the maximum quantum efficiency of PSII photochemistry (F_v/F_m), leading to a lower efficiency of energy transfer to PSII reaction centers (Singh *et al*. 2013).

Under water shortage, phosphorus application can improve soil water-use efficiency, root growth, and nutrient uptake and consequently increase crop yield (Zheng 2008). The photosynthetic activity of mesophyll cells is higher under phosphorus application compared to no phosphorus application (Wu *et al*. 2002, Girma *et al*. 2007). The period and ways of phosphorus application also affect the crop yield. Compared to traditionally complete basal application and solid phosphorus fertilizer, fertigation can increase cotton yield by 15.2%. Compared to divided applications of solid phosphorus, fertigation causes an increase of the biomass, phosphorus uptake, and fertilizer-use efficiency in corn by 27.1, 34.6, and 61.4%, respectively (Zhang *et al*. 2013, Wang *et al*. 2015). When the ratio of basal application of phosphorus fertilizer to the topdressing was 5:5, the seed cotton yield reached the peak (Hu *et al*. 2010). It also demonstrated that the seed cotton yield could be increased effectively by changing the application amount and period of phosphorus fertilizer. Although, there are extensive studies on phosphorus uptake and usage and their effects on cotton yield improvement under the condition of different water and phosphorus application regimes (Sun 2006, Zhang *et al*. 2014), scarce studies are on responses of the photosynthesis to water and phosphorus, such as the absorption, transfer, dissipation, and distribution of light energy in cotton.

Located at the typical continental semiarid to arid zone, Xinjiang is characterized by a unique irrigation agriculture in the oasis region of the desert and provides particularly favorable natural conditions for cotton growth. However, water deficit and poor nutrient-use efficiency are the main restricting factors in the improvement of cotton yield (Schachtman *et al.* 1998, Raghothama 1999). Hence, achieving a higher cotton yield through optimizing the application of water and fertilizer and exploring the potential of photosynthesis yield increase is both a hot and difficult topic for current Xinjiang cotton research (Hou *et al*. 2007, Luo *et al*. 2014). Previous research on optimal water and nitrogen application regimes has found that an adequate water and nitrogen management not only sustained leaf photosynthetic functioning; it also helped in the distribution of photosynthetic products to reproductive organs (Luo *et al.* 2013a), but also effectively adjusted roots and leaves growth, delayed the senescence of plants (Luo *et al*. 2013b), and improved nitrogen-use efficiency (Norton 2014). Now, the next question to be answered is whether the synergic application of water and phosphorus can affect cotton growth. Thus, the objectives of this study were to investigate the effects of water and phosphorus application on leaf area, chlorophyll (Chl) content, gas exchange, and Chl fluorescence at the cotton production stage and to explore the relationship between photosynthetic characteristics and dry mass. This study explores the mechanism of drought tolerance and improved lint yield as well as an efficient use of water and nutrients under different phosphorus and irrigation regimes.

Materials and methods

Experimental site: The experiment was carried out from April to October 2017 at the Agricultural Test Station of Shihezi University (45º19'N, 86º03'E), Xinjiang, China. Hard polyvinyl chloride (PVC) pipes with a diameter of 30 cm, thickness of 1 cm, and length of 40 cm were used in this experiment. One cotton variety (*Gossypium hirsutum* L. cv. Xinluzao 45) was sown. The soil was medium loam, with a pH of 7.6, a soil organic matter of 12.5 g kg^{-1}, a total nitrogen of 1.45 g kg^{-1}, alkali-hydrolyzable nitrogen of 54.9 mg kg^{-1}, an available phosphorus of 0.23 g kg^{-1}, and an available potassium of 149 g kg^{-1}.

Experimental design: The experiment was designed with two variables in randomized groups, where the two variables were soil water and phosphorus application. The water treatment included normal water supply (W_1: drip irrigation under the film mulch in the field with a specific quota of 3,750 m^3 hm^{-2}) and limited water supply (W_2: drip irrigation under the film mulch with a reduced quota of 2,500 m^3 hm^{-2}, namely 2/3 of the normal irrigation quota). The phosphorus treatment included the group without phosphorus application (P_0) and the group with phosphorus application (P_1: applying P_2O_5 with the ratio of the fertilizer to dry soil being 0.15 g kg^{-1}). The nitrogen source was urea (N, 46%) with 20% being basal application and 80% topdressing. The phosphorus source was KH_2PO_4 (P_2O_5, 52%) with 50% being basal application and 50% fertigation of topdressing at cotton growth stage.

