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Effects of water stress and rewatering on photosynthesis, root activity, and yield of cotton with drip irrigation under mulch

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Abstract

Soil water deficit is a major limitation to agricultural productivity in arid regions. Leaf photosynthesis can quickly recover after rewatering and remains at a higher level for a longer period, thus increasing crop yield and water-use efficiency (WUE). We tested our hypothesis that leaf photosynthesis and root activity of water-stressed cotton (*Gossypium hirsutum* L.) plants could quickly recover after rewatering at a certain growth stage and it should not influence a cotton yield but increase WUE. Treatments in this study included two degrees of water stress: mild water stress (V_1) and moderate water stress (V_2) imposed at one of four cotton growth stages [*i.e.*, S_1 (from the full budding to early flowering stage), S_2 (from early flowering to full flowering), S_3 (from full flowering to full bolling), and S_4 (from full bolling to boll-opening)]. The soil water content before and after the water stress was the same as that in the control treatment (CK, 70–75% of field capacity). Water deficit significantly reduced the leaf water potential, net photosynthetic rate, and stomatal conductance in cotton. The extent of the decline was greater in S_2V_2 treatment compared to others. Water deficit also reduced root activity, but the extent of inhibition varied in dependence on soil depth and duration. When plants were subjected to S_1V_1, the root activity in the 20–100 cm depth recovered rapidly and even exceeded CK one day after rewatering. An overcompensation response was observed for both photosynthesis and aboveground dry mass within one to three days after rewatering. Compared with the CK, S_1V_1 showed no significant effect on the yield but it increased total WUE and irrigation WUE. These results suggest that even a short-term water stress during the S1, S2 and S4 stages mitigated, with respect to the root activity, the negative effect of drought and enhanced leaf photosynthesis compensatory effects of rewatering in order to increase cotton WUE with drip irrigation under mulch in arid areas.

Additional key words: carbon accumulation; gas exchange; irrigation patterns; root growth.

Introduction

Drought is a worldwide problem that seriously affects crop production and quality (Passioura 2007). Irrigation can overcome the problem of drought; however, ground water supplies are declining and energy costs associated with irrigation are increasing. Agricultural producers must act urgently to solve these problems in order to maintain the production of important agricultural crops, such as cotton and wheat. Drought is a universal threat to field crop growth, but not necessarily to crop yields. Water deficit at certain times of the growing season can be compensated after rewatering so that crop growth and yield are sustained (Shan and Zhang 2006). This compensation effect is a self-regulation mechanism that helps crops to adapt to hostile environments by utilizing efficiently limited water resources (Shan and Zhang 2006).

Photosynthesis is a physiological basis of the crop yield (Raines 2011). Mild drought affects leaf expansion during crop growth but does not significantly influence

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Abbreviations: CK – 70% of field capacity; DAP – days after planting; DAR – days after rewatering; g_s – stomatal conductance; OD – optical density; P_N – net photosynthetic rate; S_1 – from full budding to early flowering stage; S_2 – from early flowering to full flowering stage; S_3 – from full flowering to full bolling stage; S_4 – from full bolling to boll-opening stage; V_1 – mild water stress; V_2 – moderate water stress; WUE – water-use efficiency; WUE_{ET} – total water-use efficiency; WUE_I – irrigation water-use efficiency; ψ_w – water potential.

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photosynthesis (Miyashita *et al.* 2005). Leaf photosynthetic rates can quickly recover after rewatering and remain at high levels for long periods, thus increasing the crop yield and water utilization efficiency (Kang and Zhang 2004). When drought-affected plants are rewatered, leaf photosynthetic rates can exceed those of unaffected plants. This can increase the crop yield and water-use efficiency (Kang and Zhang 2004). Water is primarily taken by plant roots. Roots adapt morphologically and metabolically to dry soil. These adaptations directly influence crop photosynthesis and the yield (Oosterhuis *et al.* 1987, Pinheiro *et al.* 2011, Ashraf and Harris 2013). Few studies have examined root growth when water deficit was followed by a period of normal irrigation (Liu *et al.* 2009). However, information is not available on root physiology and their relationship with the cotton yield and water productivity in water deficit and rewatering. Thus, it is important to understand the relationship between photosynthesis and root activity in order to use appropriate irrigation practices (Coelho and Or 1996).

The Xinjiang Uyghur Autonomous Region is located in arid, northwest China. Light and temperature conditions in the region are favorable for cotton growth. However, water shortage has become the major factor limiting agricultural production in Xinjiang. Since the 1990s, cotton growers in Xinjiang have been using a combination of plastic mulch, high planting density, and drip irrigation to save water and to maintain high yields (Zhang *et al.* 2003). This system, called drip irrigation under mulch, is the most common cultivation technique for cotton production in the Xinjiang Province (Wang *et al.* 2004). Most studies about drip irrigation under mulch have focused on drip volume and drip frequency (Zhang *et al.* 2003, Wang *et al.* 2011). The objective of this study was to clarify the ability of cotton plants to recover after water stress and to investigate how it is affected by two dependent factors: (*1*) severity of water stress and (*2*) the growth stage when water stress occurred.

Materials and methods

Site description: The experiment was performed during the 2006 and 2007 growing seasons in an experimental field near Shihezi University, Xinjiang, China (45°19'N, 86°03'E). The maximum/minimum temperatures were 33/18°C in 2006 and 34/17°C in 2007. The relative humidity ranged between 43–61% in 2006 and 52–71% in 2007. The mean precipitation was 26–30 mm in April, 45–50 mm in May, 46–52 mm in June, 35–38 mm in July, 30–35 mm in August, 20–25 mm in September, and 16–20 mm in October. Evapotranspiration was 1400–1500 mm during the growing season. Cotton is normally irrigated in this area. The soil is composed of purple clay loam (pH = 7.6), with 1.45 g(total N) kg^{-1}, 0.21 g(P_2O_5) kg^{-1}, 152 g(total K) kg^{-1}, and 12.5 g(organic matter) kg^{-1}.

