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Photosynthesis and biomass allocation of cotton as affected by deep-layer water and fertilizer application depth

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Abstract

Available water stored in deep soil layers could increase the photosynthetic capacity of cotton. It was hypothesized that the photosynthesis of cotton would be enhanced by changing the fertilizer application depth under different deep-layer water conditions. We examined two deep-layer water levels, *i.e.*, well-watered (W_{80}) and not watered (W_0), combined with surface application (F_{10}) and deep application (F_{30}) of basal fertilizer. Compared to W_0, W_{80} resulted in increased leaf area (LA), photosynthetic pigment contents, maximal PSII efficiency (F_v/F_m), effective quantum yield of PSII (Y_{II}) and PSI (Y_I), electron transport rate of PSII (ETR_{II}) and PSI (ETR_I). W_{80} also increased the aboveground and root dry mass by 39 and 0.6%, respectively, and decreased the root/shoot ratio by 40–73%. Under the W_0 condition, higher values of F_v/F_m, Y_{II}, Y_I, ETR_{II}, and ETR_I were measured for F_{10} compared to F_{30} after 69 d from emergence. Under the W_{80} condition, cotton plants with F_{10} showed higher LA, F_v/F_m, Y_{II}, Y_I, ETR_{II}, and ETR_I, but there were no significant differences in the photosynthetic pigments compared to F_{30}. Our results suggest that sufficient water in deeper soil layers and the surface application of basal fertilizer could increase photosynthetic activity and efficiency, which promoted aboveground dry mass accumulation and partitioning towards reproductive organs.

Additional key words: chlorophyll fluorescence; dry mass; fertigation; gas exchange.

Introduction

Photosynthesis is one of the most important factors driving crop productivity and is also the main process through which material is recycled and energy transported in ecosystems (Evans 1983). Crop photosynthetic efficiency represents the comprehensive effect of solar radiation, atmospheric CO_2 concentration, air temperature, relative humidity, as well as other environmental factors and water-nutrient management measures on crop photosynthetic characteristics (Mayoral *et al*. 2015). Water and nutrients are the most important factors limiting crop growth (Wang *et al*. 2015). Thus, modern agricultural research focuses on principles and practices for improvements of the water- and fertilizer-use efficiency that could enhance the photosynthetic activity of plants in order to achieve higher yields in terms of quality and quantity (Mandal *et al*. 2006, Yahdjian *et al*. 2011).

Water deficit might cause a decline in the leaf water potential and stomatal conductance (g_s) with decreasing net photosynthetic rate (P_N) in cotton (Lawlor *et al*. 2002, Flexas *et al*. 2006), induction of photodamage in PSII of *Sophora davidii* (Wu *et al*. 2008), and reduced electron transport rate of PSI of spinach (Jia *et al*. 2008). The nitrogen nutrient deficiency mainly decreased the accumulation of some ions or compound (*e.g.*, NO_3^- and NH_4^+) in roots and leaves of crops and limited moisture absorption (Lopes *et al*. 2006), the leaf water potential, and

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Abbreviations: C_i – intercellular CO_2 concentration; DAE – days after emergence; DM – dry mass; ETR_{II} – electron transport rate of PSII; ETR_I – electron transport rate of PSI; F_{10} – surface fertilizer application; F_{30} – deep fertilizer application; FM – fresh mass; F_v/F_m – maximal PSII efficiency; g_s – stomatal conductance; LA – leaf area; P_N – net photosynthetic rate; W_{80} – well watered; W_0 – no water; YI – effective quantum yield of PSI; Y_{II} – effective quantum yield of PSII; Y_{NA} – acceptor side limitation of nonphotochemical quantum yield of PSI; Y_{ND} – donor side limitation of nonphotochemical quantum yield of PSI; Y_{NO} – quantum yield of nonregulated energy dissipation of PSII; Y_{NPQ} – quantum yield of regulated energy dissipation of PSII.

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g_s, which caused declining activity of operative enzymes in the Calvin cycle and impaired capacity of carboxylation (Evans 1989) and then reduced P_N. In addition, under water- and nitrogen-deficient conditions, increasing rate of nitrogen-nutrient application might improve g_s, thereby increasing leaf gas exchange in winter wheat (Livingston *et al.* 1999). Based on vast studies, examining effects of water and fertilizer supply rate and timing on the photosynthetic activity of crops (Chapin *et al.* 1980, Clarkson *et al.* 1980, Evans 1983, Radin *et al.* 1986, Sinclair *et al.* 1989), researchers began to focus on the effect of water-fertilizer spatial coupling (water-nutrient application depth in root zone) on crop photosynthesis. The depth of irrigation (at 40 cm) and nutrients application (at 30 cm) in the root zone limited stomatal opening to reduce P_N of wheat. The deep-layer irrigation mainly generated stress signals (ABA) in the roots above watered depth and caused transport of signals to the crop leaves, limiting stomatal opening (Tardieu *et al.*1993). Deep fertilizer application decreased the absorption of water and available nutrients in the soil to reduce stomatal opening (Zhang *et al.* 2006, Shen *et al.* 2007). Thus, the photosynthetic capacity of leaves was sensitive to the rate and availability of water and nutrients. However, there is little information available on the question whether photosynthetic efficiency or light conversion is affected by water-fertilizer coupling.

