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PHOTOSYNTHETIC CHARACTERISTICS AND WATER USE EFFICIENCY OF SWEET SORGHUM UNDER DIFFERENT WATERING REGIMES

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Abstract

Sweet sorghum (*Sorghum bicolor* (L.) Moench) has been recognized as an important ethanol crop which can be planted in marginal lands in China, but little is known about its photosynthetic characteristics in this environment. We investigated gas exchange parameters and biomass yield under different watering regimes along the oases chain of the Hexi Corridor in China. The results showed that the net photosynthetic rate (Pn) exhibited a mid-day depression under serious drought stress (SD). However, during the soft dough stage, the diurnal changes in maximum photochemical efficiency of photosystem II, PSII (F_v/F_m) showed an obvious decline, indicating the existence of photoinhibition. Under normal water (NW) and moderate drought stress (MD) conditions, there was a unimodal pattern except in the jointing stage under MD, and there was no evidence of photoinhibition. The highest water use efficiency (WUE) occurred under MD in the early and middle growth stages, while it was highest under SD in the late growth stage. With increasing drought stress, the light compensation point (LCP) increased, whereas the light saturation point (LSP), the apparent quantum yield (AQY) and dark respiration rate (Rd) declined. The stem fresh biomass was highest under MD (77 $t{\cdot}hm^{-2}$). The main conclusion of the study was that SD caused photoinhibition of sweet sorghum and decreased WUE and stem biomass. Under NW, photoinhibition was avoided and stem biomass increased, however, WUE decreased. As a result, the highest WUE and stem biomass of sweet sorghum was achieved under MD.

Introduction

Energy is an important basis for the development of a national economy. The main energy sources that people have used for a long time include petroleum, natural gas and other fossil fuels, but these energy sources are non-renewable and draining away (Jia & Xu, 2006). China is the second largest petroleum consumer in the world and plans to blend 2 million tons ethanol annually into gasoline by 2010 and 10 million tons by 2020. However, China also has the largest population and no longer approves bioethanol projects using corn and wheat. It plans on using non-grain materials which will be planted in marginal land for fuel ethanol production (The National Development and Reform Commission, 2007). Although a native to the tropics, sweet sorghum (*Sorghum bicolor* (L.) Moench) is well adapted to temperate climates (Gnansounou *et al*., 2005; Kangama & Rumei, 2005). It is also highly resistant to drought and salinity, and has a remarkable yield potential even in marginal environments (Cosentino, 1996; Foti *et al*., 1996; Steduto *et al*., 1997; Amaducci *et al*., 2004). For these merits, sweet sorghum has been recognized as one of the most promising ethanol crops in China (Gnansounou *et al*., 2005; Kangama & Rumei, 2005).

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Water deficiency is a major factor limiting plant yield in arid areas (Fuhrer, 2003), and many researchers have focused on the response of plants to drought conditions (Santosl *et al*., 2009; Noorka *et al*., 2009; Ahmed *et al*., 2009). At present, research on sweet sorghum has focused on chemical composition of biomass (Zhao *et al*., 2009), biomass yield and sugar content (Mastrorilli *et al*., 1995, 1999; Wang *et al*., 2009; Thomas *et al*., 2008), genetic diversity and breeding (Menz *et a1*., 2004; Barnaud *et a1*., 2007; Deu *et a1*., 2008), water use efficiency, and other physiological characteristics (Ruzica & Endre, 1997; Steduto *et al*., 1997; Ge *et al*., 2007). However, little is known about the photosynthetic characteristics of sweet sorghum under drought stress.

The Hezi corridor is one of the most seriously desertified areas of China and has an arid desert climate. The soils are only poorly developed and water is deficient, especially along the oases chain of the Hezi corridor, owing to higher rates of evapotranspiration than precipitation. The cultivation of sweet sorghum has an important role in using marginal land effectively in this region. How sweet sorghum can adapt to drought and infertile soil conditions. In an effort to answer this question, we compared photosynthesis and water status in sweet sorghum under different watering regimes along the oasis chain of the Hezi corridor in China. We aimed to elucidate the adaptive mechanism of photosynthesis in sweet sorghum and determine the suitable soil water conditions which can lead to higher aboveground biomass and higher water use efficiency. We hypothesized that stem biomass declines with increasing drought, while water use efficiency increases. Through gaining an understanding of temporal variations in these parameters, we will be better able to provide an important theoretic foundation for the production of sweet sorghum in marginal environments.

Materials and Methods

Study site: The experiment was carried out in 2009 at the Linze Inland River Basin Research Station (39º21′ N 100º02′ E, 1400 m a.s.l.). It is located in the oasis edge region of the northern part of Linze in the middle reach of Hexi Corridor in Gansu Province in northwest of China, It is a typical desert oasis and relies on the Heihe river. It is an arid desert climate where the mean annual precipitation is 116.8mm. The mean annual evaporation is 2390mm which is 20 times higher than the precipitation. The average daily temperature is 7.6°C with a total range of 39.1°C to -27°C. The accumulated annual temperature of ≥10°C is around 3088°C and the frost-free period is 165 d. The main wind is northwest and the windy season is from April to May with an annual wind velocity of 3.2 m/s and there are about 15 days with heavy wind per year. The annual total number of sunlight hours is 3045. The depth of frozen soil is about 10m. The drought, high temperatures and strong wind are the main climate characteristics (Su *et al*., 2004).

Plant material and experiment design: The seeds of sweet sorghum (*Sorghum bicolor* (Linn.) Moench) hybrid BJ0601 were sown on 12, March 2009 in 9 plots (4m × 4m) and planted at 60×40×20cm spacing (100050 five-leave plants per ha). The volumetric soil water content at field capacity of 23.2% and the bulk density was $1.47 g·cm^{-3}$. The seeds began to germinate on March 23. Sweet sorghum reached the flowering stage on August 19 and the soft dough stage on September 1. The crop was harvested on 25 September 2009.

Table 1. Soil moisture content of sweet sorghum under different watering regimes.

Treatment	**Percentage of field moisture capacity (%)**	**Soil moisture content (%)**
NW	70 ± 5	16.2 ± 1.0
MD	50 ± 5	11.6 ± 1.0
SD	30 ± 5	6.9 ± 1.0

Note: NW, normal water supply; MD, moderate drought stress; SD, serious drought stress.

The experimental design was a completely randomized sampling plot design with three replications under three water levels (Table 1). Controlled water regimes started on May 23 2009, which maintained the soil moisture at the main distributed range of sweet sorghum roots (0–60 cm) within three water levels (Table 1). The soil moisture (0–20 cm, 20–40 cm, 40–60 cm,) was measured every 2 days by gravimetric determination. Then the water requirement of each plot was calculated according to the differences between the designed soil moisture and measured soil moisture, and we added the required water the next day. Therefore, we maintained the soil moisture at the main distributed range of sweet sorghum roots (0–60 cm) within the design level during the study. The amount of water added to each plot during the experimental period was 20 m^3, 10 m^3, and 6 m^3 for normal water supply (NW), moderate drought stress (MD) and serious drought stress (SD), respectively.