Before sowing, pits were dug out 6.5 m in length, 35 cm in width, and 80 cm in depth, and the pit spacing was 25 cm. The soil layer of 0–40 cm and that of 40–80 cm were placed separately. Every two PVC pipes were connected vertically into an integrated pipe and the connected place was sealed with waterproof tape. Pipes, 80 cm long, were arranged into the pit. Every treatment included twenty pipes. First, a sandy layer of 3–5 cm was laid on the pit. Next, nylon mesh (100 µm) was placed on the sand. Then the sieved soil was put into the pipe according to its original layers. After that, about 6 L of water was charged into every pipe to settle the soil naturally, making the soil in the soil column similar to that in the field. Before manually sowing the cotton seeds on 25–27 April, we mixed the basal fertilizer into the top soil (0–10 cm) and placed a layer of film mulch. Four holes were dug inside and outside of every soil column (the hole spacing inside a pipe was 10 cm and the hole spacing between neighboring pipes was 20 cm). The hole was 3 cm deep and contained two to three cotton seeds. When the seed sprouted and grew the first true leaf and one terminal bud, we only kept one seedling by pulling out the other for every hole. When the seedling had three true leaves and one terminal bud, we implemented the water treatment. During the cotton growth stage, we pulled out weeds as well as prevented and treated pest diseases in a timely manner.

Photosynthetic pigments: We used a punch (8.5 mm in diameter) to obtain five leaf discs and applied 13 mL of acetone (80%) to extract Chl. The tube, covered with a piece of black cloth, was placed in the dark and was regularly shaken to mix the dipped matter for Chl extraction. The spectrophotometer (*UV-2401*, *Shimadzu Corporation*, Japan) was utilized to measure the optical density (OD) with the wavelengths of 663 and 645 nm. The control group was acetone (80%). The formulas were as follows (Li 2000): ρ (Chl *a*) = $12.71OD_{663} - 2.59OD_{645}$, ρ (Chl *b*) = $12.71OD_{645} - 2.59OD_{663}$, and $C = (\rho Vt)/(FV \times 1{,}000)$, where ρ (Chl *a*) and ρ (Chl *b*) were the Chl concentrations (mg mL^{-1}); OD_{663} and OD_{645} were the values of OD under the wavelengths of 663 and 645 nm, respectively; C was the amount of photosynthetic pigments (mg cm^{-2}); Vt was the total volume of the extracted solution, and FV was the area of the small discs (dm^2).

Gas exchange: A portable photosynthesis system (*Li-6400*, *Li-COR Inc.*, NE, USA) was used to measure net photosynthesis (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) of the functional main stem leaf. Open gas circuit was applied. The air flow rate was 500 µmol s^{-1}. In line with the natural light intensity, temperature, and humidity between 10:00 and 13:00 h in Xinjiang, the light intensity provided by the red and blue LED light source was adjusted to 1,800 µmol(photon) m^{-2} s^{-1}, and the temperature was controlled to be 25–32°C. When the CO_2 concentration was stabilized generally to 380 µmol(CO_2) mol^{-1} and the relative humidity was 30–32%, the measurement of gas exchange was carried out.

Chl fluorescence: PSII and PSI were simultaneously measured by a modulated fluorometer (*PAM 100*, *Walz*, Effeltrich, Germany). Each leaf was dark-adapted (30 min) before the measurement. To avoid the interference of stray light, the measurements of minimal fluorescence (F_0), maximum fluorescence (F_m), and the maximum $P700^+$ signal (P_m) were first carried out. Then actinic light (AL) with an intensity of 1,030 µmol(photon) m^{-2} s^{-1} was applied. When the fluorescence signal reached the stable stage (4–5 min), the saturation pulses (SP) with an intensity of 10,000 µmol(photon) m^{-2} s^{-1} were applied for 300 ms. Then the measurements of actual fluorescence yield (F_s) at any time, the maximal fluorescence in the light-adapted state (F_m'), F_0, and the actual fluorescence (F) were conducted. The quantum efficiency of PSII (Y_{II}) was computed according to Genty *et al.* (1989), maximum quantum efficiency of PSII photochemistry (F_v/F_m) was assessed according to Krause and Weis (1991), quantum yield of regulated energy dissipation of PSII (Y_{NPQ}) was determined by Kramer *et al.* (2004) method, and the photochemical quenching (q_P) was calculated according to Schreiber *et al.* (1995).

Leaf area (LA) and dry mass (DM): At the beginning of budding stage (39 d after sprouting), samples were taken every 15 d from three pipes for each treatment. In each pipe, the aboveground part from the cotyledon node was cut and divided into separate parts of stems, leaves (main stem leaves, fruit-branch, and vegetative-branch), cotton bolls, and other organs. After the total LA of single cotton was measured by using a leaf area meter (*LI-3100*, *Li-Cor*, USA), all these separate parts were placed into separate paper bags with labels on. Then all these paper bags were placed into an oven at 105°C for 0.5 h and dried at 80°C to a constant mass.

Statistical analysis: Analysis of variance (*ANOVA*) was performed using *SPSS software version 16.0*. Differences between treatments were considered significant at $P<0.05$ according to least significant difference (LSD) tests. The figures were plotted using software *Sigma Plot version 12.5*. The data were presented as means ± SD.