Experimental design: A randomized complete block design was used to set up the field experiment with three replicates in 27 plots (6 × 4 m each). The experiment included nine treatments including the control. The soil water content (SWC) of the first treatment was maintained at 70% of field capacity throughout the entire experiment. This treatment was used as the control (CK). During the remaining eight treatments, cotton plants were subjected to water stress for 7–12 d and then the SWC was restored to the control level (*i.e.*, 70% of field capacity). The water stress was imposed at one of four cotton growth stages and there were two levels of water stress:

Stage	Description	Year	Time after planting [d]	Water stress	SWC [%]
S_1	full budding – early flowering	2006	53-77	V_1, mild	50–55
		2007	54-78		
S_2	early flowering – full flowering	2006	78-98		
		2007	79-99		
S_3	full flowering – full bolling	2006	99-119	V_2, moderate	40–45
		2007	100-120		
S_4	full bolling – boll-opening	2006	120-144		
		2007	121-145		

Cotton (*Gossypium hirsutum* L. cv. Xinluzao 13) was sown on 24 April in 2006 and on 18 April in 2007. The rows were 10 cm apart and the plant density was 2.4 × 10^5 plants ha^{-1}. Two alternate unequal row spacing, 30 and 60 cm, were adopted. Plastic film mulch covered alternate rows. Drip tapes with emitters were positioned under the mulch. The plots were fertilized with 240 kg(N) ha^{-1} and 172.5 kg(P_2O_5) ha^{-1}. Pests and weeds were controlled according to local practices. Guard rows (150 cm wide) were planted between every two plots. The management practices in the guard rows were the same as those in the plots.

The SWC in each plot was measured every two to three days using a time-domain reflectometer (*Trime T*$_3$, Germany). The plots were drip irrigated every six days to maintain the SWC within the designed limits for each treatment. The amount of irrigation water applied to the plots was controlled with a water meter (*DN20*, *Beijing Lvyuan*, China).

Predawn leaf water potential, leaf gas exchange, and root functions were measured on the last day of water stress (*i.e.*, day 0 of the rewatering period, DAR) and then the plots were drip irrigated to return the SWC to the control level. The ability of the water-stressed plants to recover was evaluated by measuring the predawn leaf water potential, leaf gas exchange, and root function each day for the next six days (*i.e.*, 1– 6 d DAR) in the S_1 and S_3 treatments. The variables were measured for only five days (*i.e.*, 1–5 DAR) in the S_2 treatment because it rained at 6 DAR. In the S_4 treatment, the variables were only measured on 1 DAR because low temperatures were causing rapid plant senescence. Each variable was measured four times in each plot.

Soil moisture and evapotranspiration: Soil moisture was measured using time-domain reflectometry as mentioned above. The measurements were made in 10 cm increments at depths between 10 and 100 cm. At the end of the water stress period, the plots were irrigated. The relative SWC generally returned to the control level (*i.e.*, 70% of field capacity) within two days after irrigation (Fig. 1S, *supplement available online*).

Evapotranspiration was calculated using the soil water balance method for the growing season (Jiftah and James 1990). The equation was: $ET = R + I - D \pm \Delta W$, where ET is evapotranspiration, R is the amount of precipitation, I is the amount of irrigation water, D is the drainage, and ΔW is the variation in the water content in the soil profile. Rainfall was very low during the cotton growing season in both years. Irrigation only brought the SWC to 70% of field capacity. Therefore, drainage was considered negligible, and ET was calculated as $ET = I \pm \Delta W$.

Predawn leaf water potential, gas exchange and dry matter partition measurements: Predawn leaf water potential and photosynthesis measurements were taken on the fourth fully expanded main stem leaf from the top of the plant in each plot. The predawn leaf water potential (ψ_w) was measured using a digital pressure chamber (*SKPM 1400*, *Skye*, UK) between 05:00 and 06:30 h. The net photosynthetic rate (P_N) and the stomatal conductance (g_s) of each leaf were both measured with a *LI-6400* photosynthesis system (*LI-COR Inc*., NE, USA) under 1,800 μmol(photon) m^{-2} s^{-1} light intensity between 10:00 and 12:00 h.

Four plants from each treatment were cut at the cotyledonary node after the measurement of photosynthesis during the 2007 growing season. The plants were separated into leaves, stems, branches, flowers, and bolls and then oven dried at 80°C until a constant mass was achieved.

Root activity: A block of soil (25 cm long × 25 cm wide × 100 cm deep) was excavated around each of four cotton plants in each plot. It was estimated that the blocks contained approximately 95% of the total root biomass of each plant (Yang *et al*. 2008). The blocks were cut into three parts by depth: 0–20, 20–40, and 40–100 cm. The soil samples were immersed in water for about 60 min and then rinsed with running water. Roots were collected in a 0.5 mm sieve with the aid of a jet of water. Debris, weeds, and dead roots were removed by hand. The root samples were then combined so that there was one root sample for each depth per plot. The surface of young, white roots were blotted dry with tissue paper and then root fresh mass was measured. Root activity measurement was performed according to the triphenyl tetrazolium chloride (TTC) method (Li 2000). Approximately 0.5 g roots were placed in tubes filled with 5 mL of 0.4% TTC and 5 mL of phosphate buffer (0.06 mol l^{-1}, pH 7.0). The tubes were incubated at 37°C for up to 3 h. The chemical reaction was stopped by adding 2 mL of 1 mol l^{-1} sulphuric acid in the tubes. This step was followed by the extraction with triphenyl formazan (TPF). And then, the roots were transfer to a mortar and grinded with a pestle. Meanwhile about 3–4 mL of ethylacetate and a little quartz sand were added to the mortar. After grinding, the extraction was deposited at room temperature for 0.5 h. The liquid phase was placed into a test tube. Ethylacetate was added up to 10 mL, and optical density (OD) values were recorded using a UV-VIS recording spectrophotometer (*UV-2401, Shimadzu Corporation*, Japan) at 485 nm. The OD values were used to calculate equivalent TPF concentrations that determined the root activity for each fresh root mass, the root activity was expressed in μg(TPF) g^{-1}(FM) h^{-1}.

