

Full Length Research Paper

# Photosynthetic, chlorophyll fluorescence and growth changes in hot pepper under deficit irrigation and partial root zone drying

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There is increasing evidence that the spatial distribution of water within the root zone, as well as total soil water status, determines plant physiological and agronomic responses. To examine the response of photosynthesis, chlorophyll fluorescence and growth of hot pepper (*Capsicum annuum* L.) to deficit irrigation (DI50, 50% of the control) and partial root-zone drying (PRD, with half of the root system exposed to soil drying and the other half watered with 50% irrigation water of the control), two water deficit treatments were imposed on greenhouse grown hot pepper during the growing period in 2006. Control plants received irrigation to both halves of the root system when soil water content was < 80% of field capacity. Both PRD and DI50 treatments decreased total dry mass by 33 to 44%, shoot biomass by 31 to 44% compared to the control. These treatments increased root-shoot ratio by 35 to 44% in relation to the control, with significant differences between PRD, DI50 and the control. Deficit irrigation led to a relative leaf water content of about 77.91 to 92.71%. Two water deficit treatments reduced photosynthetic rate ( $P_n$ ) slightly and transpiration rate ( $Tr$ ) significantly, thus improving leaf water use efficiency ( $WUE_L$ , defined as the ratio of  $P_n$  to  $Tr$ ) by 24 to 26%. During water stress, a down-regulation of PSII activity was observed along with some impairment of photochemical activity, as revealed by decreases in the maximum quantum yield of PSII ( $F_v/F_m$ ). Although  $F_v/F_m$  did not significantly differ between the deficit treatments and the control,  $F_v/F_m$  of PRD plants was higher than that of DI50 plants. The mean values of  $F_v$ ,  $F_m$ ,  $qP$  at four stages decreased and  $F_o$  and  $qN$  increased in the soil drought environment. Development of non-radiative energy dissipation mechanisms was evidenced during stress by increases in non-photochemical quenching and decreases in efficiency of excitation capture by open centers.

**Key words:** Photochemical parameters, relative leaf water content, DI50, partial root-zone drying (PRD).

## INTRODUCTION

Photosynthesis is one of the main metabolic processes determining crop production, and it is directly affected by drought. The response of photosynthesis to water stress has been a subject of controversy among researchers for many years, since conflicting results have been reported (Comic and Massacci, 1996). It has not been well established how and where the chloroplasts are damaged

under water stress, and how damage can be detected and evaluated easily. Under mild water deficit conditions, it has been shown that stomata play the dominant role in controlling the decline of net  $CO_2$  uptake, by decreasing leaf internal  $CO_2$  concentrations (Cornic and Briantais, 1991; Cornic, 2000). Nonetheless, the limitations to  $CO_2$  assimilation imposed by stomatal closure may promote an imbalance between electron requirement for photosynthesis and photochemical activity at photosystem II (PSII), leading to an overexcitation and subsequent photoinhibitory damage of PSII reaction centers

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(Krause, 1988; Long et al., 1994). As water stress progresses, the plants must dissipate excess light energy, since photosynthesis is unable to efficiently utilize photochemical energy (Ennahli, 2005). In this way, the photosynthetic apparatus may be damaged eventually, imposing an additional non-stomatal limitation to the process. Chlorophyll fluorescence parameters can evaluate the influence of environmental stress on growth and yield, since these traits were closely correlated with the rate of carbon exchange (Fracheboud et al., 2004; Guo and Li, 2000; Araus et al., 1998) and can be used as reliable indicators to evaluate the metabolic imbalance of photosynthesis and yield performance under water stress (Araus and Hogan 1994; Araus et al., 1998). The relationship between chlorophyll fluorescence parameters and water status in hot pepper will be affected by many factors, particularly as chlorophyll content changes over time. The minimum fluorescence ( $F_0$ ) parameter, for instance, has been positively correlated with the chlorophyll concentration in plant materials under water deficit (Toivonen and DeEll, 1998).

Hot pepper (*Capsicum annuum* L.) is one of the vegetable crops commonly grown in the greenhouse and consumed in China, USA, East Indies, Korea, and many other countries, for the nutritional value of its fruits, which are an excellent source of antioxidant compounds and natural colors, like carotenoids and vitamin C (Howard et al., 2000; Russo and Howard, 2002; Navarro et al., 2006; Shao et al., 2008). In the greenhouse, water availability is an important factor affecting plant growth and yield, because hot pepper is considered one of the most susceptible horticultural crops to water stress (Shao et al., 2010). The morphological and physiological responses to water stress may vary considerably among species. In general, strategies of drought-avoidance or drought-tolerance can be recognized; both involving diverse plant mechanisms that allow plants to respond and survive water stress.