Results

Leaf area: The total LA of cotton showed the unimodal curve with the peak reached at 69 DAE (Fig. 1). W_1 combined with P_1 increased the total LA by 3.2% at the whole stage. Of which, the average growth of the main stem leaf, fruit branch, and vegetative branch were 1.4, 18.3, and 20.6%, respectively. The combination of W_2P_1 resulted in 18.4% greater total LA. The combination of W_2P_1 resulted in 18.4, 16.8, 19.7, and 18.2% greater total LA, main stem leaf, fruit branch, and vegetative shoot, respectively, compared to other counterparts. During the whole growth period, vegetative-branch LA was higher under normal irrigation and fruit-branch LA under the limited irrigation conditions. W_2 resulted in a higher rate of fruit-branch LA than that of W_1 at the whole growth stage. Under P_1 conditions, rate of fruit-branch LA with W_2 was 12.6% higher than that of W_1 at 69–84 DAE.

Chlorophyll: At 69–99 DAE, Chl *a* and *b* were significantly higher under the W_1P_1 treatment than that of W_1P_0 combination (Table 1), but there were no significant differences in Chl *a* and Chl *a*/*b* under W_2P_1 and W_2P_0 treatment.

Leaf gas-exchange parameters: P_N declined during the whole growth stage (Fig. 2). At the same irrigation level, P_N under P_1 treatment was higher compared with P_0, at 39–84 DAE. Under W_1, P_N for P_1 treatment was 14.4% higher than that of P_0 treatment and under W_2, P_N for P_1 increased by 24.9% over the P_0 treatment. These data showed that phosphorus application could mitigate the negative effects of drought stress on cotton leaf photosynthesis. At the same phosphorus application level, P_N under W_1 treatment was 32.7% higher than that in W_2. Under W_1, leaf P_N under P_1 treatment was 9.8% higher than that of P_0 treatment. Under W_2, P_N for P_1 treatment was 16.1% higher compared with P_0 treatment.

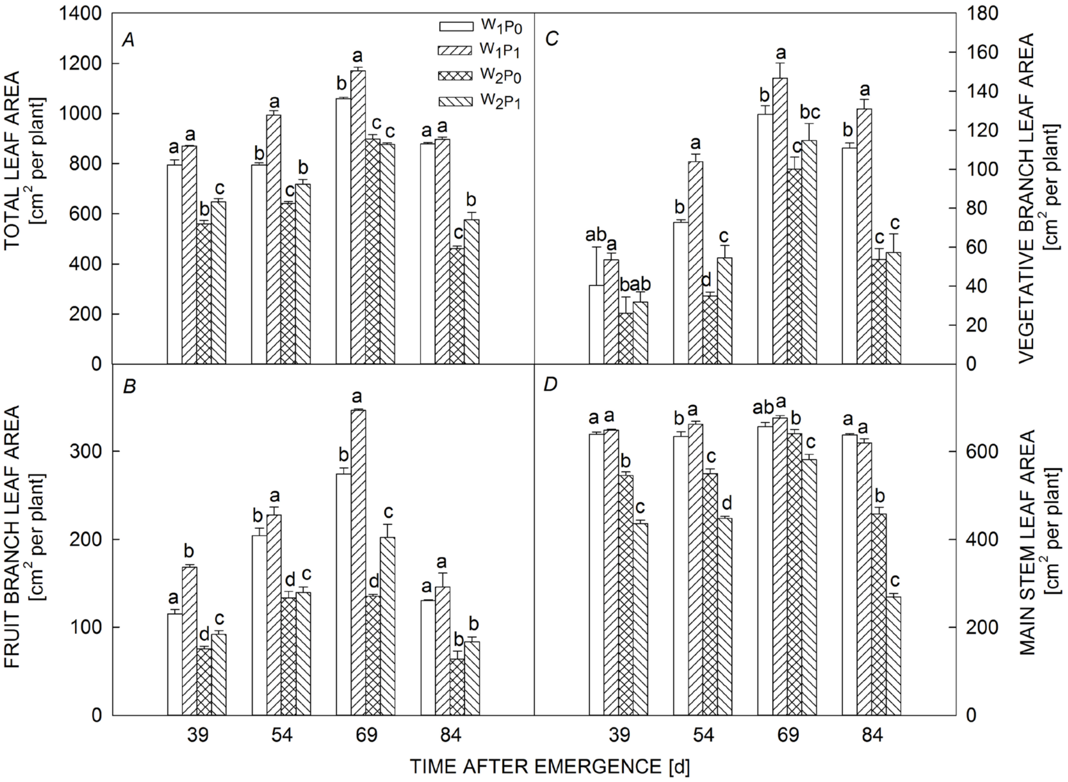

Fig. 1. Changes of total leaf area (LA) (*A*), fruit-branch LA (*B*), vegetative-branch LA (*C*), and main stem LA (*D*) after application of P_2O_5 (0.15 g kg^{-1}) (P_1) and without phosphorus application (P_0) under normal irrigation (W_1) and limited irrigation (W_2). Bars indicate SD (*n* = 3). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

Table 1. Changes in chlorophyll (Chl) *a*, Chl *b*, Chl (*a*+*b*), and the Chl *a*/*b* ratio in cotton leaves after application of P_2O_5 (0.15 g kg^{-1}) (P_1) and without phosphorus application (P_0) under normal irrigation (W_1) and limited irrigation (W_2). Values are means ± SD (*n* = 3). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level. DAE – days after emergence.

