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The interactive effects of water and fertilizer on photosynthetic capacity and yield in tomato plants

Juanjuan Zhu[1], Yinli Liang[1, 2*], Yanli Zhu[1], Wanglin Hao[1], Xingjun Lin[2], Xing Wu[1], Anrong Luo[1]

[1]College of Life Science, Northwest A & F University, Yangling, Shaanxi, 712100, P. R. China
[2]Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resource, Yangling, Shaanxi, 712100, P. R. China

*Corresponding author: liangyl@ms.iswc.ac.cn

Abstract

An experiment was carried out with potted tomato (*Lycopersicon esculentum* Mill.) plants to investigate the interactive effects of soil moisture (low: 55% of field capacity [FC]; moderate: 75% FC; and high: 95% FC) and fertilizer application rates (low: N 0.187 g/kg + P_2O_5 0.131 g/kg + K_2O 0.224 g/kg; high: N 0.267 g/kg + P_2O_5 0.187 g/kg + K_2O 0.320 g/kg) on leaf photosynthetic pigments, gas exchange, chlorophyll (Chl) fluorescence, and fruit yield for the entire fruit growing season. The correlations among photosynthetic parameters of interest, fruit yield, and plant biomass were also analyzed. Results indicated that there were significant interactive effects of soil moisture and fertilization rates in tomato plants. Soil moisture had greater effects on fruit yield, plant biomass, and root/shoot ratio than did fertilizer rates. The high fertilizer rate decreased leaf photosynthetic pigment contents, gas exchange, and Chl fluorescence when soil moisture was 55% FC, but it increased those values when soil moisture was 95% FC. When soil moisture was 75% FC， the high fertilizer rate increased leaf photosynthetic pigment contents, decreased gas exchange, and had little effect on Chl fluorescence. Linear correlations between net photosynthesis rates (P_N) and photosynthetic pigment contents (Chl a/b, carotenoids, Chl/carotenoids) and Chl fluorescence parameters (Fv′/Fm′, Φ_{PSII}, Φ_{PSII}/Φ_{CO2}, ETR, and Fv/Fm) were found. Leaf photosynthetic pigment content was positively related to dark-adapted Chl fluorescence (Fv/Fm) but negatively related to the ratio of the quantum yield of PSII to the quantum efficiency of CO_2 fixation (Φ_{PSII}/Φ_{CO2}). P_N was quadratically correlated with fruit yield, indicating that improving P_N with in a suitable range could increase fruit yield for tomato plants.

Keywords: chlorophyll fluorescence; gas exchange; photosynthetic pigment.

Abbreviations: Car (carotenoid), Chl (chlorophyll), D (light absorbed by the PSII antenna that is subsequently thermally dissipated), FC (field capacity), Fv/Fm (maximal PSII photochemistry efficiency in a dark-adapted state), Fv′/Fm′ (maximal PSII photochemistry efficiency in a light-adapted state), Ls (stomatal limitation), NPQ (non-photochemical quenching coefficient), qP (photochemical quenching coefficient), P (light absorbed by the PSII antenna that is subsequently used in photochemistry), PSII (photosystem II), SWC (soil water content), WUE (water use efficiency), X (light absorbed by the PSII antenna that is neither used in photochemistry nor thermally dissipated), Φ_{CO2} (quantum efficiency of CO_2 fixation), Φ_{PSII} (quantum yield of PSII).