Cotton (*Gossypium hirsutum* L.) is one of the most important fiber-producing crops all over the world. Light and temperature conditions in the Xinjiang region of northwestern China are favorable for cotton growth. However, scarcity of water is a major limiting factor for agricultural production in Xinjiang. Consequently, improving the water and nutrient efficiency is indispensable for a yield improvement (Hou *et al.* 2007, Luo *et al.* 2014). In our previous studies, irrigation and precipitation before sowing replenished deep-layer water (below 60 cm) which was beneficial to root development and distribution in the deeper soil layers and simultaneously improve the water-use efficiency, resulting in the improved cotton yield (Luo *et al.* 2009, 2014). It can also reduce the inhibitory effect of a root-origin signal (abscisic acid, ABA) on wheat growth, which allows crop to maintain higher water content and physiological activity in leaves (Siddique *et al.* 1990, Blum *et al.* 1993, Li *et al.* 1997). Moreover, basal fertilizer enhances root growth in cotton and absorptive capacity during early growth period, which is conducive for obtaining moisture and nutrient in soil and achieving high photosynthetic efficiency and yield of wheat (Garrido-Lestache *et al.* 2004, Shen *et al.* 2011). Based on our previous studies concerning the fertilizer rate (Luo *et al.* 2015) and mode (Yang *et al.* 2011), the present study was planned to determine whether the depth of basal fertilizer application can be modified in order to enhance the photosynthetic activity and crop yield through water and fertilizer spatial coupling. Thus, the objectives of this study were (*1*) to characterize changes in the photosynthetic traits resulting from different depths of the fertilizer application under different deep-layer water conditions and (*2*) to analyze the physiological mechanisms that lead to the differences in photosynthetic traits and product accumulation.

Materials and methods

Experimental site: The experiment was conducted at a research station of Shihezi University, Xinjiang, in northwestern China (45º19′N, 74º56′E) from April to October 2015. The maximum and minimum temperatures were 26.9 and 9.4°C, respectively. The mean precipitation was 34.0, 23.4, 37.2, 11.5, 31.2, 15.4, and 10.5 mm in April, May, June, July, August, September, and October, respectively. Cotton was grown in polyvinyl chloride (PVC) tubes, 30 cm in diameter and 120 cm in height. The bottom of the tube was covered with a wire mesh fine enough to hold the soil while allowing the water to pass through. Clay loam soil collected from the station field was passed through a 2 mm sieve and packed in the PVC tubes in increments of 0.1 to 1.2 m and then air-dried. The bulk density of the soil was 1.43 g m^{-3}. The soil composition was purple clay loam (pH = 7.6), with 1.45 g(total N) kg^{-1}, 0.23 $g(P_2O_5)$ kg^{-1}, 149 g(total K) kg^{-1}, and 12.5 g(organic matter) kg^{-1}. Four seeds were sown at a depth of 3 cm in each tube on 13 May. The seeds were spaced 10 cm apart in one direction and 20 cm apart in the other. Drip laterals (*Beijing Lvyuan Inc.*, China) were installed on the top of the tubes, and one emitter per tube was fixed at the center. The top of the tube was covered with a polyethylene film in order to reduce evaporation. Standard local pest control measures were adopted.

Experimental design: Cotton (*Gossypium hirsutum* L.) cv. Xinluzao 45 was selected for experiments. Randomized complete block design was employed for four treatments having four replications of each. Twelve tubes per treatment were buried vertically in the field. Two water treatments included (*1*) deep-layer watering (W_{80}), with 0.28 m^3 of water (*i.e.*, 80 ± 5% of field capacity) per tube at the 80–120 cm deep layer before sowing, or (*2*) no water added (W_0), when no water was applied throughout the entire depth of the tube. According to our earlier study (Luo *et al.* 2015) we applied a fertilizer [more than 2,300 kg(settled fertilizer) ha^{-1}] at two depths, *i.e.*, as a surface application (F_{10}) of sufficient basal fertilizer [2.76 g(N), 6.38 $g(P_2O_5)$, and 9.36 $g(K_2O)$ per tube] at the 10–20 cm layer before sowing, and as a deep application (F_{30}) of basal fertilizer (of the same amount and content as above) at the 30–40 cm layer before sowing. Nitrogen was applied at a rate of 0.22 g kg^{-1}(dry soil), with ratios of basal fertilizer to top dressing of 1:4; the phosphate and potassium fertilizer application rates were 0.15 $g(P_2O_5)$ kg^{-1} and

0.22 g(K_2O) kg^{-1}(dry soil), respectively. Nitrogen was applied in the form of $CO(NH_2)_2$ (N = 46%), and phosphate and potassium were applied in the form of KH_2PO_4 (P_2O_5 = 52%, K_2O = 35%). Each pot was drip-irrigated once every four days. The total amount of water supplied to the plants was 434 mm. At 39, 54, 69, 84, and 99 days after emergence (DAE), functional leaves (fourth fully expanded leaf from the top on the main stem) were selected to measure the photosynthesis, chlorophyll (Chl) contents, Chl fluorescence, and gas exchange of cotton plants. The plants were used also for the determination of root and shoot dry mass (DM).