Yield and WUE: The cotton yield was determined by hand harvesting each plot on 15 October 2006 and 8 October 2007. Total water-use efficiency (WUE_{ET}) was calculated as the seed yield (kg ha^{-1}) divided by seasonal evapotranspiration (mm). Irrigation water-use efficiency (WUE_I) was determined as the seed yield (kg ha^{-1}) per unit amount of irrigation water applied (mm) (Viswanatha *et al*. 2002).

Statistical analysis: Analysis of variance (*ANOVA*) was performed with *SPSS version 11.5* software. Differences between treatments were considered significant at $P<0.05$ according to least significant difference (LSD) tests. The figures were plotted using *SigmaPlot version 10.0* software. The data are presented as means ± SD.

Results

Leaf water potential (ψ_w) is an important indicator of the crop water content. The changes in ψ_w are mainly associated with transpiration and water absorption rates. The measurements on 0 DAR indicated ψ_w before the SWC returned to the control level (Fig. 1). The data indicated that the water deficit treatments (*i.e.*, V_1 and V_2) caused significant declines in leaf ψ_w, regardless of the stage when the water deficit was imposed (*i.e.*, S_1, S_2, S_3, or S_4). The lowest leaf ψ_w was observed after the S_2V_2 treatment in 2006 and 2007. The ψ_w recovered quickly as SWC returned to the control level, independently on the stage. Interestingly, the ψ_w of the plants treated by S_1V_1 and S_3V_1, was the same or even higher than that of CK plants. In contrast, ψ_w never fully recovered when soil water deficit was imposed at the S_2 stage.

Leaf photosynthesis and stomatal conductance: The water deficit treatments significantly reduced leaf P_N, regardless of the stage when water deficit was imposed (Fig. 2). The lowest P_N was observed in the S_2V_2 treatment in 2006 and 2007. Leaf P_N increased after SWCs returned to the control level. The ability of plants to recover their photosynthetic activity depended on the degree of drought stress. Specifically, leaf P_N in the S_1V_1, S_2V_1, S_3V_1, and S_4V_1 treatments were as high or higher than those in the corresponding CK treatment within 1 to 3 DAR after the SWCs were restored to control levels. In contrast, leaf P_N in the S_1V_2, S_2V_2, and S_3V_2 treatments were always lower than those in the corresponding CK treatment.

Stomata are the major gas exchange channel between crop leaves and the environment. Crops control CO_2 absorption for photosynthesis by adjusting the diameter of their stomata. In this study, water deficit followed by rewatering had similar effects on both stomatal conductance (g_s) and leaf P_N (g_s data not listed). There was significant, linear correlation between g_s and P_N (Fig. 3). This indicated that g_s was closely associated with P_N.

Root activity is a physiological index reflecting the ability of roots to absorb water and nutrients, to synthesize certain compounds, and to either oxidize or reduce elements in the surrounding rhizosphere. The results indicated that mild water deficit (*i.e.*, V_1) at the S_1 stage increased root activity in the 0 to 40 cm depth by 88% compared with the CK treatment (Fig. 4). In contrast, mild and moderate water deficit (*i.e.*, V_1 and V_2) at the S_2, S_3, and S_4 stages both reduced the root activity compared with the CK treatment. The root activity decreased most when water deficit was imposed at the S_4 stage. The root activity in the S_1V_1 treatment was significantly greater than that in the CK treatment during the first 1–3 DAR. The root activities in the 0 to 40 cm depth were greater after the S_2V_1 and S_2V_2 treatments than those in the CK treatment on 1 DAR. The root activities in the S_2V_1 and S_2V_2 treatments decreased slightly and were the same as those in the CK treatment at 4–6 DAR. The root activities in both the 0 to 40 cm depth and the 40 to 100 cm depth of the S_3V_1 treatment were the same or higher than those in the CK treatment on 1 DAR. The root activity in the 0 to 40 cm soil depth of the S_3V_2 treatment was significantly greater than that in the CK on 1–3 DAR; however, the root activity in the 40 to 100 cm depth of the S_3V_2 treatment was always lesser than that in the CK treatment.

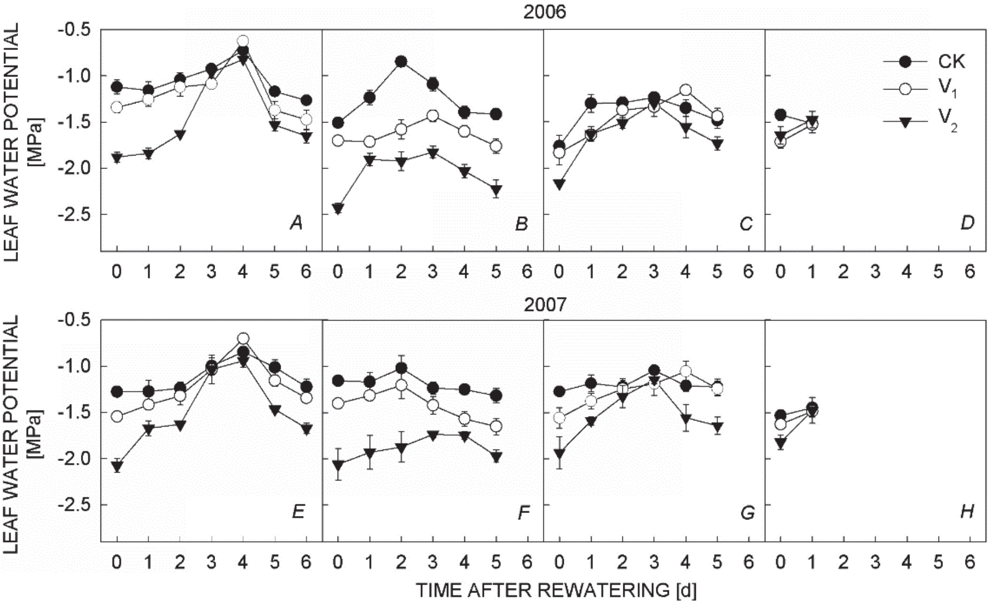

Fig. 1. Recovery of leaf water potential (Ψw) of cotton at the S_1 stage (*A*,*E*), S_2 stage (*B*,*F*), S_3 stage (*C*, *G*), and S_4 stage (*D*,*H*) after water stress in 2006 and 2007. Values are means ± SD, *n* = 4.