Deficit irrigation is an irrigation strategy that aims to supply less water than crop evapotranspiration, and has recently seen renewed interest due to positive impacts on crop quality and the decline in water availability for irrigation in many parts of the world (Feres and Soriano, 2007; Dorji et al., 2005; Wakrim et al., 2005; Paul and Goodwin, 2003; Zegbe-Dominguez et al., 2003; FAO, 2002). Partial rootzone drying is a particular form of deficit irrigation that aims to supply water to only one part of the rootzone while allowing the other to dry the soil, and has shown increased yield when compared to conventional deficit irrigation at the same irrigation levels (Kang et al., 2001; Dodd, 2009). Both techniques were proposed to reduce irrigation water use while maintaining farmers' net profits, and they are common practices worldwide (Shao et al., 2010). However, for many crop systems the best deficit irrigation strategy for improving water productivity has not yet been established (Feres and Soriano, 2007). The partial rootzone drying method and deficit irrigation provide the means to control plant-water stress to slow

down vegetative growth and promote a favorable vegetative: reproductive balance in crop production. To date, little is known about changes of traits such as photosynthesis, chlorophyll fluorescence parameters under partial rootzone drying method and deficit irrigation in hot pepper under glasshouse conditions.

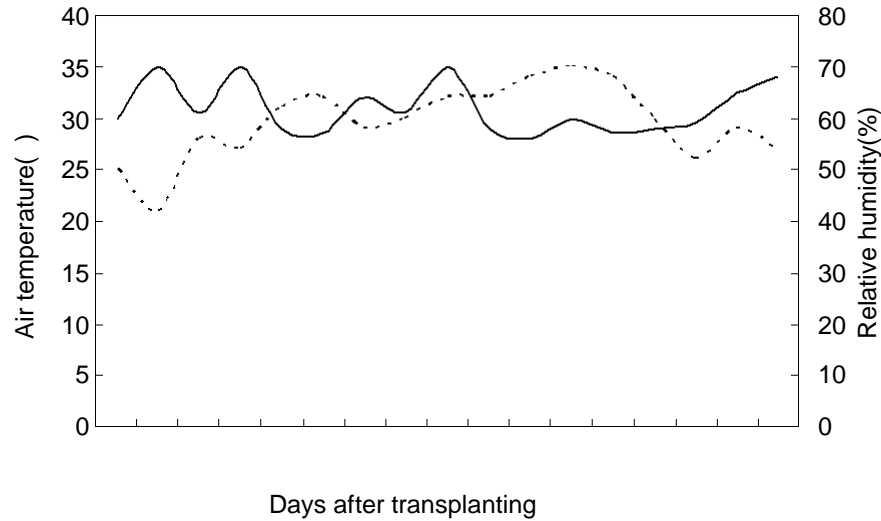
This study analyzed the responses of photosynthesis to partial rootzone drying method and deficit irrigation in hot pepper plants, both in terms of the functionality of the photosynthetic apparatus, as assessed by chlorophyll fluorescence measurements, and of stomatal conductance, as measured by leaf gas exchanges. Additionally, growth was simultaneously analyzed in order to detect possible metabolic alterations in hot pepper leaves. The underlying hypothesis is that photosynthesis in hot pepper under water stress is limited by non-stomatal and stomatal factors, both contributing to the occurrence of metabolic alterations at the leaf level.

## MATERIALS AND METHODS

The experiment was conducted under glasshouse conditions at Key Laboratory of Efficient Irrigation-Drainage and Agricultural Soil-Water Environment in Southern China, Ministry of Education (latitude 31°57' N, longitude 118°50' E 144 m above sea level) during May 2006 through October 2006. Glasshouse air temperature and relative humidity at 1.5 m above the soil were measured daily. Mean daily temperature during the experiment ranged from 21 to 38°C (Figure 1). The soil type was clay loam with a pH of 6.4% and organic matter content of 0.86%, soil bulk density for 0 to 50 cm depth was 1.35 g cm<sup>-3</sup>, field capacity was 25.6%, as weight of water on dried soil. Zaofeng variety of hot pepper were raised in a nursery and transplanted at the six-leaf stage. A week before transplanting, the experimental site was ploughed and harrowed to depths of 25 cm. In all treatments, fertilizers (15:10:15 N:P<sub>2</sub>O<sub>5</sub>:K<sub>2</sub>O) at the rate of 300 kg ha<sup>-1</sup> were applied and incorporated into soil. All the furrows were irrigated and allowed to drain to field capacity. After 24 h, the seedlings were transplanted into 9 plots. Each plot consisted of three rows of 2 m in length, among which plants were grown 50 cm apart with 40 cm spacing in each row. The one central row was the only harvested for production measurements. It was followed by a light irrigation to ensure seedling establishment. The treatments were imposed 2 weeks after transplanting. Calcium Ammonium Nitrate (26% N) fertilizer was applied as side dressing at the rate of 250 kg ha<sup>-1</sup> in two equal split doses at 5th and 7th week after transplanting when the plants were at flowering and first fruit set stages, respectively. The plots were manually weeded three times in the season. The plants were sprayed against fruit worms, white flies and other pests with insect powder at the rate of 0.8 l ha<sup>-1</sup> at the 6th week.