Water relations measurements: Diurnal time courses of leaf water potential (from 6:00 to 20:00) were measured on 3 leaves of 3 plants from each plot by using WP4 dew point water potential apparatus (Decagon, USA) every 2 hours during different growth stages (five-leaf stage- June 17; jointing stage- July 11; flowering stage- August 19; soft dough stage- September 1). Another leaf on the same plants, which was used to measure leaf water potential, was cut and the fresh leaf weight (FW) was measured on 11th July. Then the same leaf was put in water in the dark and after 12 hours the turgid leaf weight (TW) was measured. Finally leaf dry weight (DW) was obtained after drying the leaf at +80□ for 48h. The relative water content (RWC, %) was calculated with the following formula:

$$RWC = \frac{(FW - DW)}{(TW - DW)} \times 100 \qquad (1)$$

Gas exchange measurements: Diurnal time courses of gas exchange parameters (from 9:00 to 19:00) were measured on typical cloudless days during different growth stages (five-leaf stage- June 17; jointing stage- July 11; flowering stage- August 19; soft dough stage- September 1) and the responses of net photosynthetic rate (Pn) to photosynthetically active radiation (PAR) were measured on a sunny day (August 1 2009) using a LI-6400 Portable Photosynthetic System (LI-COR, Lincoln, NE, USA). A fully expanded leaf in the middle of each plant was used for the measurements. Each measurement (3 readings per leaf) was replicated on 3 plants (per treatment). Net photosynthetic rate (Pn), transpiration rate (Tr), photosynthetically active radiation (PAR), air temperature (Ta), and other parameters were automatically recorded. Instantaneous water use efficiency (WUE) was calculated as a ratio of Pn to Tr and expressed in mmol $CO_2 \cdot mol^{-1}$ H_2O.

Chlorophyll fluorescence measurements: To determine the efficiency of light absorption, chlorophyll fluorescence was measured with a portable pulse amplitude modulation fluorometer (PAM-2100, Walz, Effeltrich, Germany) in the same leaf that was used to measure gas exchange. We estimated the maximum photochemical efficiency of photosystem II, PSII (F_v/F_m) in a day (from 9:00 to 19:00) during different growth stages by:

$$\frac{F_v}{F_m} = \frac{(F_m - F_o)}{F_m}$$

where F_0= minimal fluorescence yield as measured at weak irradiance after adaptation to the dark, F_m= maximal fluorescence yield after adaptation to the dark, F_v= variable fluorescence after adaptation to the dark.

The sampled leaves were pre-adapted to the dark 30 minutes before measurements occurred.

Sugar and biomass yield measurements: The sugar content of the middle part of stem was measured in 10 plants in each plot on September 24 using a Brix refractometer. The stem biomass, leaf biomass and ear biomass in 30 plants in each watering regime were harvested on September 25. The fresh weight was measured before they were dried in an oven at 80°C for at least 72 hours, and then the dry weight was measured.

Statistical analysis: Differences in gas exchange responses, water relations and biomass yield under different watering regimes were analyzed by one-factorial analysis of variance (ANOVA). A multiple comparison of the different levels was made using Duncan's new multiple range test. The light compensation point (LCP) was obtained from fitting a linear regression of Pn against PAR ($\leq$200μmolCO_2·m^{-2}·s^{-1}). Apparent quantum yield was determined from dPn/dPAR (Von Caemmerer & Farquhar, 1981). The light saturation point (LSP) was obtained by fitting a quadratic equation of Pn against PAR ($>$200μmolCO_2·m^{-2}·s^{-1}) (Su *et al*., 2004). The Rd was obtained by the rate of PAR (=0μmolCO_2·m^{-2}·s^{-1}) (Forseth *et al*., 2001). All statistics and graphs were produced using the Origin 7.0 software package.

Results

Diurnal changes of the meteorological factors: The photon flux density (PFD) was highest on July 11 where it peaked at 13:00 with 2023μmol·m^{-2}·s^{-1} (Fig. 1A); it was lowest on September 1 and the maximum value was also reached at 13:00 with 1285μmol·m^{-2}·s^{-1} (Fig. 1A). The daily variations of air temperature (Ta) were all higher on June 17, July 11 and August 19 than on September 1, with temperatures at 14:00 of 40.6°C, 38.6°C and 37.2°C, respectively; (Fig. 1B). The variation of ambient CO_2 concentrations (C_a) were higher on August 19 and September 1 (mean: 377.1μmol·mol^{-1} and 386.6μmol·mol^{-1}, respectively; Fig. 1C) and lower on June 17 and July 11 (mean: 344.6μmol·mol^{-1} and 344.5μmol·mol^{-1}, respectively; Figure 1C). The daily mean air relative humidity (RH) was lowest on June 17 with 16.9% and it was highest on September 1 with 33% (Fig. 1D).

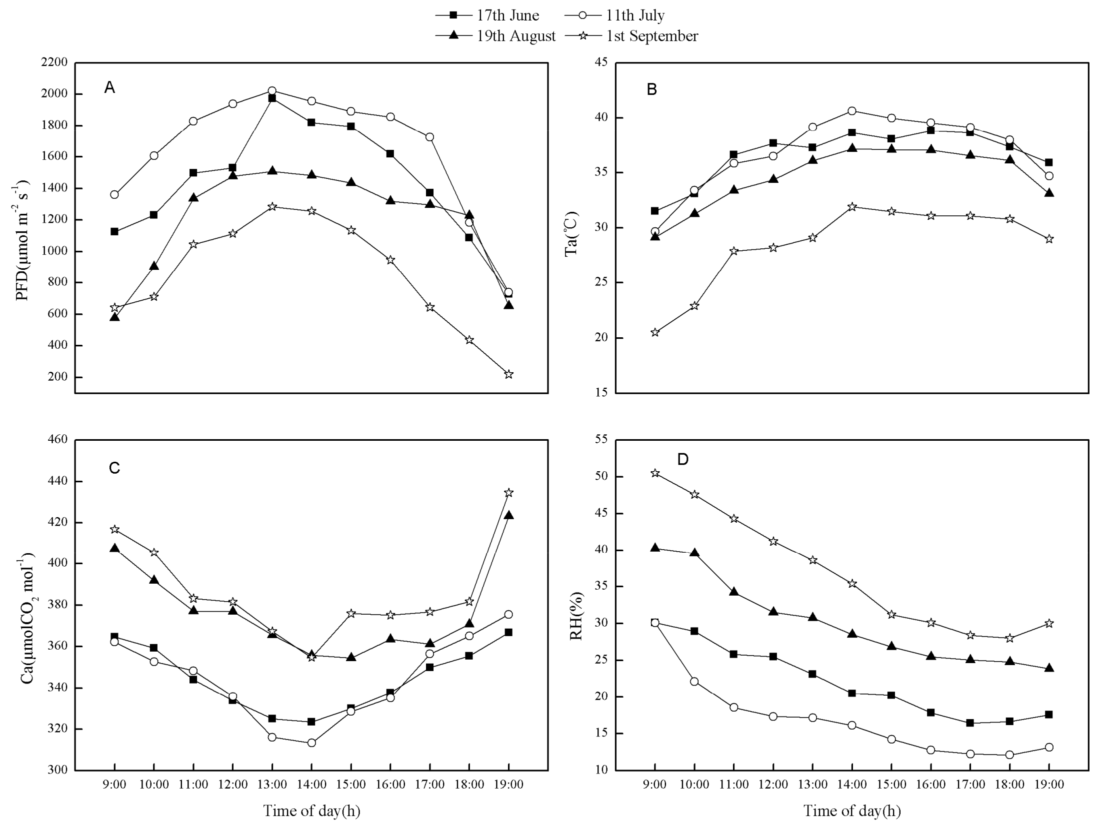

Fig. 1. Diurnal changes of meteorological factors. PFD: photon flux density; Ta: air temperature; RH: relative humidity; C_a: ambient CO_2 concentration.