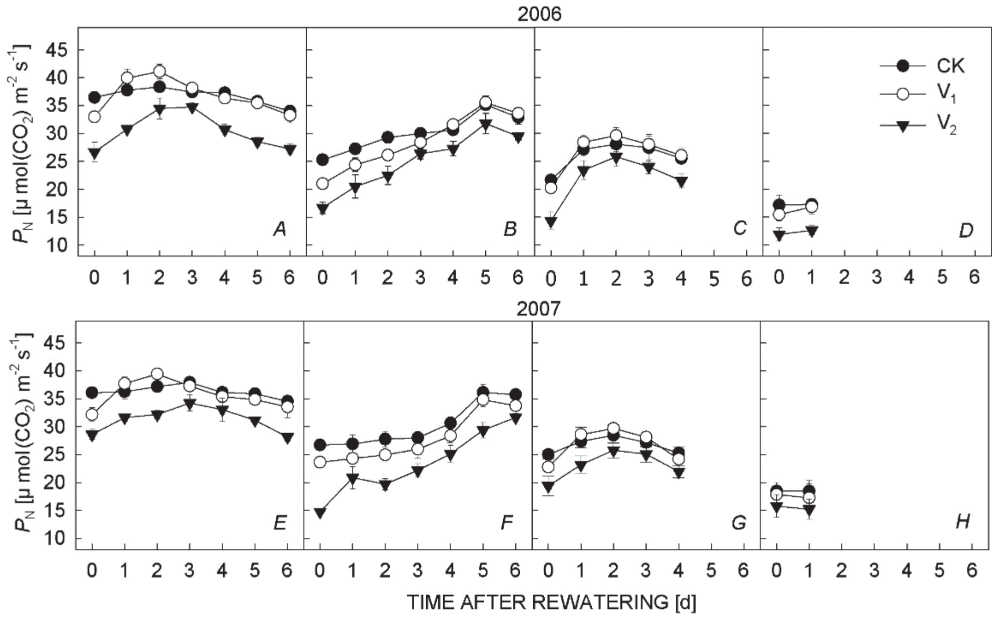

Fig. 2. Recovery of leaf net photosynthetic rate (P_N) of cotton at the S_1 stage (*A,E*), S_2 stage (*B,F*), S_3 stage (*C,G*), and S_4 stage (*D,H*) after water stress in 2006 and 2007. Values are means ± SD, *n* = 4.

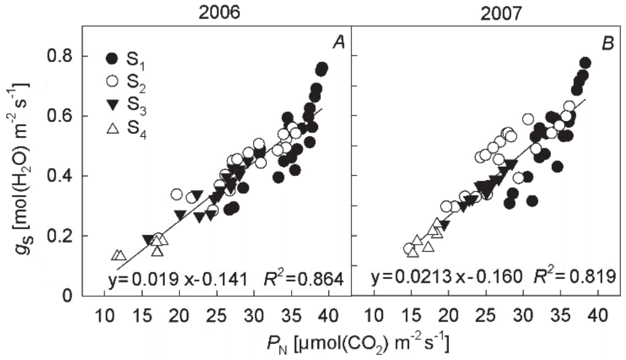

Fig. 3. Relationship between stomatal conductance (g_s) and net photosynthetic rate (P_N) of cotton as affected by water stress at different times during the growing stages (S) in 2006 (*A*) and 2007 (*B*).

Relationship between root activity and P_N: The recovery of the root activity was calculated as the change (*i.e.*, difference) in the root activity between the first and second day after the SWC was returned to the control level. The recovery of P_N was calculated in the same way. When the SWC was restored after imposing water deficit at the S_1 stage, the recovery of P_N was significantly and linearly correlated with the root activity in both the 0–20 cm and the 20–40 cm depths (Fig. 5). When the SWC was restored after imposing water deficit at the S_3 stage, the recovery of P_N was significantly and linearly correlated with the recovery of the root activity in both the 20–40 cm and 40–100 cm depths. When the SWC was restored after imposing water deficit at the S_2 stage, the root activity quickly recovered, whereas P_N recovered more slowly.

Aboveground biomass: The water deficit treatments reduced aboveground biomass by 2 to 49% compared with the CK treatment (Fig. 6). Among water deficit treatments, aboveground biomass was the largest in the S_4V_2 treatment and smallest in the S_2V_2 treatment. Aboveground biomass in the S_1V_1, S_3V_1, S_4V_1, and S_4V_2 treatments increased rapidly after the SWC was restored to the control level. At the boll-opening stage (115 DAP), aboveground biomass in the S_1V_1, S_3V_1, S_4V_1, and S_4V_2 treatments was similar to those in the CK treatment. This result indicated that appropriate drought and timely rewatering could contribute to a compensatory or even overcompensatory response in dry matter accumulation. There was no significant difference in boll dry mass between the S_1V_1 treatment and the CK treatment. In contrast, the other water deficit treatments caused the significant boll dry mass decline, with the largest declines observed in the S_2V_2 and S_3V_2 treatments.

There was no significant difference in a dry matter distribution between the S_1V_1, S_2V_1, S_3V_1, and S_4V_1 treatments and the CK treatment (Fig. 7). The dry matter distribution was 4.2% higher in the S_1V_1 treatment than that in the CK treatment. In contrast, the dry matter distribution was 26% higher in the S_2V_2 treatment and 16% higher in the S_3V_2 treatment than that in the CK treatment. The S_1V_1 treatment significantly increased the transport of dry matter to the bolls, whereas the S_3V_2 treatment had the opposite effect.