Photosynthetic pigments and leaf area (LA): After the determination of Chl fluorescence, all leaves were harvested. Chl *a* and *b* were determined spectrophotometrically in selected fresh leaves (0.1 g), when ground and extracted in 80% acetone for 96 h. Absorbance was read at 663 and 645 nm (*UV-2401*, *Shimadzu Corporation*, Japan) and the Chl content was calculated according to Li *et al.* (2000) as follows: $\rho(\text{Chl } a) = 12.71\ D_{663} - 2.59\ D_{645}$, $\rho(\text{Chl } b) = 22.88\ D_{645} - 4.67\ D_{663}$, where ρ(Chl *a*) or ρ(Chl *b*) were the content of the Chl *a* or *b*, D_{663} or D_{645} were the absorbances read at 663 or 645 nm by the spectrophotometer. LA was measured using an *LI-3000* leaf area meter (*LI-COR Inc.,* NE, USA).

Gas exchange: The net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of the leaves were measured between 10:00–12:00 h using a photosynthesis system (*Li-6400, Li-COR Inc.,* NE, USA) at a light intensity of 1,800 μmol(photon) m^{-2} s^{-1} under uniform conditions [25–32°C, 330–350 μmol(CO_2) mol^{-1}].

Chl fluorescence, PSI and PSII: Chl fluorescence was determined on the same leaves employed for the photosynthesis measurements, using a modulated fluorometer (*PAM 100, Walz,* Effeltrich, Germany). Initial fluorescence (F_0) and maximal fluorescence (F_m) were measured after a 30-min dark adaptation. The intensity of the saturation pulses, used to determine the maximal fluorescence emission in the presence (F_m') and absence (F_m) of quenching, was 10,000 μmol(photon) m^{-2} s^{-1}, 0.4 s, whereas the actinic light was 1,028 μmol(photon) m^{-2} s^{-1}. After manual balancing of the 830 and 875 nm signals in the dark, the extents of the difference signals corresponding to P_{700} fully oxidized by a saturating pulse superimposed on (*1*) far-red light (P_m) or (*2*) actinic light (P_m') were measured. Maximal PSII photochemical efficiency (F_v/F_m), effective quantum yield of PSI and II (Y_I and Y_{II}), quantum yield of nonregulated energy dissipation of PSII (Y_{NO}), quantum yield of regulated energy dissipation of PSII (Y_{NPQ}), donor side limitation of nonphotochemical quantum yield of PSI (Y_{ND}), acceptor side limitation of nonphotochemical quantum yield of PSI (Y_{NA}), electron transport rate of PSI and PSII (ETR_I and ETR_{II}) were calculated using the methods reported by Demmig-Adams (1992) and Kramer (2004).

Dry mass (DM) production, partitioning and root/shoot ratio: A total of twelve cotton plants (three PVC tubes) were selected from each treatment and cut at the cotyledonary node after the measurement of photosynthesis and Chl fluorescence. Plants were uprooted from the soil and were separated into leaves, stems, buds, flowers, bolls, and roots. DM was obtained from samples oven-dried at 80°C.

Statistical analysis: Analysis of variance (*ANOVA*) was performed using *SPSS software v. 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 10.0.* The data were presented as means ± SD.

Results

LA and photosynthetic pigment contents: LA increased with the number of the DAE (Fig. 1). All treatments exhibited similar response patterns during the growth period. The W_{80} resulted in significantly higher LA compared with the W_0; maximum values were observed at 84 DAE under the W_{80} condition, compared with 69 DAE for the W_0 condition. The LA in the F_{10} was significantly higher than that in the F_{30}. Among all treatments, the highest LA was recorded for the combination of $W_{80}F_{10}$.

From 39 to 84 DAE, Chl *a* (Fig. 2*A*) and Chl *b* (Fig. 2*B*) increased in all treatments but decreased from 84 to 99 DAE, and the Chl *a/b* ratio (Fig. 2*C*) decreased continuously throughout the growing period. Enhanced Chl *a* and *b* contents were recorded for W_{80}, but the Chl *a/b* ratio was lower than that in the W_0 (Fig. 2). Significantly higher Chl *a* and *b* contents were observed in F_{10} compared to F_{30}, but the Chl *a/b* ratio was lower in the F_{10} under both the W_0 and W_{80} (Fig. 2*C*). The highest Chl *a* and *b* contents and the lowest Chl *a/b* ratio were observed in the $W_{80}F_{10}$.