## Experimental design and irrigation treatments

All plants were fully irrigated (field capacity) in the evening before starting the experiment. The following irrigation treatments were applied with the help of furrow irrigation system (three replicates per treatment): (1) control (WW) in which irrigation water was applied to both sides of root system when soil water content was lower by 80% of field capacity; (2) DI50: Deficit irrigation in which 50% irrigation water of WW supplied to both sides of the root system; (3) PRD: partial rootzone drying with half of the root system exposed to soil drying and other half kept well-watered with 50% irrigation water of



**Figure 1.** Mean temperature (°C; dashed line) and relative humidity (%; solid line) during the experiment.

WW. At each irrigation time, the soil water content was measured and controlled with the time domain reflectometry (TDR) and by gravimetric method. Soil water contents were used to adjust the irrigation schedule to ensure that the envisaged irrigation treatments were realized, and there was no deep percolation.

#### Measurements of growth

Leaf area was measured in four plants per replicate plot which were sampled four times during the experiment, on 28, 51, 80, 102 days after transplanting with a planimeter Li-Cor Model LI-3000A (Li-Cor, Lincoln, NE, USA) and calculated from the average specific leaf area. Leaf area index (LAI) was determined using a LAI 2000 Plant Canopy Analyzer (Li-Cor Biosciences USA). Shoots were removed and shoot dry weight was determined by drying the material at 70°C for at least 48 h. The roots were washed carefully for each and dried and weighed as described above. In addition, plant development characteristics were determined including height, branches, and leaf number.

#### Measurements of relative leaf water content and photosynthetic parameters

Three leaves per plant from the third and fourth fully expanded leaf from the tip were detached to determine their relative leaf water content (RWC) with three replicates for each treatment. The leaves were weighed immediately after the treatment to obtain the fresh weight (FW), and were subsequently rehydrated in distilled water for 4 h to obtain the turgid weight (TW). The dry weight (DW) was then measured after oven drying at 80°C for 48 h. RWC was calculated as:

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

Photosynthesis, stomatal conductance and transpiration rates were measured with LI 6400 (Li-Cor Inc, Lincoln NE, USA) on two occasions from the newly expanded leaf to the 5th older leaf under a saturating photosynthetic photon flux density of 1800 mol m<sup>-2</sup> s<sup>-1</sup>

provided by an external halogen lamp. Measurements were taken between 10:00 and 12:00 h. Fluorescence measurements were done with OS5-FL (Opti-Science, USA) using the saturation pulse method, prior to the photosynthetic parameters measurements on the same sampled leaves. Chlorophyll fluorescence measurements were initially taken on dark-adapted leaves for 30 min and then for the same leaves after a 30 min acclimation period to the growth chamber. Immediately before measurements under light, leaves received a 2 s exposure of a saturating light of 6000 mol m<sup>-2</sup> s<sup>-1</sup> provided by the fluorometer's fiber optic. The following parameters were assessed: Fo, initial/minimal fluorescence, a measure of the stability of the light-harvesting complex; Fv/Fm, represents the maximum quantum yield of PSII, which in turn is highly correlated with the quantum yield of net photosynthesis. Where Fm is the maximal fluorescence value, and Fv is variable fluorescence = Fm - Fo. Photochemical quenching coefficient (qP), Stern-Volmer non-photochemical quenching coefficient (qN). All the above measurements were carried out at ambient (400 ± 10 mol mol<sup>-1</sup>) CO<sub>2</sub>, 23 ± 2°C air temperature and 80 ± 2% relative humidity.

#### Statistical analysis

Experiments were designed as randomized complete blocks, with each replicate representing a separate block. Treatment effects in the experiment were analyzed using analysis of variance (ANOVA) procedure of SPSS software Version 14.0. Treatment means were separated by least significant difference (LSD) test at p 0.05 unless otherwise specified.

## RESULTS

#### Leaf water status

Changes in relative leaf water content at four growing stages were respectively shown in Table 1. The single-factor ANOVA indicated RWC was significantly reduced in both PRD and DI50 treatments. As soil water content decreased over time, RWC of the deficit treatment decreased by 7.3 to 9.0% at the seedling stage, 10.7 to 13.6% at bloom and fruit setting stage, 16.5 to 20.9% at