Cotton yield and WUE: The timing of moisture stress had a significant effect on the cotton seed yield. The seed yields decreased by 42%, when moisture stress occurred

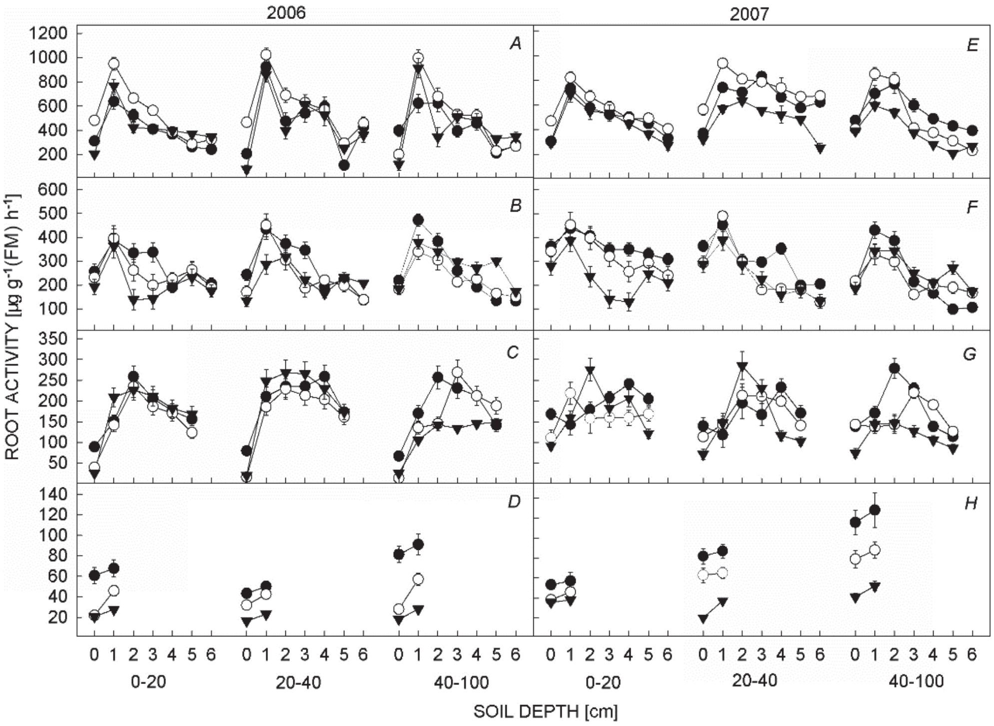

Fig. 4. Recovery of root activity in cotton at the S_1 stage (*A*,*E*), S_2 stage (*B*,*F*), S_3 stage (*C*,*G*), and S_4 stage (*D*,*H*) during the course of rewatering after no water stress (●), mild water stress (○), or moderate water stress (▼) in 2006 and 2007. Values are means ± SD, $n = 3$.

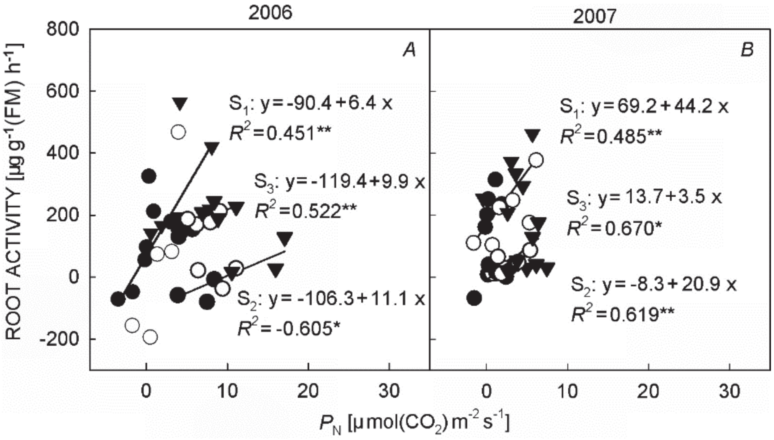

Fig. 5. Relationship between leaf net photosynthetic rate (P_N) and change of root activity in 0–20 cm soil layer during rewatering at the S_1 stage, in 0–20 cm soil layer at 4 d after rewatering at the S_2 stage, and in 20–40 cm soil layer at 4 d after rewatering at the S_3 stage under no water stress (●), mild water stress (○), or moderate water stress (▼) in 2006 (*A*) and 2007 (*B*). *The solid lines* represent the best-fit linear regressions for each treatment. * – P<0.05, ** – P<0.01.

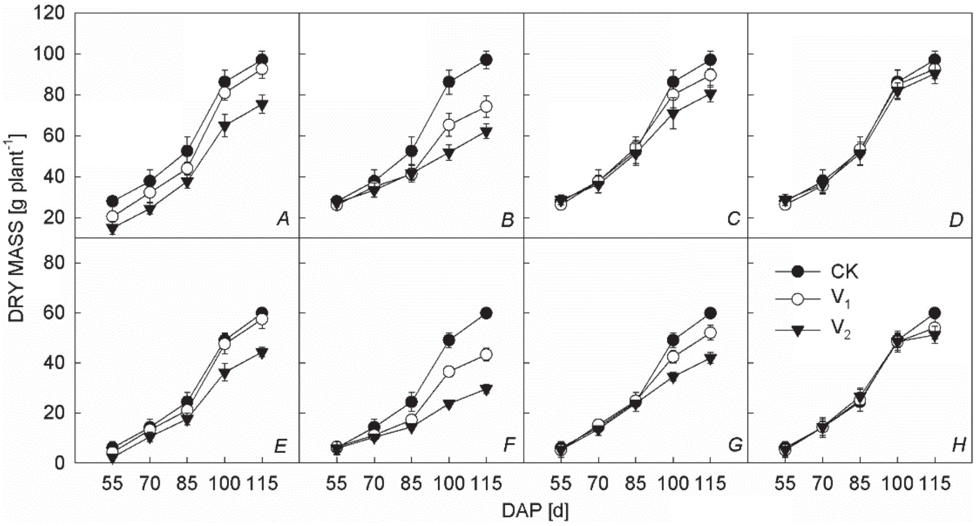

Fig. 6. Temporal changes in the dry mass of cotton shoots at the S_1 stage (*A*), S_2 stage (*B*), S_3 stage (*C*), and S_4 stage (*D*) and reproductive organs at the S_1 stage (*E*), S_2 stage (*F*), S_3 stage (*G*), and S_4 stage (*H*) during the course of rewatering after water stress in 2007. Values are means ± SD, $n = 4$.