Changes in gas exchange: The gas-exchange parameters (P_N, g_s, and C_i) increased initially and then declined (Fig. 3). All parameters exhibited similar response patterns to the treatments during the growth period. P_N and g_s of W_{80} were lower than that of W_0 from 39 to 54 DAE. In contrast, P_N, g_s, and C_i in the W_{80} were higher as compared to that of W_0 from 59 to 99 DAE. The W_{80} resulted in peak P_N, g_s, and C_i values at 69 DAE, compared with 54 DAE in the W_0. P_N, g_s, and C_i in the F_{10} were consistently higher than that in the F_{30} under both the W_0 and W_{80} conditions during the growth period. In contrast, the highest P_N, g_s, and C_i values were observed in the $W_{80}F_{10}$.

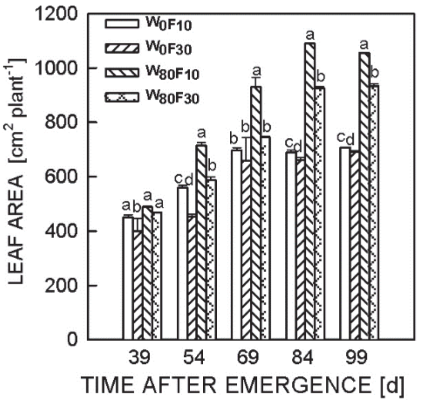

Fig. 1. Changes of leaf area (LA) at watered (W_{80}) or nonwatered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence. *Bars* indicate SD (*n* = 3).Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

Chl fluorescence parameters, PSI and PSII: F_v/F_m (Fig. 4), Y_{II}, Y_{NO}, and ETR_{II} (Fig. 5*A,B,D*) increased initially and then decreased. On the contrary, Y_{NPQ} decreased initially and then increased (Fig. 5*C*); all treatments exhibited similar trends during the growth period. Maximum values of F_v/F_m, Y_{II}, Y_{NO}, and ETR_{II} were observed at 69, 69, 54, and 54 DAE, respectively, while minimum values of Y_{NPQ} were observed at 44 DAE. F_v/F_m, Y_{II}, Y_{NO}, and ETR_{II} were higher in the W_{80} than that of W_0, while the Y_{NPQ} values presented the opposite pattern during the growth period. The F_v/F_m, Y_{II}, Y_{NO}, and ETR_{II} values in the F_{10} were significantly higher than that in the F_{30}, while the Y_{NPQ} values presented a controversial pattern. The highest values of F_v/F_m, Y_{II}, Y_{NO}, and ETR_{II} were found in the $W_{80}F_{10}$, while the Y_{NPQ} values presented the opposite pattern during the growth period. Y_I, Y_{NA}, and ETR_I tended to increase and then decrease (Fig. 5*E–G*). Y_I, Y_{NA}, and ETR_I showed high values from 54 to 69 DAE, but Y_{ND} continued to increase slowly in all treatments, regardless of stage (Fig. 5*F*). The Y_I and ETR_I values in the W_{80} were higher, but the Y_{ND} and Y_{NA} values were lower than in the W_0 throughout the whole growth period. Over the period from 54 to 99 DAE, Y_I, Y_{ND}, and ETR_I were significantly higher, but Y_{ND} and Y_{NA} were lower in W_0F_{10} compared to W_0F_{30}. Maximum values of Y_I and ETR_I and the lowest values of Y_{ND} and Y_{NA} were observed in the $W_{80}F_{10}$ treatment throughout the whole growth period.

Root/shoot ratio: Across all stages, the aboveground DM exhibited a rapidly increasing trend, and the belowground DM exhibited a slowly increasing trend (Fig. 6), while the root/shoot ratio tended to increase and then decrease (Fig. 7). The total DM in the W_{80} treatments increased by 22.4%, the aboveground DM increased by 38.6%, the belowground DM increased by 0.6%, and the root/shoot ratio decreased by 39.5–72.5% compared with the W_0. W_0F_{10} increased the total DM by 14.9%, the aboveground DM by 26.6%, and the belowground DM by 3.4%, while the root/shoot ratio decreased by 0.03–22.8% in comparison with W_0F_{30}. In the case of $W_{80}F_{10}$, total DM increased by 5.5%, the belowground DM increased by 5.8%, and the root/shoot ratio increased by 16.3–88.3% as compared to $W_{80}F_{30}$. However, there was no significant difference in the aboveground DM during the growth period. In the $W_{80}F_{10}$, the total DM, aboveground DM, and belowground DM increased by 2.0–33.6%, 0.1–57.0%, and 1.8–6.0%, respectively, and the root/shoot ratio decreased by 6–58.2% compared with the other treatments.