Relative water content and leaf water potential: The RWC under MD and SD were all lower than that of NW (95%, 89% and 77%, respectively; Fig. 2). Compared with NW, the RWC decreased by 6.32% and 18.95% under MD and SD, and it had a significant difference under different watering regimes ($P < 0.05$).

Diurnal variation of leaf water potential in different growth stages first decreased and then increased in the afternoon under relaxed conditions of evaporational demand, with lowest values at 14:00 (Fig. 3). The daily mean leaf water potential was lower in drought stressed plants than that in NW. Changing through time, the daily mean leaf water potential was lowest in the jointing stage (July 11) in every watering regime because this growth stage occurs in the hottest period in this region and the plants are under much more stress. The daily mean leaf water potential under SD was significantly different than NW ($P < 0.05$), but there was no significant difference between MD and NW ($P > 0.05$).

Changes of leaf gas exchange parameters: The diurnal course of Pn under different watering regimes in different growth stages showed different trends (Fig. 4). It presented a unimodal pattern under NW and MD except in the jointing stage of MD (Fig. 4B) and a bimodal pattern under SD except in the soft dough stage (Fig. 4D). It had a midday depression under SD in the early and middle growth stages but had a midday depression under MD in the jointing stage (Fig. 4B). The maximum daily mean Pn occurred in the jointing stage and the values were 36.38±2.07$\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$, 33.30±1.8$\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ and 27.45±1.83$\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ for MD, MD and SD, respectively. It decreased by 8.47% in MD and 24.55% in SD than NW, respectively. Compared to NW, the daily mean Pn was significantly different in the SD treatment ($P < 0.05$) while there was no significant difference in MD for different growth stages ($P > 0.05$).

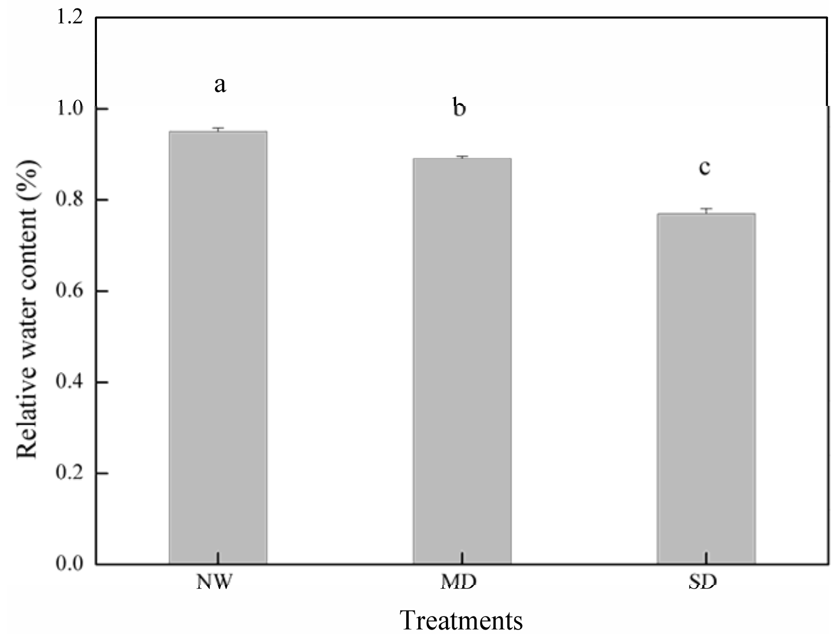

Fig. 2. Changes in relative water content on July 11 under different watering regimes. Different letters indicate significant differences at P < 0.05.

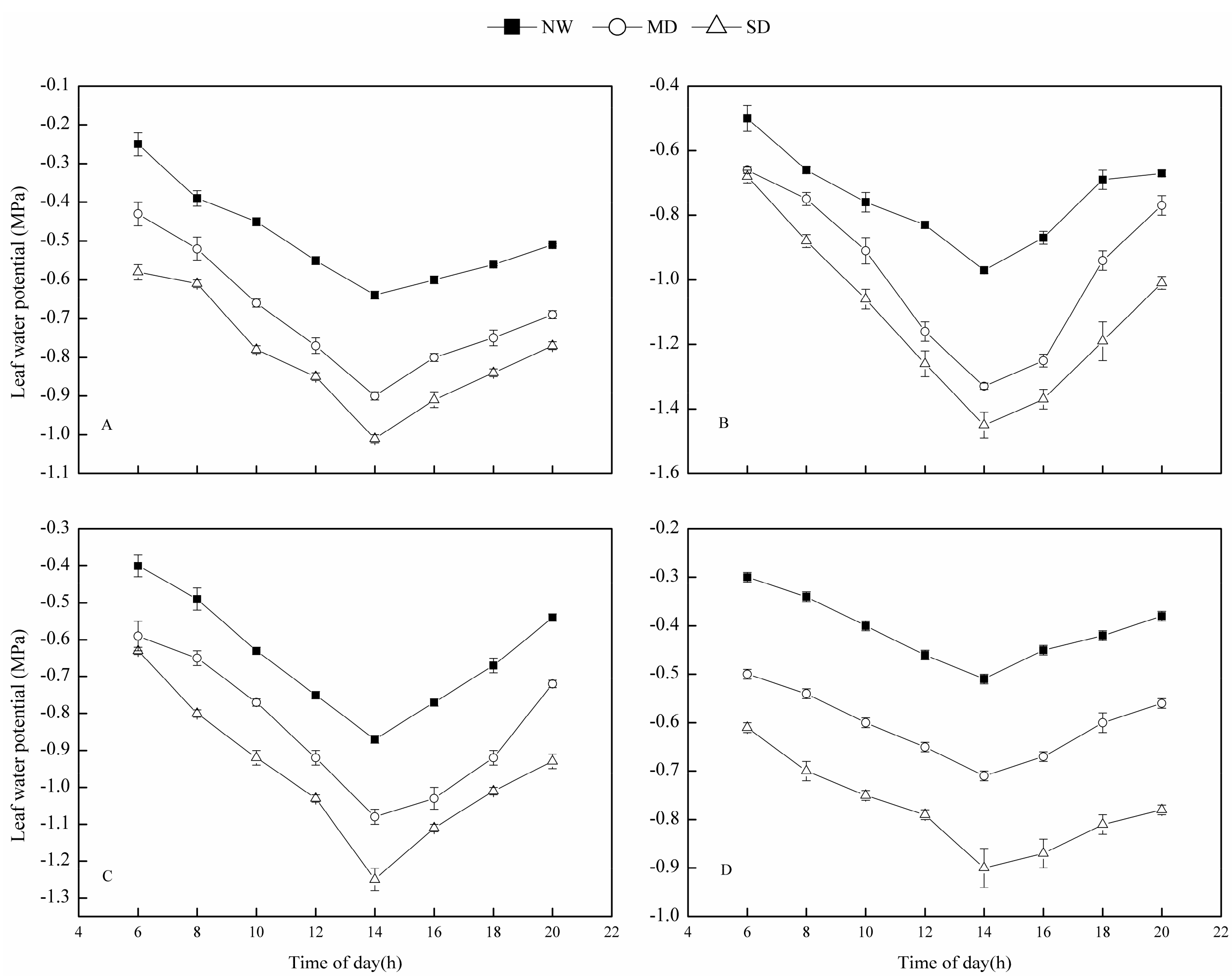

Fig. 3. Diurnal patterns of leaf water potential under different watering regimes in different growth stages. a, b, c, d refers to five-leaf stage- June 17; jointing stage- July 11; flowering stage- August 19; soft dough stage-September 1.