**Table 1.** Relative water content (%) of greenhouse-grown hot pepper under three treatments.

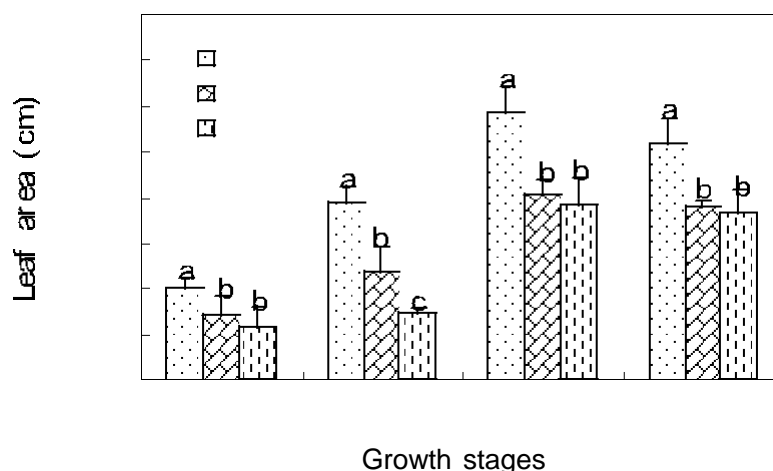
Treatments	Seedling stage	Bloom and fruit setting stage	Vigorous fruit-bearing stage	Later fruit-bearing stage
WW	93.3 ± 1.2 <sup>a</sup>	92.1 ± 0.8 <sup>a</sup>	92.6 ± 0.05 <sup>a</sup>	91.0 ± 0.8 <sup>a</sup>
PRD	84.9 ± 1.5 <sup>b</sup>	79.6 ± 1.3 <sup>b</sup>	77.3 ± 0.21 <sup>b</sup>	73.9 ± 1.5 <sup>b</sup>
DI50	86.5 ± 1.7 <sup>ab</sup>	79.2 ± 0.6 <sup>b</sup>	73.2 ± 0.14 <sup>b</sup>	70.9 ± 2.1 <sup>b</sup>

WW indicates the treatment of well watered, PRD and DI50 are the treatments of partial rootzone drying and deficit irrigation. The values represent means ± standard error (SE). (n = 3). For a given variable, mean values not sharing common letters are significantly different (p 0.05).

**Table 2.** Effect of irrigations treatments on root weight (RW) ,shoot weight (SW), root–shoot ratio (RSR), root density (RD) and total dry mass (TDM) of plant including roots and fruits in hot pepper at the 109th day after transplanting.

Treatments	RW (g plant <sup>-1</sup> )	SW (g plant <sup>-1</sup> )	RSR (g g <sup>-1</sup> )	RD (mg cm <sup>-3</sup> )	TDM (g plant <sup>-1</sup> )
WW	1.89 ± 0.03 <sup>a</sup>	19.78 ± 0.57 <sup>a</sup>	0.096 ± 0.002 <sup>b</sup>	0.042 ± 0.001 <sup>a</sup>	82.56 ± 1.34 <sup>a</sup>
PRD	1.86 ± 0.02 <sup>a</sup>	13.57 ± 0.87 <sup>b</sup>	0.138 ± 0.009 <sup>a</sup>	0.041 ± 0.000 <sup>a</sup>	54.87 ± 1.57 <sup>b</sup>
DI50	1.44 ± 0.04 <sup>b</sup>	11.11 ± 0.15 <sup>c</sup>	0.130 ± 0.003 <sup>a</sup>	0.031 ± 0.001 <sup>c</sup>	46.15 ± 0.72 <sup>b</sup>

WW indicates the treatment of well watered, PRD and DI50 are the treatments of partial rootzone drying and deficit irrigation. The values represent means ± standard error (SE). (n = 3). For a given variable, mean values not sharing common letters are significantly different (p 0.05).



**Figure 2.** Influence of different irrigation pattern on leaf area of hot pepper at different stages. ST1, ST2, ST3 and ST4 denote the stages of seedling stage, bloom and fruit setting stage, vigorous fruit-bearing stage and later fruit-bearing stage, respectively. Vertical bars represent ± S.E. of the mean. (n = 3). For a given variable, mean values not sharing common letters are significantly different (p 0.05).

vigorous fruit-bearing stage, and 18.8 to 22.1% at the later fruit-bearing stage, respectively. At the seedling stage, the RWC of PRD was lower than that in DI50 plants, but at other growth stages it was higher than the PRD treatment.

### Growth measurements

There were significant differences in the plant growth of hot pepper with different levels of irrigation. PRD and DI50 significantly reduced shoot and root dry weight, shoot

weight and total leaf area compared to the control (Table 2 and Figure 2). However, the root-shoot ratio under the DI50 and PRD treatments was significantly 35 to 44% higher than the WW treatment. Although the PRD and WW treatments had a similar root density, root density of the PRD plants was 32% higher than the DI50 plants. Similarly, the PRD plants had a significantly greater total root weight than the DI50 plants. Leaf area index of plants exposed to non-stress water regimes was the highest and that of plants exposed to the DI50 treatment was the lowest