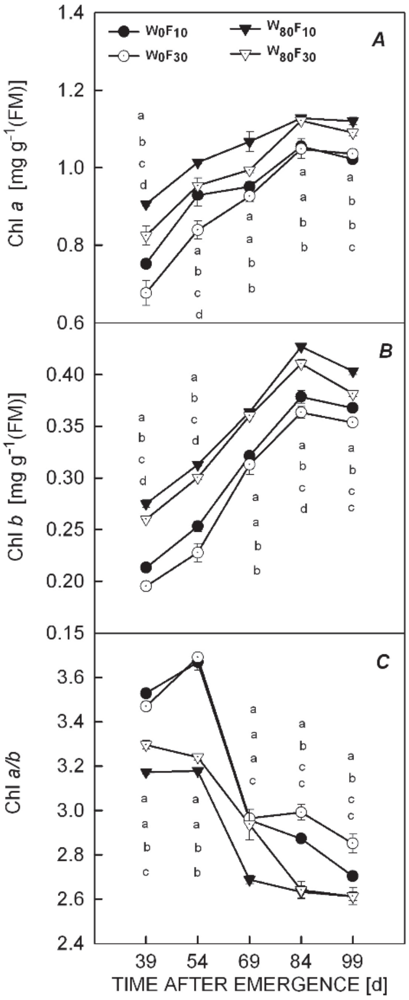

Fig. 2. Changes of chlorophyll (Chl) *a* (*A*) and Chl *b* (*B*) contents, and the ratio Chl *a/b* (*C*), in leaf at watered (W_{80}) or nonwatered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence. *Bars* indicate SD (*n* = 3).Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

DM partitioning: Throughout the whole growth period, the stem and leaf DM increased rapidly from 69 to 99 DAE, while the DM of the reproductive organs increased rapidly from 84 to 99 DAE in all treatments (Fig. 6). In the W_{80}, the DM of the leaf, stem, and reproductive organs were 29.7, 31.6, and 48.1% higher, respectively, than the corresponding values in the W_0 treatments (Fig. 6). Under W_{80} condition, F_{10} decreased leaf and stem DM by 12.3 and 7.7%, respectively, while the DM of the reproductive organs increased by 11.9% in comparison to the F_{30} treatment. The W_0F_{10} increased leaf, stem, and reproductive organ DM by 22.1, 20.3, and 33.1%, respectively, as compared to W_0F_{30}. In the case of $W_{80}F_{10}$, the DM of the leaf, stem, and reproductive organs increased by 10.1–34.5, 15.7–39.1, and 37–82%, respectively, compared to the W_0F_{10} and W_0F_{30}, while the DM of the leaf and stem decreased by 14.1 and 8.3%, respectively, and the DM of reproductive organs increased by 12% compared to $W_{80}F_{30}$.

Discussion

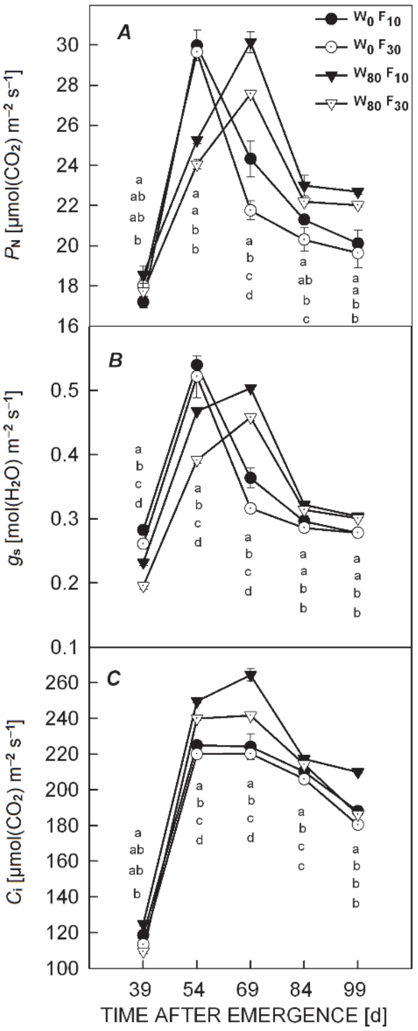

Fig. 3. Changes of net photosynthetic rate (P_N, *A*), stomatal conductance (g_s, *B*), and intercellular CO_2 concentration (C_i, C) in leaf at watered (W_{80}) or nonwatered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence. *Bars* indicate SD ($n = 3$). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

Higher photosynthetic capacity (per unit of leaf area or photosynthetic pigments or leaf gas exchange) plays an important role in yield improvement of plants (van Kooten *et al.* 1990, Li *et al.* 2003) and is significantly affected by the water and fertilizer application rate, application modes, and stage of growth (Wang *et al.* 1999, DaMatta *et al.* 2002, Flexas *et al.* 2006, Makoto *et al.* 2007). Our study showed that changes in P_N were accompanied by changes in g_s. Compared to W_0, the peak of P_N was delayed in the W_{80} treatment and appeared at 69 DAE, and P_N and g_s in W_{80} were higher than that in W_0 after that peak (Fig. 3). However, P_N, g_s, and C_i in F_{10} under W_{80} condition were the highest in comparison to other treatments after 54 DAE. It indicated that $W_{80}F_{10}$ could promote the g_s-stimulated beneficial effect on leaf gas exchange during the whole growth stage. Many studies have shown that g_s has a positive relation with the soil water content (Chen *et al.* 2015, Luo *et al.* 2016). Our early research revealed that deep-layer water resulted in relatively higher root surface area and the root vigor in middle-deep soil layer (40–50 cm) that increased the use of soil moisture and nutrients in the deep soil layer. However, surface fertilizer application increased relatively the distribution of the root system in soil layer above 20 cm that was beneficial to reach and absorb water from irrigation (Li *et al.* 2009), thereby increasing leaf water potential and g_s (Luo *et al.* 2009). It increased CO_2 availability at the mesophyll level (Ball *et al.* 1994, Rouhi *et al.* 2007) and ensured a higher P_N. It is possible that $W_{80}F_{10}$ could better coordinate a relationship among nutrients, moisture, and root in soil profile, declining the water-nutrient stress on root and formation root signal (ABA), allowing a plant to maintain higher water content and physiological activity in leaves (Siddique *et al.* 1990, Blum *et al.* 1993). Lower water and nutrient stress on root could also increase accumulation of some ions or compounds in roots and leaves and then promote moisture absorption (Lopes *et al.* 2006), leaf water potential, and g_s and increase activity of enzymes in the Calvin cycle promoting carboxylation (Evans 1989). Moreover, C_i in $W_{80}F_{10}$ showed the higher value that was caused by stomatal opening, and the carboxylation efficiency did not decrease, though Rouhi *et al.* (2007) found that higher C_i decreased the carboxylation efficiency of