Introduction

Tomato (*Lycopersicon esculentum* Mill**.**) is a widely grown plant of great economic importance, especially in warm and rather dry areas (Cuartero and Fernandez-Munoz, 1999), due to the high nutritional value of its fruit (Savić et al., 2008). The yield and quality of fresh fruit are influenced by many factors, including genetic factors and growing conditions (Viskelis et al., 2008). Irrigation and nutrient supply are considered to be the two environmental inputs that contribute most to crop productivity (Lenka, et al., 2009; Wang et al., 2011). Water deficiency is the main constraint for tomato production in the arid and semi-arid areas of north-western China because of the low precipitation (about 40-200 mm per year), the high annual potential evaporation (about 1,500–3,000 mm), and the scarce water resources (only 4.7% of national resources) in those areas (Xie et al., 2005). It is very common to apply excess fertilizer (>1000 kg N ha^{-1}) to plants for maximal yield (He et al., 2007), leading to low fertilizer use efficiency, especially nitrogen use efficiency, and producing environmental contaminants. Therefore, the influences of irrigation and fertilizer on tomato plants have attracted considerable interest (Savić et al., 2008). Many controlled experiments have been done on the physiological processes involved (Nieves-Cordones et al., 2007; Sánchez-Rodríguez et al., 2010; Wang et al., 2011). Photosynthesis is the primary physiological process that is affected by changes in growing conditions. Leaves are the major contributors to net productivity throughout the growing season for crops (Ashraf and Bashir, 2003), and their photosynthetic activities are crucially important for harvestable fruit yield (Hansen, 1969). Many researchers have investigated changes in leaf photosynthesis in plants grown with different soil moisture or different fertilizer application rates. Leaf photosynthetic capacities can be estimated by using leaf gas-exchange parameters based on CO_2 assimilation or by using chlorophyll (Chl) fluorescence parameters based on the operating quantum efficiency of electron transport through photosystem II (PSII). Water deficit decreases the water potential of growing plants, resulting in dehydration, reduced stomatal conductance, changes in Chl fluorescence and PSII photoinhibition, conformational changes in the membrane-bound ATPase enzyme complex, and decreases in rubisco concentrations (Pessarakli, 2005). The reduction in photosynthesis can be attributed to a decline in intercellular CO_2 concentration (Ci), partly due to the closure of stomata, which leads to overexcitation and subsequent photoinhibitory damage of PSII reaction centers (Cornic 2000; Souza et al. 2004) and partly to metabolic factors (Lawlor and Cornic, 2002). Moreover, applied fertilizer can be used to synthesize the components of the photosynthetic apparatus (Sugiharto et al., 1990), including rubisco as well as chlorophyll- and carotenoid-containing membrane proteins (Bungard et al., 1997). A lack of fertilizer, therefore, can disturb photosynthetic activities directly and can also restrict partitioning of assimilates to the fruits from the leaves (Kanai et al., 2011). Leaf contents of photosynthetic pigments, proteins, lipids, and thylakoid membranes, which are related to photosynthesis, are also affected strongly by soil moisture or fertilizer application. Plant growth and development are frequently dependent on photosynthesis, as this is the process through which all living green plants produce their own food (Ashraf and Bashir, 2003). It is clear that photosynthetic capacity is the basis of agricultural yield (Pessarakli, 2005). Leaf photosynthesis accounts for the majority of the variation in biomass production and yield (Takai et al., 2010). However, three contradictory relationships between leaf photosynthesis and crop yield have been found: positive (Faville et al., 1999; Ashraf, 2001 and 2003; Lin et al., 2005; Hubbart et al., 2007), negative (Evans, 1993; Long et al., 2006), and no correlation (Berdahl et al., 1972; Chongo and McVetty 2001). Lawlor (1995) showed that these contradictory results could be explained by the fact that limiting environmental and plant factors interact strongly to regulate photosynthesis and yield. It is important, therefore, to improve understanding of the mechanisms underlying biomass production under a range of conditions (Jaimez et al., 2008). Photosynthetic responses of tomato plants to either irrigation regimes or fertilizer application rates have been well documented; however, there is little literature reporting how these factors interact to influence photosynthetic capacity throughout the entire reproductive season in tomato plants. Furthermore, could increasing the leaf photosynthetic capacity increase fruit yield? What are the relationships between fruit yield and leaf photosynthetic parameters in tomato? Therefore, the objectives of current research were to assess the interactive effects of soil water contents and fertilizer application rates on leaf photosynthetic pigments, gas exchange, and Chl fluorescence, as well as the effects on marketable yield and plant dry weight in tomato crops and to evaluate the relationships between tomato marketable yield and leaf photosynthetic capacity and photosynthetic sustainability index throughout the fruit growing season.

Results and Discussion

Photosynthetic pigment contents

Leaf Chl content is one of the most important factors determining photosynthetic capacity, as it contains the reaction centers (Mao et al., 2007), and carotenoids (Car) play an important role in light harvesting complexes and in photoprotection of the photosystems (Netto et al., 2005). The evaluation of photosynthetic pigments is used to evaluate environmental stress, and changes in Chl a/b and total Chl/Car ratios may be good indicators of tolerance and physiological status of plants under stress conditions (Netto, et al., 2005; Camejo et al., 2005). In the current study, high variability in levels of all photosynthetic pigments throughout fruit growth (Fig. 1) made it difficult to ascertain treatment effects; however, incorporating the continuous impacts of soil water content (SWC), fertilizer (F), and sampling time (Table 1) into the analysis alleviated the problem and showed that among all effects in the full model, SWC levels, fertilizer, time, and their interactions had significant effects on leaf Chl contents throughout fruit growth in tomato plants, with the exception of Chl a/b (Table 1). It indicated that 55% of field capacity (FC) could not cause significant damage to chloroplasts leading to changes in pigment composition of the photosynthetic apparatus during tomato fruit growth. SWC had a significant effect on the ratios of the total Chl contents to the carotenoids contents (TChl/Car) only under high fertilizer condition. Fertilizer rates had different impacts on Chl a, TChl, and Chl/Car ratio at different SWC (Table 1). Fertilizer did not affect Chl a and TChl in the Wl treatment but had significant effects in other SWC levels. Chl/Car ratios were significantly different between fertilizer treatments only in the Wm treatment. Comparisons among combined irrigation and fertilizer treatments, averaged over the entire fruit growth season, showed that Chl contents were highest in the WmFh treatment (Table 1).