**Table 3.** Changes in lead area index of greenhouse-grown hot pepper under three treatments.

Treatments	Seedling stage	Bloom and fruit setting stage	Vigorous fruit-bearing stage	Later fruit-bearing stage
WW	1.32 ± 0.06 <sup>a</sup>	1.82 ± 0.08 <sup>a</sup>	2.85 ± 0.05 <sup>a</sup>	2.43 ± 0.38 <sup>a</sup>
PRD	1.04 ± 0.13 <sup>ab</sup>	1.78 ± 0.09 <sup>a</sup>	2.61 ± 0.21 <sup>a</sup>	2.16 ± 0.21 <sup>a</sup>
DI50	0.87 ± 0.05 <sup>b</sup>	1.09 ± 0.02 <sup>b</sup>	2.26 ± 0.14 <sup>b</sup>	1.58 ± 0.07 <sup>b</sup>

WW indicates the treatment of well watered, PRD and DI50 are the treatments of partial root zone drying and deficit irrigation. The values represent means ± standard error (SE). (n = 3). For a given variable, mean values not sharing common letters are significantly different (p 0.05).

**Table 4.** Influence of different irrigation treatments on Pn, Tr, g<sub>s</sub> and WUE<sub>L</sub> of hot pepper leaf.

Index	Treatments	Date of measurement (day-month-year)				Mean values
		15-07-2006	18-08-2006	05-09-2006	20-09-2006	
Pn	WW	21.03 ± 0.23 <sup>a</sup>	17.33 ± 0.44 <sup>a</sup>	9.96 ± 2.05 <sup>a</sup>	5.68 ± 0.92 <sup>a</sup>	13.50 ± 0.91 <sup>a</sup>
	PRD	17.20 ± 2.02 <sup>a</sup>	13.96 ± 0.65 <sup>b</sup>	8.62 ± 2.24 <sup>ab</sup>	3.93 ± 0.16 <sup>ab</sup>	10.93 ± 1.27 <sup>a</sup>
	DI50	18.50 ± 0.69 <sup>a</sup>	12.34 ± 0.31 <sup>b</sup>	8.32 ± 0.32 <sup>b</sup>	2.85 ± 0.81 <sup>b</sup>	10.50 ± 0.53 <sup>a</sup>
Tr	WW	8.27 ± 0.30 <sup>a</sup>	5.93 ± 0.08 <sup>a</sup>	4.56 ± 0.46 <sup>a</sup>	3.60 ± 0.84 <sup>a</sup>	5.59 ± 0.42 <sup>a</sup>
	PRD	4.81 ± 0.85 <sup>b</sup>	3.88 ± 0.09 <sup>b</sup>	3.19 ± 0.38 <sup>b</sup>	2.19 ± 0.43 <sup>b</sup>	3.52 ± 0.55 <sup>b</sup>
	DI50	5.22 ± 0.41 <sup>b</sup>	3.62 ± 0.11 <sup>b</sup>	3.12 ± 0.11 <sup>b</sup>	1.52 ± 0.62 <sup>b</sup>	3.37 ± 0.31 <sup>b</sup>
g <sub>s</sub>	WW	1.43 ± 0.13 <sup>a</sup>	1.03 ± 0.00 <sup>a</sup>	0.48 ± 0.09 <sup>a</sup>	0.16 ± 0.04 <sup>a</sup>	0.78 ± 0.07 <sup>a</sup>
	PRD	0.93 ± 0.08 <sup>b</sup>	0.72 ± 0.00 <sup>b</sup>	0.32 ± 0.14 <sup>b</sup>	0.10 ± 0.02 <sup>b</sup>	0.52 ± 0.06 <sup>b</sup>
	DI50	0.96 ± 0.03 <sup>b</sup>	0.63 ± 0.00 <sup>b</sup>	0.20 ± 0.01 <sup>b</sup>	0.10 ± 0.03 <sup>b</sup>	0.47 ± 0.02 <sup>b</sup>
WUE <sub>L</sub>	WW	2.54 ± 0.09 <sup>b</sup>	2.92 ± 0.24 <sup>b</sup>	2.18 ± 0.25 <sup>b</sup>	1.58 ± 0.07 <sup>a</sup>	2.31 ± 0.16 <sup>b</sup>
	PRD	3.58 ± 0.26 <sup>a</sup>	3.60 ± 0.35 <sup>a</sup>	2.70 ± 0.17 <sup>a</sup>	1.79 ± 0.15 <sup>a</sup>	2.92 ± 0.23 <sup>a</sup>
	DI50	3.55 ± 0.16 <sup>a</sup>	3.38 ± 0.18 <sup>b</sup>	2.66 ± 0.17 <sup>a</sup>	1.88 ± 0.10 <sup>a</sup>	2.87 ± 0.15 <sup>a</sup>