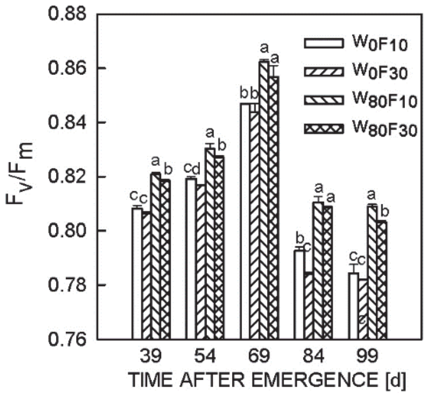

Fig. 4. Changes of maximal PSII photochemical efficiency (F_v/F_m) in leaf at watered (W_{80}) or nonwatered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence. *Bars* indicate SD (*n* = 3). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

leaf under the stomatal closure and lower P_N. Furthermore, our study also found that $W_{80}F_{10}$ could prolong the duration of photosynthetic functions. A possible reason was that the deep-layer water slowly moved from bottom to top during the experiment (Luo *et al.* 2014). Adequate availability of water and nutrients also relieved stress-induced senescence of tissues or organs in rice (Hayashi *et al.* 2013), which prolonged the function of the organs and postponed the P_N peak in $W_{80}F_{10}$. Thus, the $W_{80}F_{10}$ enhanced available water and fertilizer in soil profile which prolonged photosynthesis functioning and increased g_s that promoted P_N and the ability to assimilate carbon in cotton.

Many studies have shown that Chl fluorescence is sensitive to the amount of water and fertilizer (Jia *et al.* 2008, Luo *et al.* 2016), which affects photosynthetic efficiency and the electron transport rate (Jia *et al.* 2008, Wu *et al.* 2008). We found that Chl fluorescence and PSI parameters showed the similar tendency in all the treatments during the whole growth stage. Compared to those from other treatments, $W_{80}F_{10}$ resulted in higher F_v/F_m, Y_{II}, Y_I, ETR_I, and ETR_{II} values after 54 DAE. It indicated that plants possessed higher activity of the reaction centers and the photoprotective mechanisms of PSII, which promoted photochemical energy conversion and transfer efficiency and the electron transport rate of PSI and PSII. $W_{80}F_{10}$ also promoted the accumulation of nitrogen that resulted in higher Chl *a* and *b* contents during the whole growth period (Fig. 2) (Makoto *et al.* 2007), showing that LHC had a greater ability to capture effective light energy (Jeon *et al.* 2006). PSII and PSI are very sensitive to environmental stresses (Hayashi *et al.* 2013, Yi *et al.* 2016). Adequate moisture availability, when the plants were not simultaneously exposed to high light and high temperature, in particular at midday, decreased the photoinhibition of PSII and PSI and promoted the photochemical efficiency and the electron transport rate of PSII and PSI (Hayashi *et al.* 2013, Jia *et al.* 2008, Luo *et al.* 2016). In addition, Y_{ND} and Y_{NPQ} in $W_{80}F_{10}$ were lower, indicating that the capacity of PSI electron acceptors were higher or having more PSI electron acceptors. The electron flow from PSII to PSI *via* the cytochrome *b*$_6$/*f* complex generated proton gradient across the thylakoid membrane (pH) to form ATP and balance the ATP and NADPH energy budget (Tikkanen *et al.* 2014). A possible reason was that adequate moisture and nutrients availability may increased the stress-resistance ability of the leaf, that can tolerate intense solar radiations and temperature (>38°C) to cause over-reduction on the PSI acceptor side leading to PSI photodamage (Munekage *et al.* 2002, Kono *et al.* 2014, Tikkanen *et al.* 2014). Moreover, lower Y_{NPQ} and Y_{NO} (Fig. 5*C*,*D*) values in $W_{80}F_{10}$ further revealed that less energy was dissipated through regulated and nonregulated energy dissipation (Havaux *et al.* 1991, Lei *et al.* 2014), while most of the energy was transmitted through linear electron transport, resulting in considerable chemical energy storage (Hendrickson *et al.* 2004, Takahashi *et al.* 2013). In consequence, $W_{80}F_{10}$ increased activity of the reaction centers and the photoprotective mechanisms of PSII, promoted photochemical energy conversion and transfer efficiency, and the electron transport rate of PSI and PSII.