Leaf gas exchange

Photosynthesis converts light energy into chemical energy and has a major impact on crop productivity (Ashraf and Bashir, 2003). However, the photosynthetic rate is influenced greatly by plant growth conditions and is therefore a common criterion used to identify possible changes in crops adapted to specific environments (Ashraf, 2001; El-Sharkawy, 2006). Throughout the experiment, the photosynthetic capacities of tomato leaves were strongly affected by SWC, fertilizer, time, and their interactions. High fertilizer application rate (Fh) decreased net photosynthesis rates (P_N), intercellular CO_2 concentration (Ci), transpiration rate (E), and stomatal limitation (Ls) in the Wl and Wm treatments (WlFl *vs.* WlFh and WmFl *vs.* WmFh) but did not influence P_N or E and increased Ci and Ls in the Wh treatment (WhFl *vs.* WhFh) (Table 2). Regardless of SWC, Fh decreased stomatal conductance to water vapor (gs) and improved water use efficiency (WUE) (WlFl *vs.* WlFh, WmFl *vs.* WmFh, and WhFl *vs.* WhFh), in agreement with Latiri-Souki et al. (1998), Caviglia and Sadras (2001), and Li et al. (2004). Among tested SWC, plants grown with moderate soil moisture (Wm) had the highest P_N, gs, Ci, and E and the lowest Ls (WlFl+WlFh *vs.* WmFl+WmFh *vs.* WhFl+WhFh). Averaged over the entire reproductive stage, photosynthetic capacity was highest in the WmFl treatment and lowest in the WlFh treatment. Drought stress is often associated with high irradiance and temperature (Araus et al., 1998). The photosynthetic apparatus absorbs excess light energy, leading to the inactivation of or damage to Chl and to a reduction in photosynthetic activity (Dai et al., 2009). On average, 36% of the light absorbed by PSII was used in photochemistry (P), 46% was dissipated thermally (D), and 17% was not used in photochemistry or dissipated by the PSII antenna (X) in tomato plants (Fig. 2). The SWC and fertilizer rates and their interaction significantly affected the allocation of light absorbed by PSII, though X was not affected by SWC or fertilizer rates alone (Fig. 2). Among the treatments in this study, WlFh and WhFl could decrease P, leading to a low photosynthetic capacity, consistent with measured P_N. There was a significant correlation between P_N and Chl a/b (r = 0.43), Car (r = 0.44), and Chl/Car (r = -0.55) throughout fruit growth (Fig. 3), but no significant correlation was observed between P_N and Chl a, Chl b, or TChl contents (data not shown), in agreement with Marini (1986). This indicated that TChl con-

Table 1. Contents of chlorophyll (Chl) and carotenoids (Car), and Chl/Car least squares means computed from the time-repeated measures analysis for the entire reproductive stage of tomato plants.

Treatments	Chl a ($mg\ g^{-1}$ FW)	Chl b ($mg\ g^{-1}$ FW)	Chl a/b	TChl ($mg\ g^{-1}$ FW)	Car ($mg\ g^{-1}$ FW)	TChl/Car
WlFl	1.202 ab	0.470 b	2.565 a	1.670 b	0.273 a	6.19 b
WlFh	1.175 b	0.457 c	2.547 a	1.630 b	0.262 b	6.31 ab
WmFl	1.075 c	0.424 d	2.537 a	1.497 c	0.244 c	6.16 b
WmFh	1.235 a	0.489 a	2.511 a	1.722 a	0.269 ab	6.46 a
WhFl	0.974 e	0.388 f	2.523 a	1.435 d	0.218 e	6.33 ab
WhFh	1.031 d	0.406 e	2.560 a	1.359 e	0.233 d	6.23 ab
SWC	***	***	ns	***	***	ns
F rates	***	***	ns	***	***	*
SWC × F	***	***	ns	***	***	**
time	***	***	***	***	***	***
SWC × time	***	***	***	***	***	***
F × time	***	***	***	***	***	**
SWC × F × time	***	***	***	***	***	***
SWC at Fl	***	***	ns	***	***	ns
SWC at Fh	***	***	ns	***	***	*
F rates at Wl	ns	**	ns	ns	**	ns
F rates at Wm	***	***	ns	***	***	*
F rates at Wh	**	***	ns	**	***	ns

The different letters indicate significant difference among treatments at $p \leq 0.05$ level; SWC, soil water content; F, fertilizer; time, different sampling dates; the *, **, and *** significant at $p \leq 0.05$, 0.01, and 0.001 levels, respectively; NS, not significant.