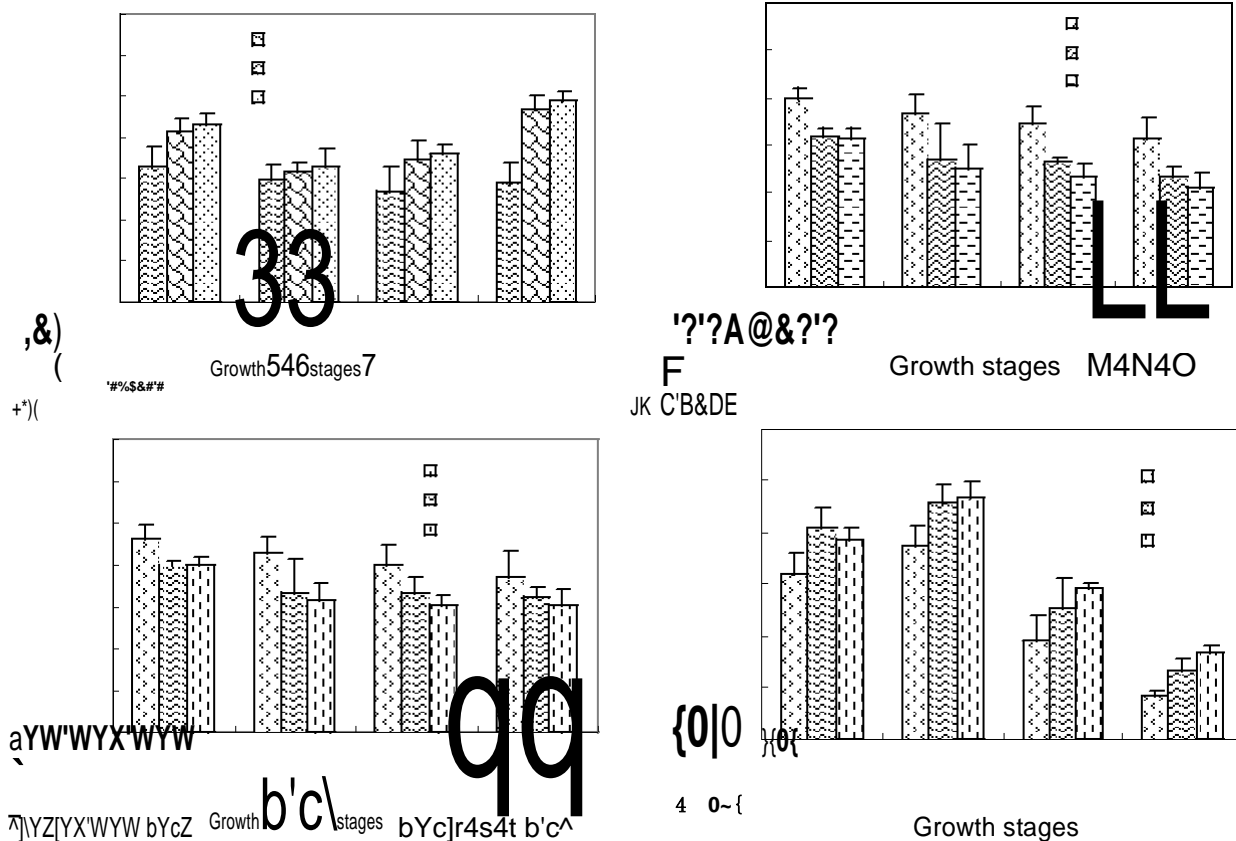
Pn, Tr, g<sub>s</sub> and WUE<sub>L</sub> denote photosynthetic rate, transpiration rate, stomatal conductance and water use efficiency of leaves. WW indicates the treatment of well watered, PRD and DI50 are the treatment of partial rootzone drying and deficit irrigation. The values represent means ± standard error (SE). (n = 3). For a given variable, mean values not sharing common letters are significantly different (p 0.05).

(Table 3 and Figure 2). The PRD treatment had a higher LAI than the DI50 treatments, with significant differences observed at the latter three growth stages. Both deficit irrigation treatments significantly inhibited leaf area per plant, but PRD plants had a higher leaf area than DI50 plants, with significant differences between the two treatments detected at the second growth stage only.

### Photosynthetic and chlorophyll fluorescence

Table 4 shows the photosynthetic rate (Pn), stomatal conductance (g<sub>s</sub>), transpiration rates (Tr) and the leaf water use efficiency (WUE<sub>L</sub>, Pn/Tr) under the different water treatments. Tr and g<sub>s</sub> significantly decreased at the first growth stage after imposing water stress, with PRD decreased more than DI50. Tr and g<sub>s</sub> were more sensitive to water deficit than Pn. Compared to the control, PRD and DI50 at the first growth stage improved WUE<sub>L</sub> by approximately 40%. Pn in PRD treatment at other growth

stages had no significant difference (P > 0.05) with exception at second stage in relation to the control, but Tr and g<sub>s</sub> had significant difference (P < 0.05), and PRD treatment at third stage also increased WUE<sub>L</sub> significantly. Averaged across the four growth stages, PRD and DI50 treatments decreased average Pn by 19 and 22% respectively, and increased average WUE<sub>L</sub> by 26.41 and 19.18%. Simultaneously, the average g<sub>s</sub> under PRD and DI50 treatments at different growth stages decreased significantly, which decreased CO<sub>2</sub> entry into the leaf, and resulted in decreasing of leaf intercellular CO<sub>2</sub> concentration and Pn, indicating that the decline of photosynthesis was mainly due to strong reversible stomatal limitation. Both of the water deficit treatments reduced leaf g<sub>s</sub> and Pn and thus the leaf intercellular CO<sub>2</sub> concentration remained unchanged or even increased (data not shown), indicating that the decline of photosynthesis was mainly due to poor reversible non-stomatal limitation, that is, due to lower photosynthetic