DAE	Treatment	Chl *a* [mg dm^{-2}]	Chl *b* [mg dm^{-2}]	Chl (*a*+*b*) [mg dm^{-2}]	Chl *a*/*b*
39	W_1P_0	5.07 ± 0.34^a	0.63 ± 0.09^a	5.70 ± 0.40^a	8.17 ± 1.02^a
	W_1P_1	5.25 ± 0.08^a	0.64 ± 0.06^a	5.90 ± 0.06^a	8.23 ± 0.76^a
	W_2P_0	5.09 ± 0.35^a	0.57 ± 0.03^a	5.67 ± 036^a	8.86 ± 0.56^a
	W_2P_1	5.21 ± 0.13^a	0.62 ± 0.04^a	5.82 ± 0.14^a	8.48 ± 0.55^a
54	W_1P_0	5.38 ± 0.13^{ab}	0.75 ± 0.03^b	6.12 ± 0.12^b	7.19 ± 0.39^a
	W_1P_1	5.65 ± 0.09^a	0.90 ± 0.13^{ab}	6.56 ± 0.14^{ab}	6.41 ± 0.98^{ab}
	W_2P_0	5.31 ± 0.16^b	0.89 ± 0.18^{ab}	6.20 ± 0.33^b	6.21 ± 1.22^{ab}
	W_2P_1	5.64 ± 0.17^{ab}	1.10 ± 0.06^a	6.74 ± 0.16^a	5.15 ± 0.16^b
69	W_1P_0	3.90 ± 0.19^b	1.55 ± 0.08^b	5.44 ± 0.12^b	2.53 ± 0.25^b
	W_1P_1	4.60 ± 0.34^a	1.77 ± 0.04^a	6.37 ± 0.35^a	2.59 ± 0.19^b
	W_2P_0	3.85 ± 0.48^b	1.41 ± 0.13^c	5.26 ± 0.61^c	2.73 ± 0.10^a
	W_2P_1	3.57 ± 0.16^c	1.36 ± 0.06^{bc}	4.93 ± 0.20^c	2.63 ± 0.10^b
84	W_1P_0	3.04 ± 0.17^b	1.30 ± 0.07^b	5.36 ± 0.24^a	2.55 ± 0.01^{ab}
	W_1P_1	3.85 ± 0.17^a	1.51 ± 0.04^a	4.34 ± 0.21^a	2.33 ± 0.07^c
	W_2P_0	3.19 ± 0.18^b	1.22 ± 0.09^b	4.40 ± 0.27^a	2.62 ± 0.05^{bc}
	W_2P_1	3.00 ± 0.15^b	1.26 ± 0.04^b	4.26 ± 0.18^a	2.39 ± 0.06^a
99	W_1P_0	3.61 ± 0.17^b	1.45 ± 0.08^a	5.24 ± 1.27^b	2.62 ± 0.26^a
	W_1P_1	3.81 ± 1.01^a	1.43 ± 0.26^a	5.06 ± 0.26^b	2.50 ± 0.02^a
	W_2P_0	2.39 ± 0.14^c	1.02 ± 0.04^{ab}	3.41 ± 0.18^b	2.35 ± 0.13^a
	W_2P_1	2.78 ± 0.34^c	1.10 ± 0.06^b	3.88 ± 0.38^a	2.52 ± 0.25^a