Dry mass production is a function of the total light energy intercepted (Monteith *et al.* 1977, Latiri-Souki *et al.* 1998). This is also readily affected by the amount of water and fertilizer (Latiri-Souki *et al.* 1998, Mahajan *et al.* 2012) and their supply depths (Ayars *et al.* 1991, Kauer *et al.* 2013). Our study revealed that total DM and aboveground DM in W_{80} were higher, root DM showed no significant difference, the root/shoot ratio was lower as compared to W_0 during the whole growth stage. Under the W_{80} conditions, the F_{10} treatment (Figs. 6, 7) exhibited the highest total DM and aboveground DM, the lowest underground DM and the root/shoot ratio compared to other three treatments throughout the whole growth stage. It indicated that $W_{80}F_{10}$ increased photosynthate partitioning to aerial parts of cotton plants. Thus, $W_{80}F_{10}$ provided adequate available water and nutrients and increased the root absorption that promoted photosynthetic capacity (per unit of leaf area or photosynthetic pigments), increased the leaf gas exchange and photochemical energy conversion and use efficiency and enhanced CO_2 fixation in leaves (Hendrickson *et al.* 2004, Takahashi *et al.* 2013), producing large amounts of photosynthates. Moreover, cotton plants could obtain adequate water by a small root system under $W_{80}F_{10}$, and the root growth of cotton mainly occurred before 69 DAE (Hu *et al.* 2009). Thus, it was beneficial for the accumulation of photosynthates in the aerial parts of the cotton plants after 69 DAE. Hence, $W_{80}F_{10}$ promoted the accumulation of DM in aerial parts of cotton plants.

The total DM increases with increasing water supply; the effect is smaller under sufficient water conditions than that under drought conditions, where applied N doubled the total DM (Lawlor *et al.* 1981, Giunta *et al.* 1993, Latiri-Souki *et al.* 1998). Partial irrigation with adequate water