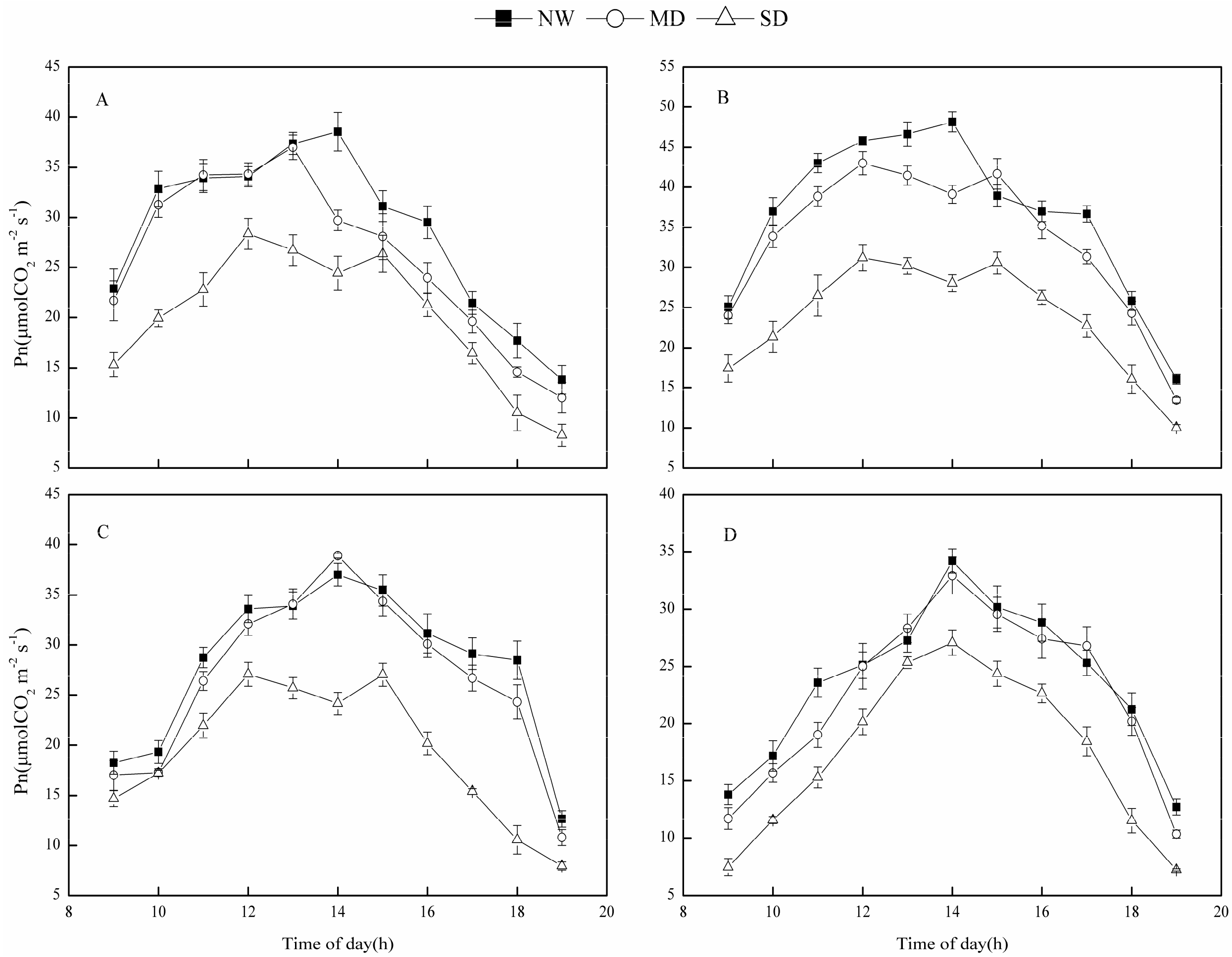

Fig. 4. Diurnal patterns of Pn under different watering regimes in different growth stages. a, b, c, d refers to five-leaf stage- June 17; jointing stage- July 11; flowering stage- August 19; soft dough stage- September 1.

Transpiraton (Tr) showed a similar pattern as net photosynthesis under the different watering regimes. As shown in Fig. 5, the diurnal variation of Tr was unimodal and reached the peak at 14:00 under NW and MD in different growth stages. On the contrary, it was bimodal under SD except in the soft dough stage (Fig. 5D). The maximum daily mean Tr was also in the jointing stage (Fig. 5B) and the values were 15.02±0.54 $mmolH_2O \cdot m^{-2} \cdot s^{-1}$, 13.42±0.48 $mmolH_2O \cdot m^{-2} \cdot s^{-1}$ and 10.95±0.43 $mmolH_2O \cdot m^{-2} \cdot s^{-1}$ for MD, MD and SD, respectively. It decreased by 10.65% in MD and 27.1% in SD than NW, respectively. Compared to NW, the daily mean Tr was significantly different under SD except the flowering stage ($P < 0.05$) and there was no significant difference to MD in different growth stages ($P > 0.05$).

The behavior of Pn and Tr followed closely a correlation with stomatal conductance as shown by the individual linear regression lines (Fig. 6).

In Figure 7, the photochemical efficiency of PSII as shown by the Fv/Fm ratio was lowest at 14:00 under different watering regimes. The minimum value of Fv/Fm was larger than 0.8 under NW and MD but lower under SD for all different growth stages except the soft dough stage. In comparison to NW, the statistical analysis showed significant difference in Fv/Fm under MD and SD in different growth stages except for the jointing stage ($P < 0.05$).