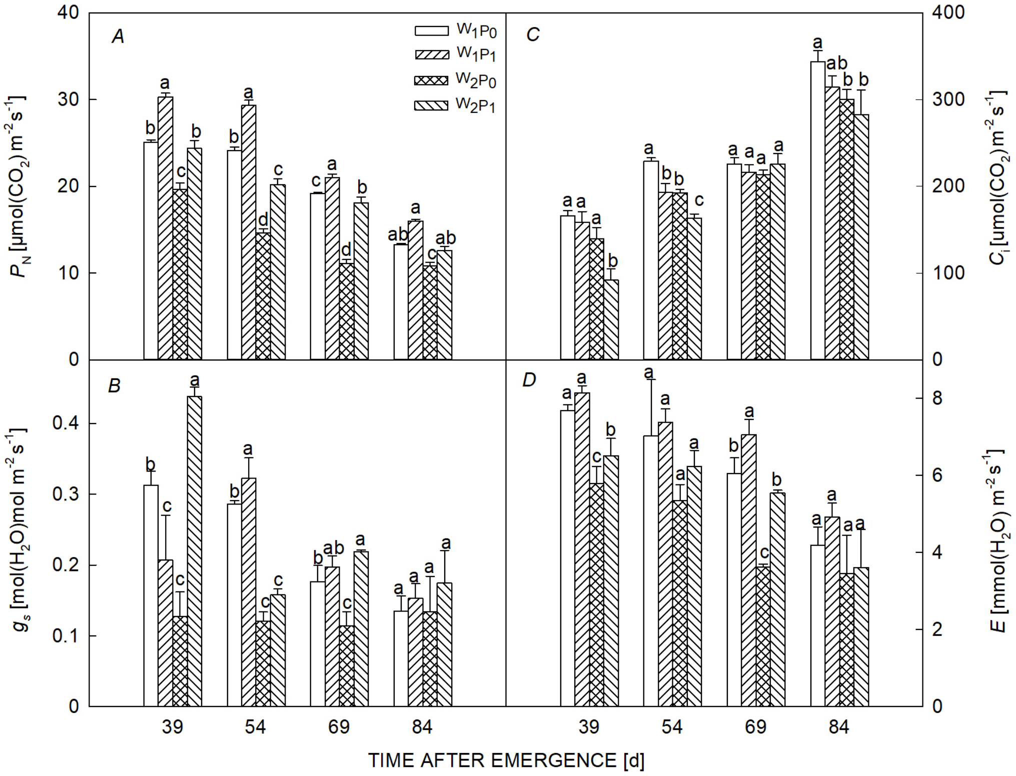

Fig. 2. Changes of net photosynthetic rate (P_N) (*A*), stomatal conductance (g_s) (*B*), intercellular CO_2 concentration (C_i) (*C*), and transpiration rate (*E*) (*D*) after application of P_2O_5 (0.15 g kg^{-1}) (P_1) and without phosphorus application (P_0) under normal irrigation (W_1) and limited irrigation (W_2). Bars indicate SD (*n* = 3). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

At the same phosphorus application level, C_i under W_1 was 14.1% higher than that under W_2 treatment. After 39 DAE, at the same phosphorus application level, g_s under W_1 treatment was 39.4% higher than that under W_2 treatment. Under the same treatment of W_2, C_i under P_1 treatment was in average 41.5% higher than that under P_0 treatment.

Chl fluorescence parameters: Both water and P application substantially influenced Chl fluorescence attributes (Fig. 3). Both the F_v/F_m and Y_{II} declined during the whole growth stage, under W_1, F_v/F_m and Y_{II} in P_1 were 6.8 and 10.4% higher, respectively, than that under P_0 treatment. Significant differences were observed at 84 DAE. Under W_2 treatment, phosphorus application exerted no obvious effect on F_v/F_m, but after 69 DAE, P_1 had 38.0% higher Y_{II} than that in P_0 treatment.

Photochemical quenching (q_P) reflects the transferring efficiency of light quantum harvested by PSII to chemical energy and stands for the openness degree of the PSII reaction center. A greater q_P stands for larger activity of electron transfer in PSII. The q_P increased first and then decreased during the whole growth stage and was at peak during 69 DAE (Fig. 3). Prior to 69 DAE, for W_1, q_P under P_1 treatment was 17.1% higher than that under P_0 treatment. Under W_2, q_P for P_1 was 40.2% higher than that under P_0 treatment. q_P under W_1 treatment was 24.3% lower than that under W_2 treatment. At the same irrigation level, prior to 84 DAE, phosphorus application lowered Y_{NPQ}. Under W_1 treatment, Y_{NPQ} declined by 15.8 and 33.0% under W_1 and W_2, respectively. These data demonstrate that phosphorus application had a significant regulatory effect on Y_{NPQ} under limited irrigation.

Dry mass accumulation: Cotton plant dry matter production under water and P application is shown in Fig. 4. DM accumulation of vegetative organs, reproductive organs, and the aboveground parts under W_2 were respectively 28.9–43.8, 29.2–64.0, and 25.8–54.4% higher than that at the W_1 treatment. In all the irrigation treatments, the vegetative organ DM, reproductive organ DM, and the total DM under P_1 were 7.5–26.7, 21.9–51.7, and 14.1–42.8% higher, respectively, than that of the P_0 treatment.

Correlation analyses showed that after 69 DAE, there was a strong positive correlation between the LA of fruiting branch and Y_{II}. There was a significant positive correlation between Y_{II} and P_N (Table 2). Data also showed a significant positive correlation between P_N and reproductive organ DM as well as total DM. These data suggest that retaining the photosynthetic area of fruiting branch and photosynthesis at 69 DAE was beneficial for the efficient DM accumulation.

Discussion

Plant leaves are the main drivers for photosynthesis and leaf area determines light harvesting, affects photosynthetic