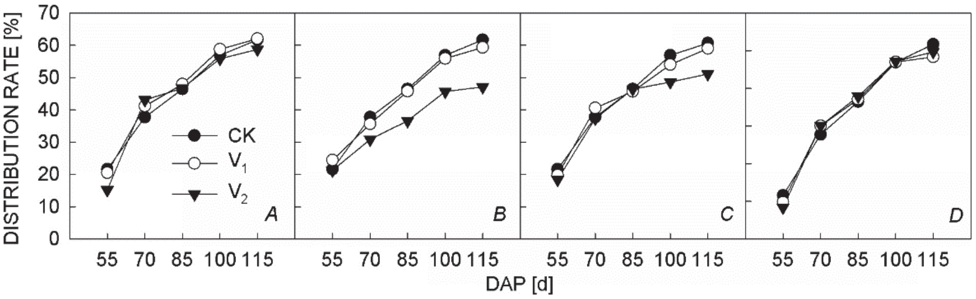

Fig. 7. Temporal changes in distribution rate of dry matter in bud and boll at the S_1 stage (*A*), S_2 stage (*B*), S_3 stage (*C*), and S_4 stage (*D*) during the course of rewatering after water stress in 2007.

during the S_2 stage, and by 31%, when moisture stress occurred during the S_3 stage. Moisture stress during the S_1 and S_4 stages had no significant effect on the seed yield. The S_2V_1 and S_2V_2 treatments showed the lowest WUE among the eight treatments in this study. In comparison, moisture stress during the S_1 stage increased WUE_{ET} by 3.9% and WUE_I by 7.4% compared with the CK treatment. This indicated that moisture stress at the S_1 stage was the most potential for saving water.

The number of bolls per plant and boll quality both decreased as water stress increased. In contrast, the lint percentage slightly increased as water stress increased. The relatively low yields in the S_1V_2, S_2V_1, and S_2V_2 treatments were mainly due to decreases in boll quality and even more, the number of bolls per plant. Water stress during the S_3 and S_4 stages reduced both the number of bolls per plant and boll quality. Between these two variables, the boll quality decreased most quickly, which was the major cause of the drought-induced yield reduction.

Discussion

Photosynthesis belongs to the most sensitive to variations in soil moisture among plant physiological processes. Many studies have reported the negative effects of drought on cotton leaf photosynthesis and light-use efficiency (Ennahli *et al.* 2005, Tang *et al.* 2005, Ko and Piccinni 2009). We observed that moisture stress at any growth stage significantly reduced P_N (Fig. 2). The S_2V_2 treatment caused the largest reduction in P_N, while the S_4V_1 treatment caused the smallest reduction. The P_N in the S_1V_1, S_2V_1, S_3V_1, and S_4V_1 treatments recovered quickly from moisture stress, reaching rates that were the same or greater than that in the CK treatment within four days after restoring the SWC to control levels. The P_N recovered most rapidly in the S_1V_1 treatment. It can explain that the leaf water potential in the S_1V_1 decreased more slowly than in the other treatments and quickly increased after rewatering, which might be due to lower leaf and vapor pressure deficiency during that treatment (Koichi *et al.* 2005).When the SWC was restored to the control level after imposing water deficit during either the S_1 or S_3 stages, both ψ_w and leaf relative water content quickly increased (Fig. 1). This was beneficial for the quick recovery of P_N. Water deficit during S_2 caused the significant decrease in ψ_w. Leaf P_N and g_s both recovered slowly after rewatering.

A pot experiment by Liu *et al.* (2008) showed that mild drought during budding led to only a slight decrease in P_N. The P_N of the S_1V_2, S_2V_2, S_3V_2, and S_4V_2 treatments remained relatively low after the SWC was restored to the control level. One explanation is that most of the excitation energy in the photosynthetic apparatus was used for thermal dissipation during the moderate water deficit treatment (*i.e.*, V_2) after rewatering (Zhang *et al.* 2011). This finding also suggests that moderate drought caused irreversible damage to the photosynthetic apparatus of cotton leaves.

Flexas *et al.* (2004) reported that g_s declines under mild or moderate drought. This results in a reduction of CO_2 supply in the chloroplasts and in a decline of P_N. The authors also indicated that photosynthetic depression in cotton leaves under severe drought was caused by non-stomatal factors, such as an increase in the impedance of gas diffusion in mesophyll cells, a reduction in CO_2 solubility, and a reduction in the affinity of Rubisco to CO_2 (Ennahli *et al.* 2005). In previous research, we concluded that the decrease in P_N in the S_3V_1 and S_3V_2 treatments was mainly caused by stomatal limiting factors (Luo *et al.* 2008). In this experiment, P_N and g_s were significantly lower in all water deficit treatments than those in the control (Fig. 3). Both P_N and g_s continuously increased when the SWC was restored to the control level after water deficit. Furthermore, there was significant linear correlation between P_N and g_s (Fig. 3). Therefore, stomatal limitation was a primary response affecting cotton photosynthesis after rewatering.