**Figure 3.** Change of  $F_0$ ,  $F_v$ ,  $F_m$  and  $F_v/F_m$  at different stages of hot pepper under three irrigation treatment; Note: ST1, ST2, ST3 and ST4 denote the stages of seeding stage, bloom and fruit setting stage, vigorous fruit-bearing stage and later fruit-bearing stage, respectively. Vertical bars represent  $\pm$  S.E. of the mean. ( $n = 3$ ). For a given variable, mean values not sharing common letters are significantly different.

activity of leaf cells.

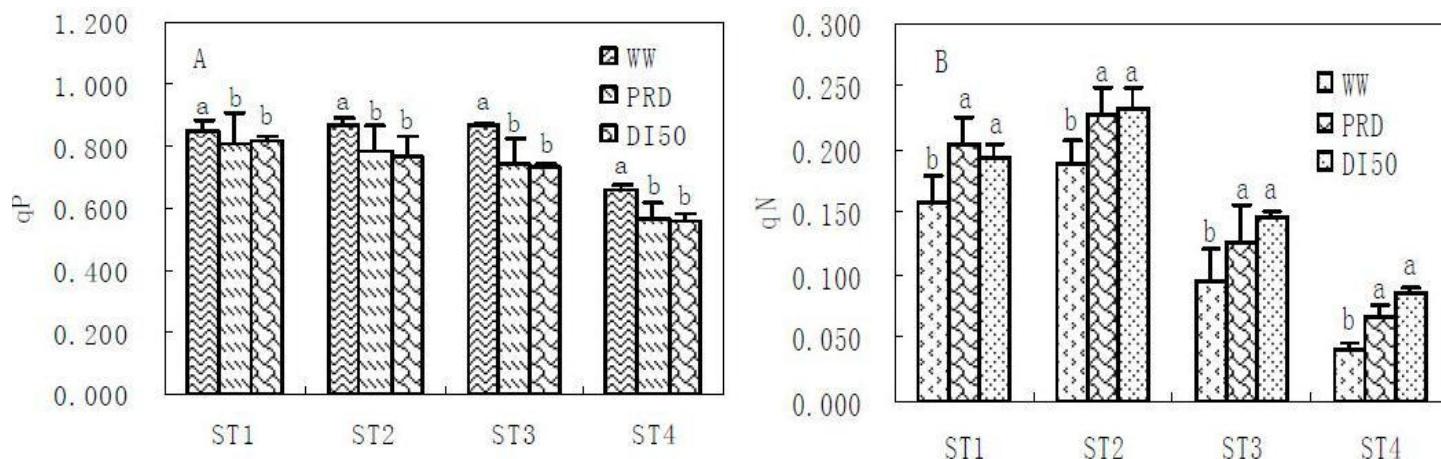
Photochemical parameters, evaluated through modulated chlorophyll a fluorescence technique, are presented in Figures 3 and 4. When drought was imposed, significant increase in  $F_0$  was found in PRD and DI50 at all the growing stages except the second stage. However, the maximal fluorescence ( $F_m$ ) and variable fluorescence ( $F_v$ ) decreased significantly in both deficit irrigation treatments. We observed that the drought stress treatments had a slight effect on the maximum yield of primary photochemistry of PSII ( $F_v/F_m$ ) as shown in Figure 2, confirming a high stability of the potential PSII photochemical efficiency during drought stress. Compared to the control, the average of  $F_v/F_m$  ratio at four stages decreased by 9.5% in PRD and by 12.0% in DI50. The decrease in the  $F_v/F_m$  ratio from both deficit irrigation treatments was due more to a decline in  $F_m$  than an increase in  $F_0$ .  $F_0$ ,  $F_v$ ,  $F_m$  and  $F_v/F_m$  and did not significantly differ between PRD and DI50 treatments.

The plants developed non-photochemical quenching ( $q_N$ ) with increasing light intensity (data not shown). Moreover, this increase was significantly stronger in the drought-stressed as compared to the well-watered hot pepper plants. However,  $q_P$  of both deficit treatments

were approximately 11% lower than well-watered plants.