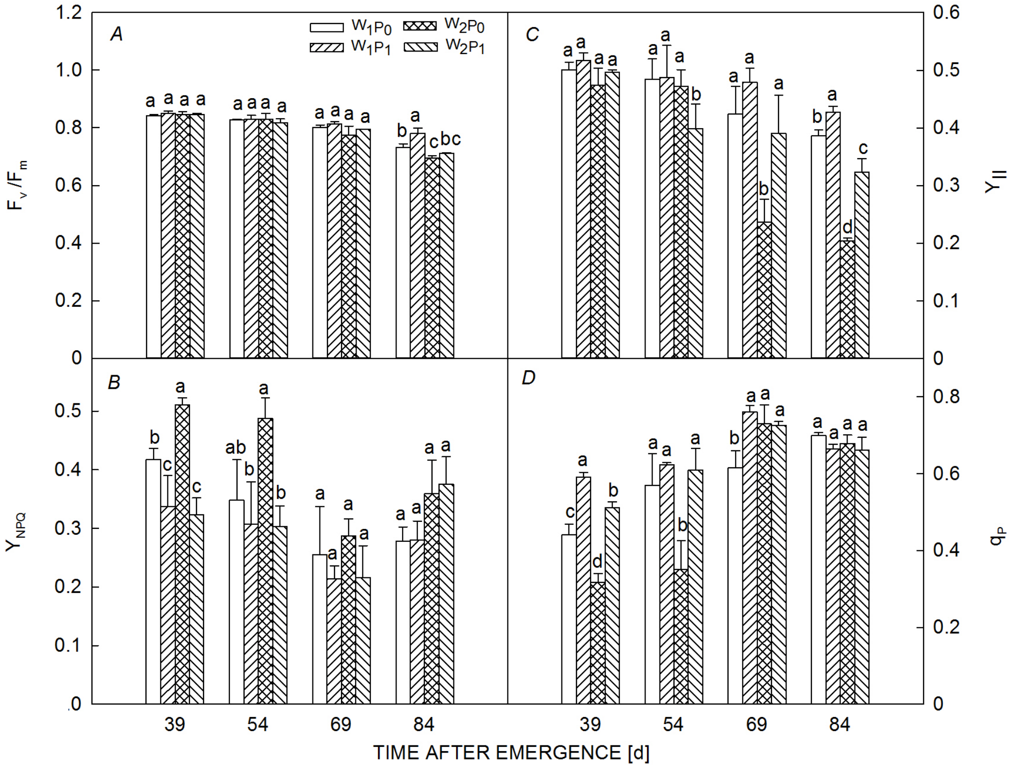

Fig. 3. Maximum quantum efficiency of PSII photochemistry (F_v/F_m) (*A*), quantum yield of regulated energy dissipation of PSII (Y_{NPQ}) (*B*), the quantum efficiency of PSII (Y_{II}) (*C*), and the photochemical quenching coefficient (q_P) (*D*) after application of P_2O_5 (0.15 g kg^{-1}) (P_1) and without phosphorus application (P_0) under normal irrigation (W_1) and limited irrigation (W_2). Bars indicate SD (n = 3). Values within columns followed *by the same letter* are statistically insignificant at the 0.05 level.

activities and the accumulation of photosynthetic products (Lawlor 1995, Dai *et al.* 2001). This research found that under all irrigation patterns, leaf area with phosphorus application was larger than that without phosphorus application. Previous studies have also found that phosphorus shortage has a large effect on wheat growth by directly influencing the extension of leaf area and the growth of tillers (Rodríguez *et al.* 1998, 1999). Subtending fruit branch transported about 85% of photosynthetic products to cotton bolls during growth (Hu *et al.* 2008). In this study, phosphorus application can guarantee a relatively larger photosynthetic area, particularly the area of fruit branch, under the condition of water shortage.

The leaf with a higher Chl content results in greater physiological activity (Jeong *et al.* 2017). P-deficient leaves can slow down the regeneration of ATP and the rate of photosynthesis and decrease the export of photosynthates (Jacob and Lawlor 1992, Rao and Terry 1995). Chloroplasts are organelles which consume phosphorus; a lack of phosphorus can greatly affect the synthesis of photosynthetic pigments (Hu *et al.* 2010). In this experiment, under normal irrigation, phosphorus application greatly improved Chl content (at 69–99 DAE), which may be the result of the application of phosphorus fertilizer and its absorption by cotton plant. The absorption of phosphorus occurs at the late stage of cotton growth (Dai *et al.* 2010). Application of phosphorus combined with irrigation (50% basal application and 50% topdressing application) apparently reduces the amount of phosphorus solidified in the soil and increases available phosphorus in the soil solution leading to higher phosphorus-use efficiency (Zhang *et al.* 2013). Drought stress decreased P accumulation and addition of P significantly increased cotton shoot P acquisition which led to a higher apparent P-fertilizer recovery when drought occurred. A complete basal phosphorus fertilization can increase cotton lint yield (Li *et al.* 2018). The ratio of basal application of phosphorus fertilizer to the topdressing (5:5), is in compliance with cotton growth need for fertilizer and fertigation satisfied cotton's demand for phosphorus at the critical period or boll stage (Wu *et al.* 1996). Meanwhile, retaining a relatively high content of Chl at the late growth stage is the main reason for cotton lint yield increment (Du et al. 2009).

P_N reflects photosynthetic capacity of crops and is the key driver to achieve the higher yield (Wang *et al.* 2018). Moisture stress can significantly depress cotton photosynthetic rate and yield (Kaiser 1987, Pinheiro *et al.* 2011, Khan *et al.* 2018). In this experiment, under limited water and low phosphorus application, both P_N and g_s decreased and C_i increased. Hence, the decline in cotton photosynthetic rate under limited water and phosphorus may be the result of nonstomatal factors which depressed photosynthetic activity of mesophyll cells (Cao *et al.* 2004, Singh *et al.*2013). Furthermore, under limited irrigation, phosphorus application can improve P_N. This might be