Recent evidence suggests that greater shoot activity may contribute partly or fully to greater root activity (Palta *et al.* 2011). Liu *et al.* (2008) demonstrated that water stress during either the blossoming or boll forming stages significantly decreased cotton root activity, which restricted the growth of a cotton root system. However, the cotton root activity quickly increased after rewatering, offsetting some damage caused by drought. In our study, the root activity in the 0 to 100 cm soil depth was significantly higher in the S_1V_1 treatment than that in the CK treatment (Fig. 4). In comparison, when water stress was applied at the S_2, S_3, or S_4 stages, root activities in the

100 cm depth were always lower than those in the CK treatment. Furthermore, the root activities declined as water stress increased.

One explanation is that mild water stress during the early growth stages enhanced the root activity in the middle and upper layers of the soil, forcing the root system to absorb water from deeper soil layers in order to offset the water shortage (Luo *et al*. 2014). Root activities in the 0 to 40 cm soil depth of S_1V_1, S_2V_1, S_3V_1, and S_4V_1 were higher than those in the CK treatment 1 DAR (Fig. 4). This indicated that after water stress, roots (*i.e.*, root activity) recovered more quickly than shoots did (*i.e.*, leaf water potential). The results also indicated that cotton root activity was enhanced in the upper and middle layers of the profile after rewatering, thus providing adequate nutrients and water for rapid shoot growth. Gallardo *et al.* (1994) reported that the root systems developed most rapidly in the part of the soil profile where water availability was high. This preference could optimize the allocation and utilization of crop resources, resulting in the highest water and nutrient availability (Ben-Asher *et al.* 1992). When water stress occurred at the S_1, S_3, or S_4 stages, the root activity recovered to the CK level within 1 to 3 DAR and then gradually declined. When water stress occurred at the S_2 stage, the root activity in the 0 to 40 cm soil depth exceeded that in the CK treatment 1 DAR. Root activities then declined in the S_2 treatment and were the same as those in the CK treatment within 4 to 6 DAR. This finding might be related to the SWC in the 0 to 40 cm soil depth, which decreased to less than 60% of field capacity within 2 to 3 DAR (Xie *et al.* 2011). This decrease in the SWC, which was due to surface evapotranspiration and percolation, quickly reduced the root activity. However, transpiration and hydraulic lift by roots would result in the transport of water from the subsurface soil to the surface soil (Chiatante *et al.* 1999), enhancing root activity in the 0 to 40 cm soil depth.

Al-Khafaf *et al.* (1989) discovered a close relationship between the root activity and P_N. We observed a significant or extremely significant linear relationship between the root activity and P_N after rewatering (Fig. 5). This relationship indicates that rewatering after drought enhanced cotton root activity, which allowed the root system to provide adequate water and minerals to leaves. P_N remained at a relatively high level after recovery, thus increasing resources for photosynthesis and ensuring the supply of photosynthates for root growth (Al-Khafaf *et al.* 1989). The correlation between root vitality and P_N varied among the treatments. The P_N in S_1V_1 and S_1V_2 significantly correlated with the root activity in the 0 to 20 cm depth, whereas P_N in S_2V_1, S_2V_2, S_3V_1, and S_3V_2 significantly correlated with the root activity in both the 0 to 20 and 20 to 40 cm depths. The differences in these results may be caused by the strong and rapid compensation response of P_N in S_1V_1.

Wang *et al.* (2009) demonstrated that short-term drought during soybean podding significantly increased photosynthate distribution to the root system, but significantly reduced photosynthate distribution to the reproductive organs. This caused a drastic drop in economic coefficient and yield. Proffit *et al.* (1985) concluded that moderate drought increased the transport of photoassimilates to wheat roots. This resulted in greater root growth and higher soil water utilization rate during grain filling. We observed that at the same growth stage, the photoassimilate distribution rates to cotton buds and bolls were similar in mild water-stressed plants (*i.e.*, V_1) and non-stressed plants (*i.e.*, CK treatment) (Fig. 6). The S_1V_1 treatment achieved a lint yield that was similar to that of the CK treatment by increasing the distribution rate of photoassimilate to cotton buds and bolls. After rewatering, the plants under the moderate water stress treatments (*i.e.*, V_2) exhibited an early, strong, and long compensation response in regard to P_N and an overcompensation response in regard to dry matter production. These compensations favor translocation of photoassimilates to reproductive organs and improvement of the water utilization rate without significantly decreasing yield (Shan and Zhang 2006).

Conclusion: Among the treatments in this study, S_1V_1 exhibited the highest ψ_w, P_N, g_s, and root activity 1 to 3 DAR. Cotton yield and water utilization efficiency were the highest in the CK and S_1V_1 treatments. Producers can save water, maintain yields, and increase irrigation water-use efficiency by using water deficit-irrigation practices plus drip irrigation under mulch to control cotton root activity and leaf photosynthesis. In this study, the optimum results were obtained when the SWC was maintained at 50–55% of field capacity during S_1, 70–75% of field capacity during S_2, and 50–55% of field capacity during S_3 and S_4.

References

Al-Khafaf S., Aziz F.G., Salih H.M. *et al.*: Shoot and root growth and nutrients uptake of wheat as affected by soil layers. – Plant Soil **117**: 59-66, 1989.

Ashraf M., Harris P.J.C.: Photosynthesis under stressful environments: An overview. – Photosynthetica **51**: 163-190, 2013.

Ben-Asher J., Silberbush M.: Root distribution under trickle irrigation: Factors affecting distribution and comparison among methods of determination. – J. Plant Nutr. **15**: 783-794, 1992.

Chiatante D., Di Iorio A., Maiuro L. *et al.*: Effect of water stress on root meristems in woody and herbaceous plants during the first stage of development. – Plant Soil **217**: 159-172, 1999.

Coelho F.E., Or D.: A parametric model for two dimensional water uptake intensity by corn roots under drip irrigation. – Soil Sci. Soc. Am. J. **60**: 1039-1049, 1996.

Ennahli S., Earl H.J.: Physiological limitations to photosynthetic carbon assimilation in cotton under water stress. – Crop Sci. **45**: 2374-2382, 2005.