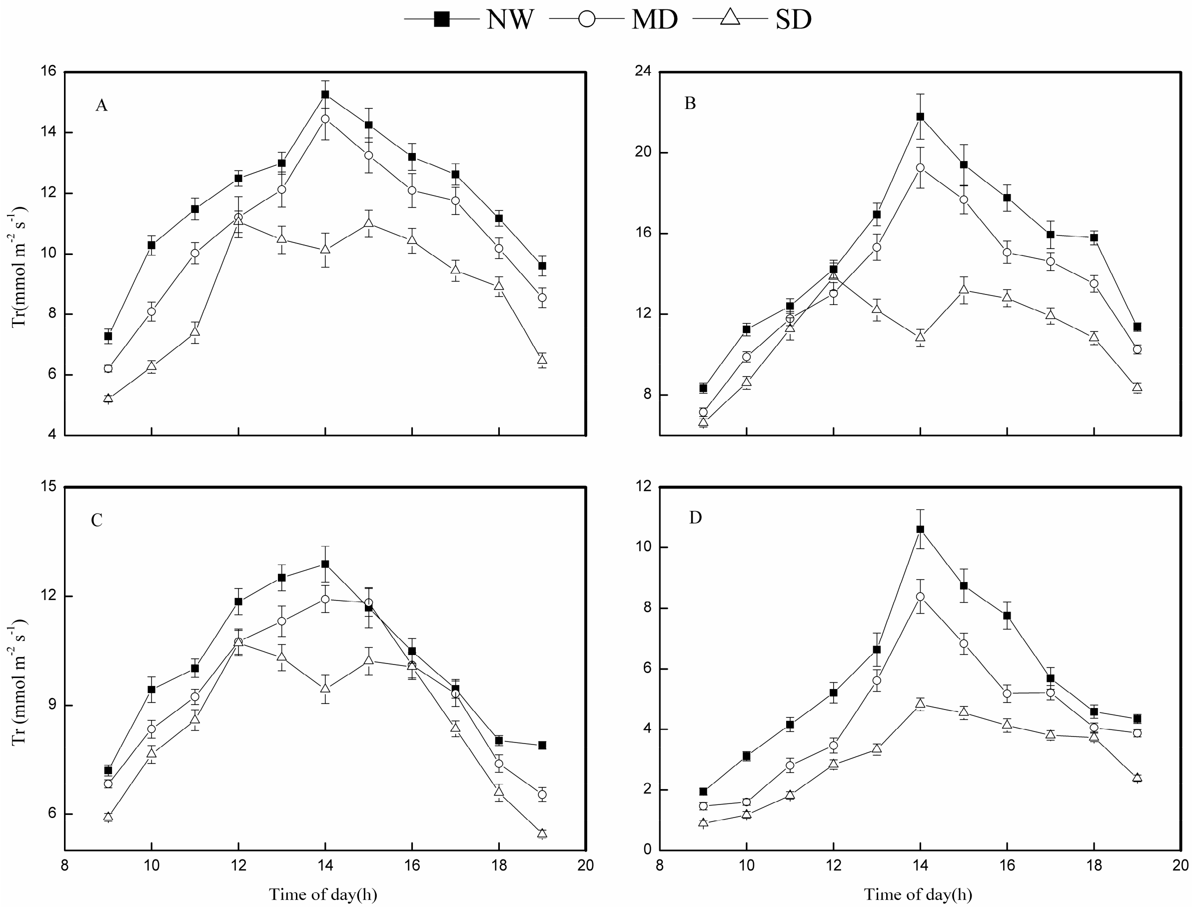

Fig. 5. Diurnal patterns of Tr under different watering regimes in different growth stages. a, b, c, d refers to five-leaf stage- June 17; jointing stage- July 11; flowering stage- August 19; soft dough stage- September 1.

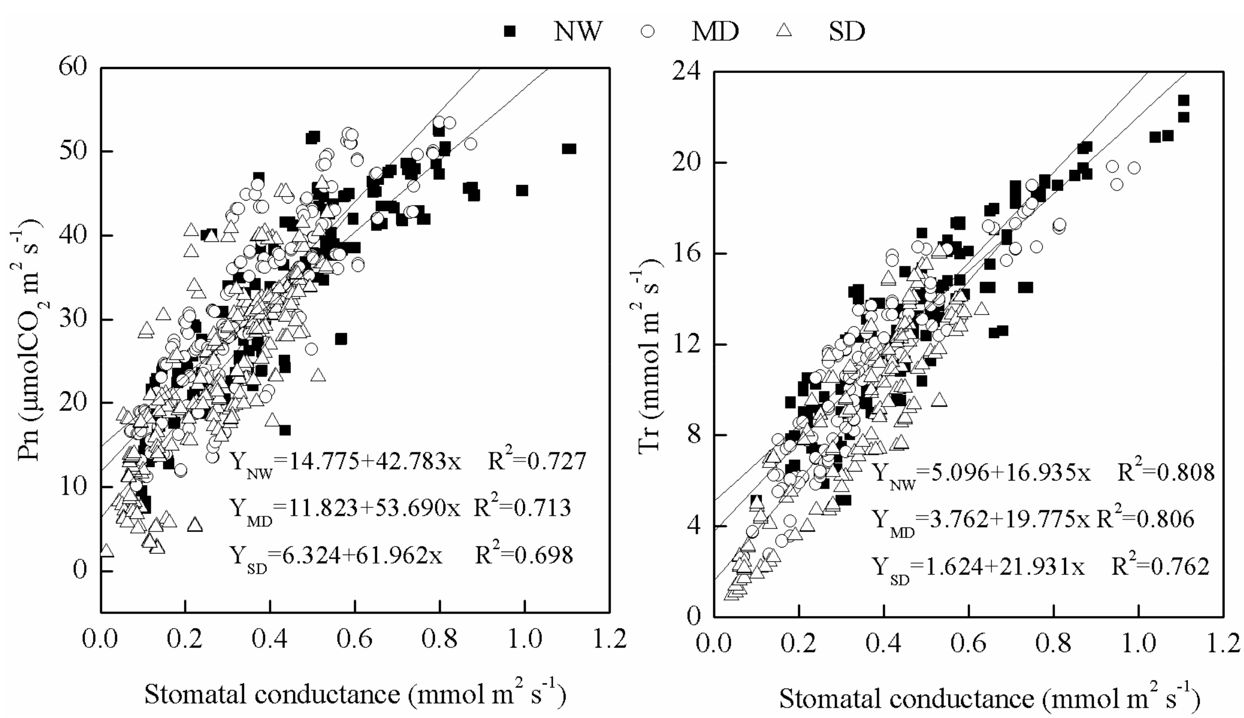

Fig. 6. Relationship between Pn, Tr and stomatal conductance during the experimental period. Regression equations are also reported ($P < 0.0001$)