## DISCUSSION

Water limitation decreases plant water use and growth (Franco et al., 2006), although the exact impact may vary depending on the pattern and intensity of the water stress imposed. Restriction of the water available to glasshouse-grown hot pepper significantly reduced the total dry mass, shoot weight and leaf area (Table 2 and Figure 2), and improved the root density. Growth responses to reduce irrigation were also influenced by the pattern of irrigation. Plants grown with PRD had a similar leaf area and total dry weight to the control treatment and showed a less pronounced decline at the end of experimental period than the plants under DI50. The root/shoot ratio of the plants under PRD was higher than in control and DI50 plants, as previously reported for PRD-grown tomato (Mingo et al. 2004). This redistribution of dry matter in favour of the roots at the expense of shoots (Montero et al., 2001) is probably due to the plants needing to maintain root surface area under soil drought conditions in order to absorb water from the substrate.



**Figure 4.** Influence of different irrigation treatment on qP and qN at different stages; ST1, ST2, ST3 and ST4 denote the stages of seeding stage, bloom and fruit setting stage, vigorous fruit- bearing stage and later fruit- bearing stage, respectively. Vertical bars represent  $\pm$  S.E. of the mean. (n = 3). For a given variable, mean values not sharing common letters are significantly different (p 0.05).

An advantage for the smaller surface area, as we can observe in our experiment, is its contribution in reducing water consumption, since canopy transpiration is a function of the net sunshine energy absorption and lower leaf area will reduce light interception (De Herralde et al., 1998; Bañón et al., 2002).

The timing and degree of water stress also influenced LAI development (Table 3). PRD did not affect LAI compared to control plants, suggesting that LAI is not modified by this pattern of deficit irrigation and meaning that plants can cope with water shortage without losing their horticultural value.

A decrease in leaf relative leaf water content may decrease stomatal conductance and leaf area development, thereby decreasing total plant water consumption (Kang et al., 2000). Alternatively, changes in root- to-shoot chemical signalling (Dodd, 2009) and/or their interaction with plant water status may influence shoot physiology.

Chlorophyll fluorescence parameters (such as  $F_o$ ,  $F_v$ ,  $F_m$ ,  $F_v/F_m$ , qP and qN) are often measured to explain the integrity or health of the photosynthetic apparatus during environmental stress (Krause and Weiss, 1991; Clark et al., 2000). Under drought conditions, in general, the mean values of  $F_v$ ,  $F_m$ ,  $F_v/F_m$ , qP decreased and  $F_o$  and qN increased which suggested that the efficiency of the photosystems decreased. This might be attributed to a reduced efficiency of the light-harvesting and antenna complexes to deliver quanta to the reaction centers and a reduced efficiency of those reaction centers to process that energy when delivered, with greater emphasis being on the latter.

The general decrease in  $F_m$ ,  $F_v$  and increase in  $F_o$  have also been observed in a number of other plants subjected to soil drought: barley, paddy rice and so on (Li et al., 2006; Alejandro et al., 2005; Angelopoulos et al.,

1996). Many researcher agree that the fluorescence emission observed at  $F_o$  emanates from Chl a molecules located in the antenna, but the source of  $F_v$  fluorescence is more controversial (Krause and Weiss, 1991). In the study, the increase of  $F_o$  values may attribute to a disassociation of the light-harvesting complexes from PSII or decreased thylakoid integrity (Beckett et al., 2000; Yamane et al., 2000). Study on maize leaves subjected to water stress sustain severe disfigurement to thylakoid structure and the chloroplast envelope, grana within the thylakoid are barely recognizable compared with unstressed controls (Ristic et al., 1992). Increased in  $F_o$  (Figure 3) may indicate leaf osmoregulation during water stress within the leaf of hot pepper. Under osmotic stress, chloroplasts may sustain their stromal volume, by either synthesizing or accumulating solutes within the stroma. However, under increased stress, osmoregulation will cease to maintain chloroplast size and the stromal volume will decrease (Santakumari and Berkowitz, 1991). Decline in chloroplast volume would likely contribute to disorder within the thylakoid membranes and reduce efficiency of photochemistry. The most convincing theory suggest that  $F_v$  is related to the decay of the primary radical pair  $P680^+Pchl^-$  in PSII (Schreiber, 2004). There are several potential factors that could lead to the reduction of  $F_v$  and thereby decrease the rate of photosynthesis. Currently, there is no agreement on the exact mechanism whereby the decay or recombination of  $P680^+Pchl^-$  leads to  $F_v$  (that is, whether the electron travels back and forth between P680 and Pchl emitting energy in the form of heat and fluorescence, or whether it is eventually transferred back into the antenna complex to be emitted as heat and/or fluorescence). Many studies have shown that plants under water stress can degrade of the D1 and D2 proteins, thereby inhibiting the electron transport chain (Giardi et al., 1996; He et al., 1995). Despite morpho- logical differences between PRD and DI plants receiving the same irrigation volumes,

there was no difference in adaptation of the photosynthetic apparatus to the two treatments (Figures 3 and 4).

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