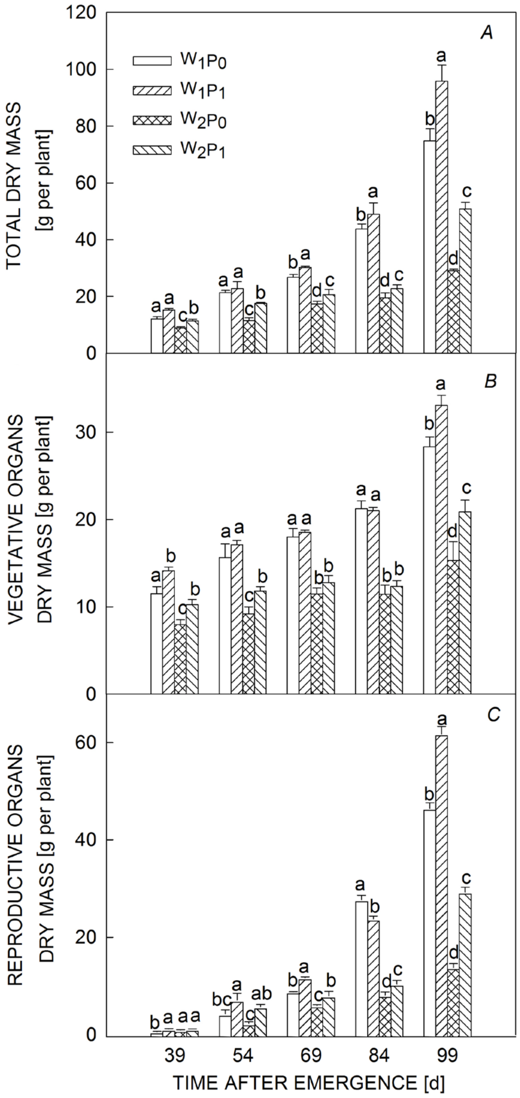

Fig. 4. Changes of total dry mass (DM) (*A*), vegetative DM (*B*), and reproductive organs DM (*C*) after application of P_2O_5 (0.15 g kg^{-1}) (P_1) and without phosphorus application (P_0) under normal irrigation (W_1) and limited irrigation (W_2). Bars indicate SD (*n* = 3). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

explained by the fact that fertilizer application under the condition of water shortage can enhance plant's capacity of absorbing and utilizing soil water (Mengel and Kirby 1987). Improvements in soil water utilization can increase leaf photosynthetic rate (Zheng 2008, Luo *et al.* 2009).

Chl fluorescence dynamics can reflect leaf absorption, transfer, dissipation, and distribution of light energy, and is extremely sensitive to water and fertilizer application (Lin *et al.* 1992, Jia *et al.* 2008). PSII is a photosynthetic component that is more sensitive to stress. Analysis of PSII function is crucial when the plants are exposed to stress conditions (Luo *et al*. 2016). The photochemical activity of PSII was reflected by the photochemical quenching coefficient (q_P) and quantum efficiency of PSII (Y_{II}) (Zhou *et al*.2009). Under normal irrigation, phosphorus application resulted in a greater F_v/F_m, Y_{II}, and q_P.

The q_P is a measure of the oxidation state of PSII primary electron acceptor Q_A reflecting the share of photochemical energy captured by PSII antenna pigments for photochemical electron transport. Low P can affect photosynthesis by changing the phosphorylated intermediate contents within the chloroplast, activation of enzymes of the Calvin cycle, and ribulose-1,5-bisphosphate (RuBP) regeneration (Sawada *et al*. 1992, Rao and Terry 1995). Phosphorus application can also improve the regeneration rate of RuBP, facilitate Calvin cycle (Zhou *et al.* 2009), decrease Chl degradation rate, and improve light-capturing capacity (Makoto and Koike 2007), thus increasing electron transfer rate.

Under drought conditions, phosphorus application brought no obvious effects on F_v/F_m but made Y_{II} increase by 38.0% after 54 DAE. Correlation analyses showed that after 69 DAE there was an extremely significant positive correlation between Y_{II} as well as P_N and the area of fruit branch. Since photosynthetic activities are strongly allied with electron transfer and leaf phosphorus concentration, it can thus maximize photophosphorylation and the production of carbohydrates (Conroy *et al.* 1986). Sufficient absorption of phosphorus can greatly improve light energy-use efficiency (Singh and Reddy 2014, Li *et al.* 2016). Phosphorus application in arid regions satisfies crop's need for nutrients at the growth stage (Brown 1971, Liu *et al*. 2005).

Low amount of effective phosphorus in soil and a shortage of water are important factors restricting dry matter accumulation and cotton yield improvement (Singh *et al.* 2006, Luo *et al.* 2016). A shortage of phosphorus decreases biomass accumulation and yield through affecting crop growth and photosynthesis (Singh *et al.* 2013). The results of this study showed that phosphorus application can improve aboveground biomass accumulation. Under limited irrigation, the highest accumulation of dry matter in reproductive organs was from 69 to 99 DAE. This might be due to deficit in phosphorus which inhibits the generation and proliferation of cells and delays plant growth (Wang *et al*. 2016). Under drought conditions, phosphorus application can improve crop's drought-resistance capacity (Gutiérrez-Boem and Thomas 1999, Jin *et al*. 2006), obviously facilitate crop growth, increase biomass, and greatly improve the ratio of distribution to reproductive organs (Rao and Terry 1989).