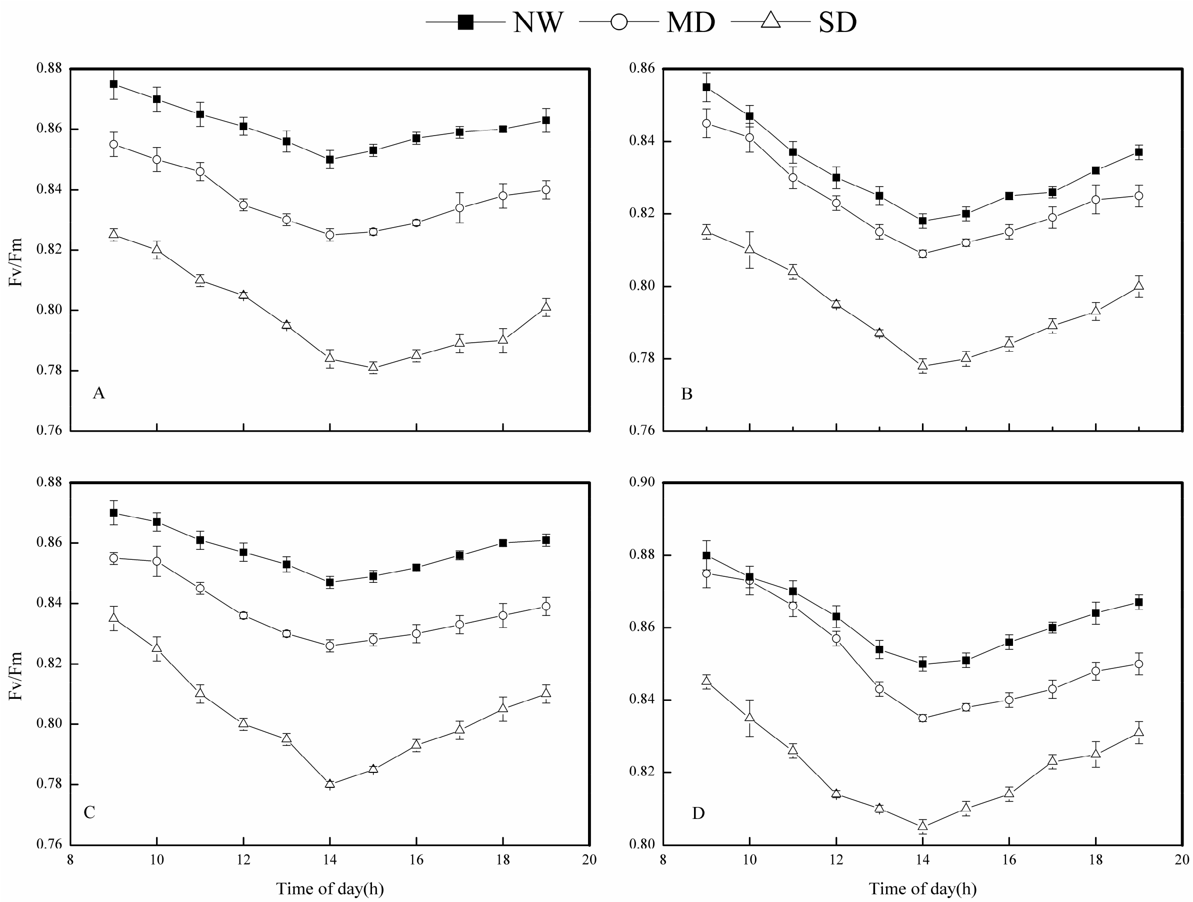

Fig. 7. Diurnal patterns of Fv/Fm under different watering regimes in different growth stages. a, b, c, d refers to five-leaf stage- June 17; jointing stage- July 11; flowering stage- August 19; soft dough stage- September 1.

Changes of water use efficiency: Compared to NW, the daily mean WUE under MD was higher in different growth stages, whereas it was lower under SD except the soft dough stage (Table 2). The daily mean WUE increased with time under NW and MD. The daily mean WUE was highest under MD in the early and middle growth stages, while it was highest under SD in the late growth stage. There was no significant difference in WUE between NW and MD in different growth stages ($P > 0.05$), but there was significant difference between NW and SD in flowering stage and soft dough stage ($P < 0.05$). (Table 2)

Responses of Pn to PAR: The Pn was very similar when PAR $< 200\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ under different watering regimes and it increased quickly at PAR $> 200\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ (Fig. 8). Compared to NW, the LSP, AQY and Rd under MD and SD were all lower which suggests more drought stress (Table 3). The response of Pn to PAR under SD was significantly different than NW and MD ($P < 0.05$), whereas there was no significant difference between NW and MD ($P > 0.05$).

Changes of stem biomass yield and sugar content: In Figure 9, the fresh stem biomass yield under MD was highest with the value $77t \cdot hm^{-2}$, which was higher by 9.03% and 41.58% in the NW and SD treatments, respectively. There was a significant difference between MD, NW and SD ($P < 0.05$).

Table 2. Changes in mean water use efficiency in different growth stage under different watering regimes (mmol CO_2·mol^{-1} H_2O).

	June 17 (Five-leaf stage)	July 11 (Jointing stage)	August 19 (Flowering stage)	September 1 (Soft dough stage)
NW	2.42 ± 0.11^a	2.49 ± 0.08^a	2.74 ± 0.09^a	4.51 ± 0.11^b
MD	2.50 ± 0.10^a	2.55 ± 0.05^a	2.77 ± 0.10^a	5.75 ± 0.13^{ab}
SD	2.31 ± 0.14^a	2.16 ± 0.02^a	2.22 ± 0.06^b	6.30 ± 0.14^a

Note: Each value is indicated by mean±SD (n=3), mean with different letters are significant difference at $P < 0.05$. NW, normal water supply; MD, moderate drought stress; SD, serious drought stress.

Table 3. Photosynthetic and physiological parameters of sweet sorghum under different watering regimes.

	Light compensation point (LCP)	Light saturation point (LSP)	Apparent quantum yield (AQY)	Dark respiration rate (Rd)
NW	μmol·m^{-2}·s^{-1}	μmol·m^{-2}·s^{-1}	mol·mol^{-1}	μmol·m^{-2}·s^{-1}
MD	52^{**}	-	0.040	2.05^{**}
SD	69^{**}	1866^{**}	0.025^{**}	1.01^{**}

Note: ** indicates difference is significant at 0.01 levels (2-tailed); -: indicating that the light saturation point had not been determined clearly. NW, normal water supply; MD, moderate drought stress; SD, serious drought stress

The sugar content of sweet sorghum was 21.9%, 22.1% and 22.4% for NW, MD and SD, respectively. Compared to NW, the sugar content increased 0.91% and 2.26% under MD and SD, individually. The sugar content of sweet sorghum was not significantly different under different watering regimes ($P > 0.05$).

Discussion

The deficiency of soil water is very common in arid and semi-arid regions. Sobrado & Turner (1983) suggested that water contents in tissues would be reduced and stomatal resistance would increase when plants suffered from drought stress. The greater the increase in drought stress, the lower the relative water content. Moreover, the leaf water potentials in sweet sorghum decreased with increasing drought stress in the same growth stage but there was no significant difference under moderate water stress and normal water supply ($P > 0.05$) which shows that sweet sorghum can adapt to soil water deficits through decreasing water potentials. Meanwhile, the transpiration in plants increased continuously through time due to higher temperatures and strong radiation in July. In order to satisfy the increasing evaporational demand in sweet sorghum, the leaf water potential decreased significantly which helped to absorb water from the soil and enhanced drought resistance. The stress from environmental conditions was reduced in August and September, when sweet sorghum reached the reproductive growth stage. The moderate transpiration rates at that time led to increased leaf water potentials.

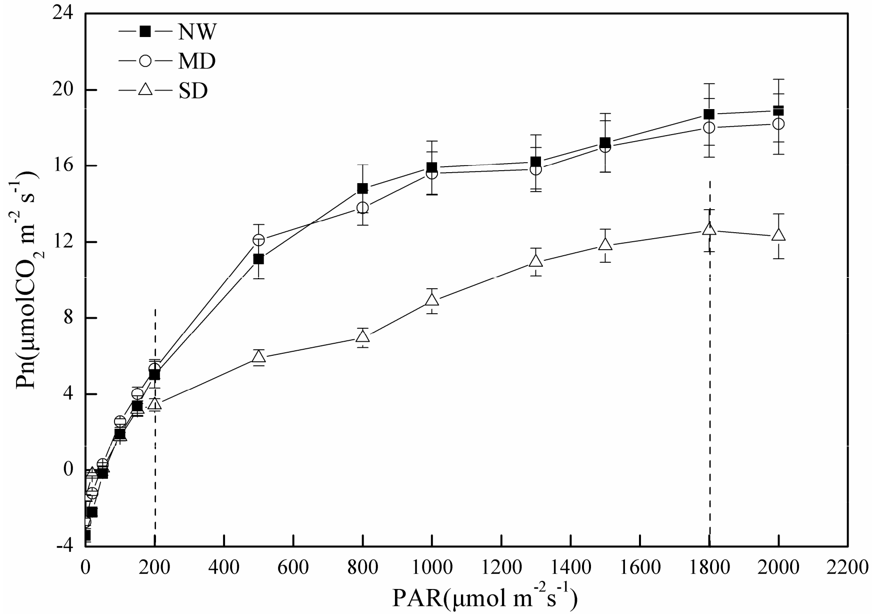

Fig. 8. Responses of net photosynthetic rate to different photosynthetically active radiations (PAR).