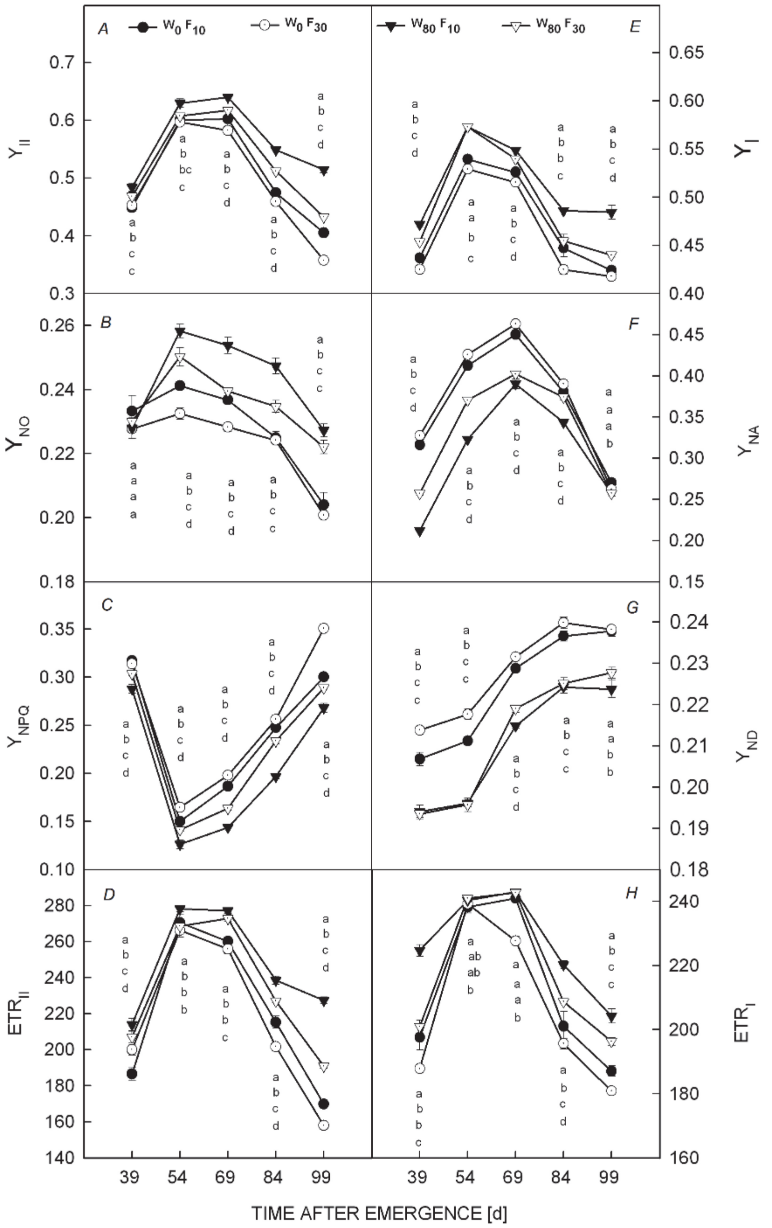

Fig. 5. Changes of effective quantum yield of PSII (Y_{II}, *A*), quantum yield of nonregulated energy dissipation of PSII (Y_{NO}, *B*), quantum yield of regulated energy dissipation of PSII (Y_{NPQ}, *C*), electron transport rate of PSII (ETR_{II}, *D*), effective quantum yield of PSI (Y_I, *E*), donor side limitation of nonphotochemical quantum yield of PSI (Y_{ND}, *F*) and acceptor side limitation of nonphotochemical quantum yield of PSI (Y_{NA}, *G*), and electron transport rate of PSI (ETR_I, *H*) in leaf at watered (W_{80}) or non-watered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence. Bars indicate SD (*n* = 3). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

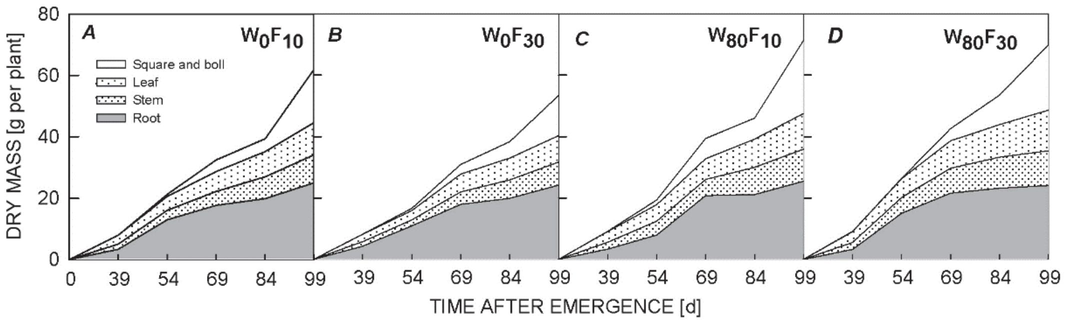

Fig. 6. Change in productive organ, leaf and stem and root dry mass (*A*: no deep layer water and base fertilizer surface application treatment; *B*: no deep layer water and base fertilizer deep application treatment; *C*: deep layer water and base fertilizer surface application treatment; *D*: deep layer water and base fertilizer deep application treatment) production of cotton at watered (W_{80}) or nonwatered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence.

and fertilization supply in the maize root zone reduced the total DM (Kirda *et al*. 2004, Liang *et al*. 2006). In addition, the DM accumulation in different organs exhibited significant differences at different growth stages (Tang *et al*. 2003, Bange *et al*. 2004). Our results showed that W_{80} partitioned the most of DM to the aerial part of cotton plants including leaves, stem, and reproductive organs compared to W_0. Under the W_{80} conditions, the F_{10} promoted a large amount of the aboveground DM partitioning to the reproductive organs compared to other treatments after 84 DAE (Fig. 6). Our results indicated that $W_{80}F_{10}$ enhanced accumulation of DM in the aerial parts of cotton plants including vegetative and reproductive organs, and promoted the greater aboveground (leaf and stem) DM partitioning to reproductive organs (square and boll), which was in accordance with the result concerning deep-layer water (Luo *et al*. 2014), base fertilizer application (Yang *et al*. 2011), and adequate water and nutrients (Radin *et al*. 1992) that were conducive to the DM accumulation and partitioning to reproductive organs.

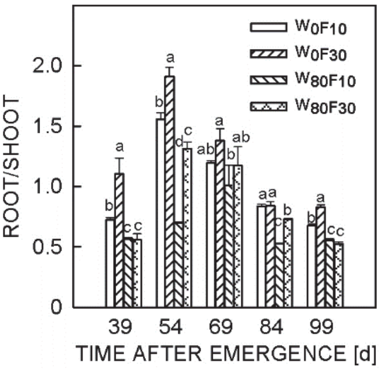

Fig. 7. Change in root shoot ratio of cotton at watered (W_{80}) or nonwatered (W_0) deep soil layer and base fertilizer surface (F_{10}) or deep (F_{30}) application with the days after emergence. Bars indicate SD ($n = 3$). Values within columns followed by *the same letter* are statistically insignificant at the 0.05 level.

Conclusion: Among the treatments in this study, $W_{80}F_{10}$ extended the duration of photosynthetic functions and exhibited the highest LA, photosynthetic pigment contents, gas exchange, and the activity of the photosystems and photochemical energy conversion efficiency after 69 DAE, which caused accumulation of aboveground and reproductive organs (square and boll) DM in $W_{80}F_{10}$. In summary, the synchronous improvement of photosynthetic capacity and the increase in the photosynthetic efficiency resulting from sufficient water in deeper soil layers and basal fertilizer applied at surface depth were the main reasons for the increase in cotton dry mass and allocation to reproductive organs.

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