Conclusions: Water shortage reduced cotton photosynthetic area, lowered the content of photosynthetic pigments, greatly decreased the actual photochemical efficiency of PSII, increased the dissipation of nonphotochemical energy, and diminished transpiration rate. Phosphorus application increased cotton leaf area, and counteracted the degradation of chlorophyll at the late full boll stage. The normal irrigation and phosphorus at 50% basal application and 50% fertigation increased photosynthetic area, especially under drought. This combination also increased the area of fruit branches, retained a relatively high content of photosynthetic pigments, greatly improved the actual photochemical efficiency of PSII at the late

Table 2. Relationship between the net photosynthesis (P_N), stomatal conductance (g_s), intercellular CO$_2$ concentration (C_i), transpiration rate (E), total leaf area (LA), main stem LA, fruit-branch LA, vegetative-branch LA, vegetative dry mass (DM), reproductive DM, total DM, maximum quantum efficiency of PSII photochemistry (F_v/F_m), quantum efficiency of PSII (Y_{II}), photochemical quenching coefficient (q_P), and quantum yield of regulated energy dissipation of PSII (Y_{NPQ}). ** – highly significant ($p<0.01$) and * – significant ($0.01<p<0.05$). $n = 46$ (before 69 DAE), $n = 12$ (after 69 DAE). DAE – days after emergence.

	P_N	g_s	C_i	E	Total LA	Main stem LA	Fruit-branch LA	Vegetative-branch LA	Vegetative DM	Reproductive DM	Total DM	F_v/F_m	Y_{II}	q_P	Y_{NPQ}
Before 69 DAE															
P_N	1	0.655*	–0.22	0.933**	0.053	0.449	–0.017	–0.241	0.191	–0.388	–0.134	0.649*	0.599*	–0.278	–0.24
g_s		1	–0.09	0.55	–0.16	0.348	–0.2	–0.232	–0.096	–0.315	–0.233	0.37	0.26	–0.368	0.095
C_i			1	–0.164	0.642*	0.676*	0.689*	0.756**	0.593*	0.698*	0.719**	–0.700*	–0.384	0.617*	0.179
E				1	0.144	0.471	0.095	–0.195	0.269	–0.309	–0.037	0.623*	0.614*	–0.208	–0.294
Total LA					1	0.744**	0.909**	0.923**	0.907**	0.815**	0.910**	–0.482	–0.135	0.821**	–0.452
Main stem LA						1	0.626*	0.611*	0.666*	0.389	0.564	–0.253	–0.008	0.484	–0.201
Fruit-branch LA							1	0.892**	0.925**	0.873**	0.963**	–0.38	0.05	0.683*	–0.223
Vegetative-branch LA								1	0.814**	0.943**	0.939**	–0.704*	–0.345	0.846**	–0.26
Vegetative DM									1	0.742**	0.929**	–0.263	0.117	0.682*	–0.36
Reproductive DM										1	0.929**	–0.684*	–0.331	0.776**	–0.174
Total DM											1	–0.529	–0.134	0.785**	–0.263
F_v/F_m												1	0.882**	–0.698*	–0.015
Y_{II}													1	–0.471	–0.003
q_P														1	–0.582*
Y_{NPQ}															1
After 69 DAE															
P_N	1	0.484	–0.121	0.415	0.574	0.479	0.627*	0.734**	0.571	0.615*	0.603*	0.682*	0.760**	–0.514	0.081
g_s		1	–0.519	–0.183	–0.111	–0.156	0.115	0.079	–0.051	–0.083	–0.072	0.137	0.157	–0.786**	0.224
C_i			1	0.233	0.619*	0.684*	0.495	0.477	0.652*	0.580*	0.610*	0.334	0.293	0.805**	–0.562
E				1	0.567	0.524	0.550	0.590*	0.591*	0.610*	0.607*	0.441	0.466	0.122	–0.055
Total LA					1	0.978**	0.896**	0.962**	0.979**	0.994**	0.994**	0.787**	0.766**	0.176	–0.536
Main stem LA						1	0.817**	0.905**	0.969**	0.952**	0.964**	0.682*	0.653*	0.260	–0.519
Fruit-branch LA							1	0.937**	0.903**	0.922**	0.921**	0.796**	0.894**	0.060	–0.559
Vegetative-branch LA								1	0.955**	0.974**	0.973**	0.877**	0.871**	0.004	–0.485
Vegetative LA									1	0.973**	0.989**	0.769**	0.783**	0.192	–0.502
Reproductive DM										1	0.997**	0.822**	0.803**	0.132	–0.503
Total DM											1	0.808**	0.801**	0.154	–0.506
F_v/F_m												1	0.804**	–0.160	–0.432
Y_{II}													1	–0.092	–0.418
q_P														1	–0.427
Y_{NPQ}															1

growth stage, enhanced light energy-use efficiency and CO_2 assimilation. Therefore, it improved photosynthetic activities and the transition of photosynthetic products to reproductive organs.

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