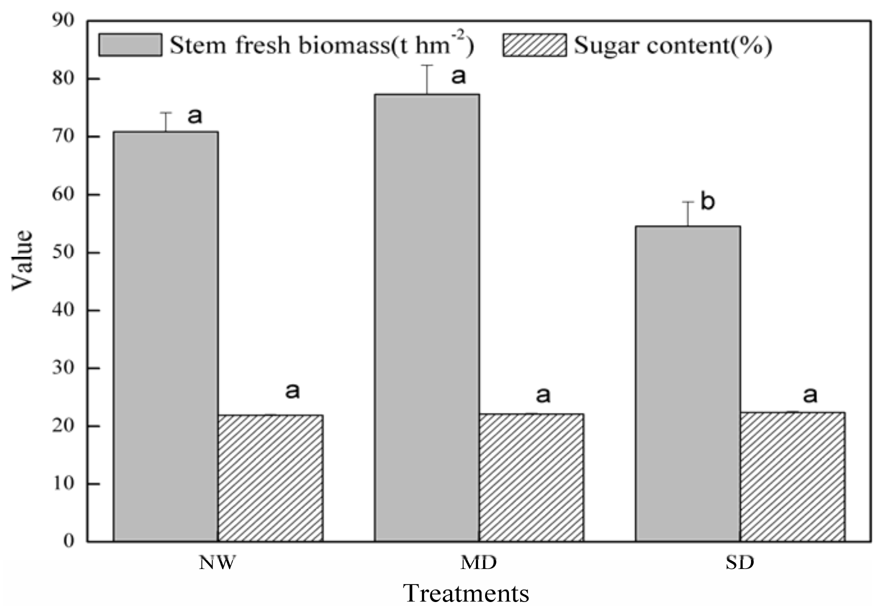

Fig. 9. Changes in stem biomass and sugar content under different watering regimes. Different letters indicate significant difference at $P < 0.05$.

The process of photosynthesis is sensitive to changing environmental conditions, and the way in which plants adapt to their environment is propitious to photosynthesis. The diurnal variation of photosynthesis in most plants declines around mid-day which is induced by high radiation and serious water deficit (Su *et al*., 2007, Saraswathi *et al*., 2008, Ge *et al*., 2004). There was mid-day depression in sweet sorghum in strong radiation under serious drought stress in the five-leaf stage, jointing stage and flowering stage. At mid-day, it is likely that PFD and temperature were stronger but RH was lower. Moreover, plants need more water for their growth in the early and middle growth stages, so the plants suffered greater stress at mid-day. Nevertheless, the PFD (1285μmol·m^{-2}·s^{-1}) and temperature (31.9°C) decreased while RH (35.4%) increased as plants needed less water for growth in the soft dough stage. As a result, the plants were under less stress and had no mid-day depression.

Photoinhibition occurs when absorbed radiation is in excessive amounts and the photosynthetic organ decreases in photosynthetic function. The Fv/Fm of leaves decrease significantly when plants suffer from photoinhibition and it is one of the fluorescence parameters most widely used to estimate the degree of photoinhibition (Oquist *et al*., 1992, Demminga & Adams, 1992). The Fv/Fm of sweet sorghum also decreased along with reduced Pn during mid-day under different watering regimes. The minimum value was less than 0.8 under serious drought stress except in the soft dough stage, and it increased in the afternoon. This reveals that photoinhibition in sweet sorghum appeared under serious drought stress but it did not induce PSII destruction which is considered to be an adapted protective mechanism against drought conditions.

Mastrorilli (1999) found that temporary soil water stress in sweet sorghum significantly reduced water use efficiency at the early stage, but it had no significant effect on water use efficiency at the late stage. In comparison, we found a perennial drought stress had no significant effect on water use efficiency at the early stage, but it increased significantly at the late stage. We also found water use efficiency of sweet sorghum was highest under moderate drought stress in the early and middle growth stages, but it was highest under serious drought stress in late growth stage. The reason may be that the crop is in a vegetative and early reproductive growth stage and is very sensitive to water deficit. Plants reduced their photosynthetic rate the most under serious drought stress when soil water deficit is the worst. However, in order to avoid the negative effects of strong radiation, transpiration rate was still kept at a suitable level, resulting in lower water use efficiency. On the one hand, a lot of water was transpired under normal water supply conditions, but the photosynthetic rate increased little which in turn led to lower water use efficiency. When a plant is in its late reproductive growth period, it needs less water for growth and can better utilize soil water under serious drought stress. Thus Pn was maintained in a stable level, but transpiration was much reduced, resulting in higher water use efficiency. We found close correlations between stomatal conductance and photosynthetic rate and stomatal conductance and transpiration rate, which also have been described elsewhere (Moriana *et al*., 2002). The parallel decline in photosynthetic rate, transpiration rate and stomatal conductance confirms the role of drought stress in similarly affecting function as plant water status decreases.

One of the important influences on carbon production and crop yield is leaf net photosynthetic rate. Higher leaf net photosynthetic rate produces more efficient dry matter production (Li *et al*., 2008). The stem fresh biomass of sweet sorghum was highest under moderate drought stress conditions in spite of its lower photosynthetic rate relative to normal water supply conditions. Although the photosynthetic rate was higher under normal water supply (Fig. 4), but the respiration rate in the dark was also significantly higher than moderate drought stress (Table 3) and less biomass was allocated to aboveground parts, so the stem fresh biomass was lower under normal water supply. The stem juice content of sweet sorghum is about 60% (Guo, 2005) and we estimated the stem juice content to be 46 $t{\cdot}hm^{-2}$ under moderate drought stress which is significantly higher sugar production than 33 $t{\cdot}hm^{-2}$under serious drought stress. Therefore we have to reject the hypothesis of stem biomass declines with increasing drought. We conclude that the highest stem biomass and sugar production of sweet sorghum was achieved under moderate drought stress, and the water use efficiency was higher. As a result, the moderate drought stress (11.6±1.0 % soil moisture condition) can be used for the cultivation of sweet sorghum in oasis edge of the

Hexi Corridor in China. This approach would reduce water waste, while increasing stem biomass, sugar production and water use efficiency.

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References

Ahmed, N., F. Ahmad, M. Abid and M. Amanullah. 2009. Impact of zinc fertilization on gas exchange characteristics and water use efficiency of cotton crop under arid environment. *Pak. J. Bot*., 41: 2189-2197.

Amaducci, S., A. Monti and G. Venturi. 2004. Non-structural carbohydrates and fibre components in sweet and fibre sorghum as affected by low and normal input techniques. *Ind. Crops Products*, 20: 111-118.