Flexas J., Bota J., Loreto F. *et al.*: Diffusive and metabolic limitations to photosynthesis under drought and salinity in C_3 plants. – Plant Biol. **6**: 269-279, 2004.

Gallardo M., Turner N.C., Ludwig C.: Water relations, gas exchange and abscisic acid content of *Lupinus cosentinii* leaves in response to drying different proportions of the root system. – J. Exp. Bot. **45**: 909-918, 1994.

Jiftah B.A., James E.A.: Deep seepage under nonuniform sprinkler irrigation. I: theory. – J. Irrig. Drain. E.-Asce **116**: 354-362, 1990.

Kang S.Z., Zhang J.H.: Controlled alternate partial root-zone irrigation: its physiological consequences and impact on water use efficiency. – J. Exp. Bot. **55**: 2437-2446, 2004.

Ko J., Piccinni G.: Characterizing leaf gas exchange responses of cotton to full and limited irrigation conditions. – Field Crop. Res. **112**: 77-89, 2009.

Koichi M., Shigemi T., Toshihiko M. *et al*.: Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. – Environ. Exp. Bot. **53**: 205-214, 2005.

Li H.S.: Principles and Techniques of Plant Physiological Experiment. Pp. 119-120. Higher Education Press, Beijing 2000.

Liu R.X., Zhou Z.G., Guo W.Q. *et al*.: Effects of N fertilization on root development and activity of water-stressed cotton (*Gossypium hirsutum* L.) plants. – Agr. Water Manage. **95**: 1261-1270, 2008.

Liu R.X., Chen B.L., Wang Y.H., *et al*.: Effects of nitrogen on cotton root growth under drought stress and after watering during flowering and boll-forming stages. – Chin. J. Plant Ecol. **33**: 405-413, 2009.

Luo H.H., Zhang H.Z., Han H.Y. *et al*.: Effects of water storage in deeper soil layers on growth, yield, and water productivity of cotton in arid areas of Northwestern China. – Irrig. Drain. **63**: 59-70, 2014.

Luo H.H., Zhang Y.L., Zhang W.F. *et al*.: Effects of re-watering after drought stress on photosynthesis and yield during flowering and boll-setting stage of cotton under-mulch-drip irrigation in Xinjiang. – Acta Agron. Sin. **34**: 171-174, 2008.

Miyashita K., Tanakamaru S., Maitani T. *et al*.: Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. – Environ. Exp. Bot. **53**: 205-214, 2005.

Oosterhuis D.M., Wullschleger S.D.: Osmotic adjustment in cotton (*Gossypium hirsutum* L.) leaves and roots in response to water stress. – Plant Physiol. **84**: 1154-1157, 1987.

Palta J.A., Chen X., Milroy S.P. *et al*.: Large root systems: are they useful in adapting wheat to dry environments? – Funct. Plant Biol. **38**: 347-354, 2011.

Passioura J.: The drought environment: Physical, biological and agricultural perspectives. – J. Exp. Bot. **58**: 113-117, 2007.

Pinheiro C., Chaves M.M.: Photosynthesis and drought: Can we make metabolic connections from available data? – J. Exp. Bot. **62**: 869-882, 2011.

Proffit A.P.B., Berliner P.R., Oosterhuis D.M.A.: Comparative study of root distribution and water extract ion efficiency by wheat grown under high- and low-frequency irrigation. – Agron. J. **77**: 655-662, 1985.

Raines C.A.: Increasing photosynthetic carbon assimilation in C3 plant to improve crop yield: Current and future strategies. – Plant Physiol. **155**: 36-42, 2011.

Shan L., Zhang S.Q.: [Is possible to save large irrigation water? – The situation and prospect of water-saving agriculture in China.] – Chinese J. Nature **28**: 71-74, 2006. [In Chinese]

Tang L.S., Li Y., Zhang J.H.: Physiological and yield responses of cotton under partial root zone irrigation. – Field Crop. Res. **94**: 214-223, 2005.

Viswanatha G.B., Ramachandrappa B.K., Nanjappa H.V.: Soil-plant water status and yield of sweet corn as influenced by drip irrigation and planting methods. – Agr. Water Manage. **55**: 85-91, 2002.

Wang C., Isoda A., Wang P.: Growth and yield performance of some cotton cultivars in Xinjiang, China, an arid area with short growing period. – J. Agron. Crop Sci. **190**: 177-183, 2004.

Wang L., Wang P.C., Zhang T., *et al*.: Effect of short-term drought and rewatering during the pod-setting stage on leaf photosynthesis and yield of the soybean. – Acta Ecol. Sin. **29**: 3328-3334, 2009.

Wang Y.X., Li M.S., Lan M.J.: Effect of soil wetting pattern on cotton-root distribution and plant growth under plastic mulched drip irrigation in field. – Trans. Chin. Soc. Agric. Eng. **27**: 31-38, 2011.

Xie Z.L., Tian C.Y.: Coupling effects of water and nitrogen on dry matter accumulation, nitrogen uptake and water-nitrogen use efficiency of cotton under mulched drip irrigation. – Plant Nutr. Fertil. Sci. **17**: 160-165, 2011.

Yang L., Wang Y., Kobayashi K. *et al*.: Seasonal changes in the effects of free-air CO_2 enrichment (FACE) on growth, morphology and physiology of rice root at three levels of nitrogen fertilization. – Global Change Biol. **14**: 1844-1853, 2008.

Zhang W.F., Ren L.T., Wang Z.L. *et al*.: Effect of different norms of under-mulch-drip irrigation on diurnal changes of photosynthesis and chlorophyll fluorescence parameter in high yield cotton of Xinjiang. – Sci. Agric. Sin. **36**: 533-538, 2003.

Zhang Y.L., Hu Y.Y., Luo H.H. *et al*.: Two distinct strategies of cotton and soybean differing in leaf movement to perform photosynthesis under drought in the field. – Funct. Plant Biol. **38**: 567-575, 2011.