Barnaud, A., D. Monique, G. Eric, D. McKey and H. Joly. 2007. Local genetic diversity of sorghum in a village in northern Cameroon: structure and dynamics of landraces, *Theor. Appl. Genet*., 114: 237-248.

Cosentino, S.L. 1996. Crop physiology of sweet sorghum. In: *Proceedings of First European Seminar on Sorghum for Energy and Industry*, *Tulose*, pp. 30-41.

Demminga, D.B. and W.W. Adams. 1992. Photoprotection and other response of plants to high radiation stress, *Ann. Rev. Plant Physiol. Plan. Mol. Biol*., 43: 599-622.

Deu, M., F. Sagnard, J. Chantereau, C. Calatayud, D. Hrault, C. Mariac, J.L. Pham, Y. Vigouroux, I. Kapran, P.S. Traore, A. Mamadou, B. Gerard, J. Ndjeunga and G. Bezancon. 2008. Niger-wide assessment of in situ sorghum genetic diversity with microsatellite markers, *Theor. Appl. Genet*., 116: 903-913.

Forseth, I.N., D.A. Wait and B.B. 2001. Casper, Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial, *J, Ecol*., 89: 670-680.

Foti, S., S.L. Cosentino, V. Copani, C. Patane and P. 1996. Guarnaccia, Growth and yield of C_4 species for biomass production in Mediterranean environment. In: *Proceedings of the 9th European Bioenergy Conference: Biomass for Energy and Environment*. pp. 616-621.

Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO_2, ozone, and global climate change, *Agric. Eco. Environ*., 97: 1-20.

Ge, J.L., L. Shi, W.B. Gu, Y.D. Tang, J.Z. Zhang, C.D. Jiang and D.M. Ren. 2007. Photosynthetic Characteristics and the Regulation of PhotosystemII Function in Salt-Stressed Sweet Sorghum Five-leafs, *Acta Agron. Sin*., 33: 1272-1278.

Ge, Y., Y.J. Lu, J.X. Liao, B.H. Guan and J. Chang. 2004. Photosynthetic parameters of *Mosla hangchowensis* and *M. dianthera* as affected by soil moisture, *Photosynthetica*, 42: 387-391.

Gnansounou, E., A. Dauriat and C.E. Wyman. 2005. Refining sweet sorghum to ethanol and sugar: economic trade-offs in the context of North China, *Bioresour. Technol*., 96: 985-1002

Guo, H.Y. 2005. Characteristic on growth and pole sugar contents of sweet sorghum hybrids, *Dissertation*, China: Henan Agricul. Univ.,

Jia, H.S. and Y.N. Xu. 2006. World biodiesel utilization and development strategies in China, *Acta phytoecol. Sin*., 30: 221-230.

Kangama, C.O. and X. Rumei. 2005. Introduction of sorghum (*Sorghum bicolor* (L.) Moench) into

China, *Afr. J. Biotechnol*., 4: 575-579.

Li, F.D., P. Meng, D.L. Fu and B.P. Wang. 2008. Light distribution, photosynthetic rate and yield in a Paulownia-wheat intercropping system in China, *Agrofor. Sys*., 74: 163-172.

Mastrorilli, M., N. Katerji and G. Rana.1999. Productivity and water use efficiency of sweet sorghum as affected by soil water deficit occurring at different vegetative growth stages, *Eur. J. Agron.,* 11: 207-215.

Mastrorilli, M., N. Katerji, G. Rana and P. Steduto. 1995. Sweet sorghum in Mediterranean climate: radiation use and biomass water use efficiencies, *Industr. Crops Prod*., 3: 253-260.

Menz, M.A., R.R. Klein, N.C. Unruh, W. L. Rooney, P.E. Klein and J.E. Mullet. 2004. Genetic diversity of public inbreds of sorghum determined by mapped AFLP and SSR markers, *Crop Sci.*, 44: 1236-1244.

Moriana, A., F.J. Villalobos and E. Fereres. 2002. Stomatal and photosynthetic responses of olive (*Olea europaea* L.) leaves to water deficits, *Plant Cell Environ.,* 25: 395-405.

Noorka, I.R., S.U. Rehman, J.R. Haidry, I. Khaliq, S. Tabassum and G. Mueenuddin. 2009. Effect of water stress on physico-chamical properties of wheat (*Triticum aestivum* L.). *Pak. J. Bot*., 41: 2917-2924.

Oquist, G., W.S. Chow and J.H. Anderson. 1992. Photoinhibition of photosynthesis represents a mechanism for the long-term regulation of photosystem II, *Planta*, 186: 450-460.

Ruzˇica, S. and C. Endre. 1997. Relationships between available soil water and indicators of plant water status of sweet sorghum to be applied in irrigation scheduling. *Irrig. Sci*., 18: 17-21.

Santosl, M.G., R.V. Ribeiro, E.C. Machado and C. Pimentel. 2009. Photosynthetic parameters and leaf water potential of five common bean genotypes under mild water deficit, *Biol. Plant*, 53: 229-236.

Saraswathi, S.G. and K. Paliwal. 2008. Diurnal and seasonal trends in photosynthetic performanceof *Dalbergia sissoo* Roxb., and *Hardwiewia binata* Roxb., from a semi-arid ecosystem. *Photosynthetica*, 46: 248-254.

Sobrado, M.A. and N.C. Turner. 1983. Comparison of the water relations characteristics of *Helianthus annuus* and *Helianthus petiolaris* when subjected to water deficits. *Oecologia*, 58: 309-315.

Steduto, P., N. Katerji, H. Puertos-Molina, M. Ünlü, M. Mastrorilli and G. Rana. 1997. Water-use efficiency of sweet sorghum under water stress conditions gas-exchange investigations at leaf and canopy scales. *Field Crops Res*., 54: 221-234.

Su, P.X., G.D. Cheng, Q.D. Yan and X.M. Liu. 2007. Photosynthetic regulation of C_4 desert plant *Haloxylon ammodendron* under drought stress. *Plant Growth Regul*., 51: 139-147.

Su, P.X., X.M. Liu, L.X. Zhang, A.F. Zhao and H.S. Chen. 2004. Comparison of values and gas exchange of assimilating shoots of desert plants *Haloxylon ammodendron* and *Calligonum mongolicum* with other plants. *Isr. J. Plant Sci*., 52: 87-97.

Thomas, L., Tew Robert, M., P. Cobill Edward and Jr. Richard. 2008. Evaluation of sweet sorghum and sorghum × sudangrass hybrids as feedstocks for ethanol production, *Bioenerg. Res.,* 1: 147-152.

The National Development and Reform Commission, Mid-Long Term Development Plan for Renewable Energy. 2007. Beijing, pp. 19-22.

Von Caemmerer, S. and G.D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves, *Planta*, 153: 376-387.

Wang, Y.J., Z.K. Xie, S.S. Malhi, C.L. Vera, Y.B. Zhang and J.N. Wang. 2009. Effects of rainfall harvesting and mulching technologies on water use efficiency and crop yield in the semi-arid Loess Plateau, China, *Agr. Water Manage*., 96: 374-382.

Zhao, Y.L., A. Dolat, Y. Steinberger, X. Wang, A. Osman and G.H. Xie. 2009. Biomass yield and changes in chemical composition of sweet sorghum cultivars grown for biofuel, *Field Crops Res*., 111: 55-64.

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