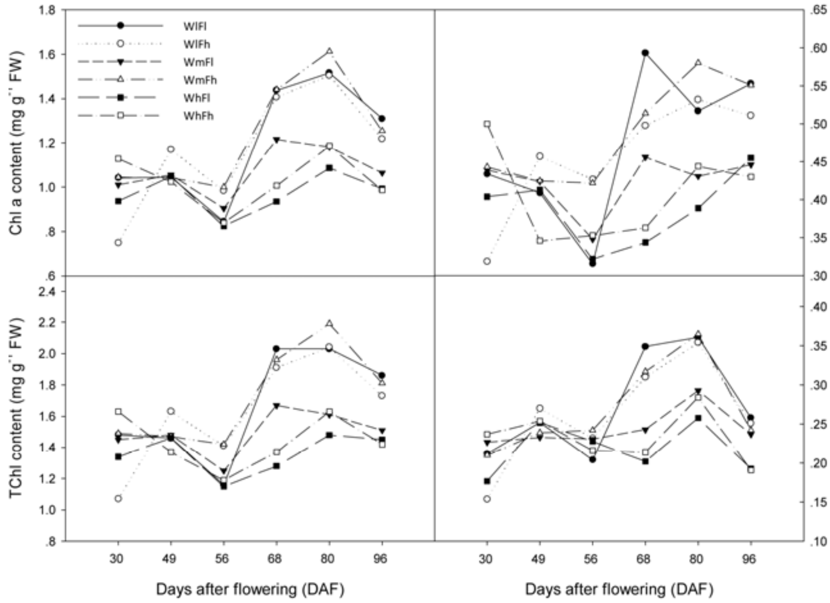


Fig 1. The interactive effects of soil water contents (SWC) and fertilizer rates on chlorophyll (Chl) and carotenoid (Car) contents at different days after florescence (DAF) for tomato plants.

tributed less to P_N than Car did during fruit growth in tomato plants under different soil moisture and fertilizer conditions.

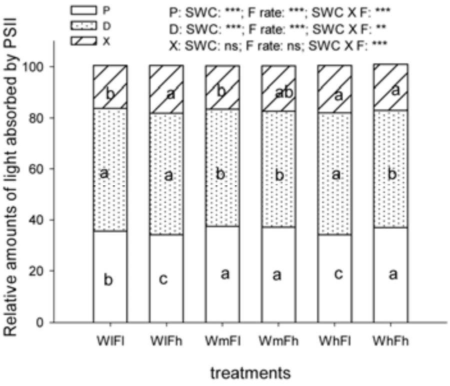
Leaf chlorophyll fluorescence

Chlorophyll fluorescence analysis allows non-invasive, near-instantaneous measurement of key aspects of photosynthetic light capture and electron transport (Campbell et al., 1998) and responds frequently to the state of energy distribution in the thylakoid membrane, the quantum efficiency of PSII, and the extent of photoinhibition (Wang et al., 2007). Values of Fv/Fm, Fv'/Fm', Φ_{PSII}, Φ_{PSII}/Φ_{CO2}, ETR, qP, and NPQ for each treatment averaged over the reproductive season are shown in Table 3. Tukey's multiple range tests conducted on these combined treatments showed significant differences among them. Soil moisture had a greater influence on Chl fluorescence of tomato leaves than did fertilizer rates, based on time-repeated measurement analysis (Table 3). However, the effects of fertilizer rates had different patterns under different SWC treatments. Fv/Fm was significantly affected by fertilizer rates in low SWC (Wl) but not in moderate (Wm) or high (Wh) SWC. Fh increased Fv'/Fm' and Φ_{PSII}/Φ_{CO2} in the Wh treatment (WhFl *vs.* WhFh) but had no significant effect in the Wl or Wm treatment (WlFl *vs.* WlFh and WmFl *vs.* WmFh). Φ_{PSII} was negatively affected by Fh in the Wl condition but was positively affected in the Wh condition. Although ETR and qP were not affected, based on the time-repeated ANOVA, fertiliz-

Table 2. Net photosynthetic rate (P_N) (μmol CO_2 m^{-2} s^{-1}), stomatal conductance to water vapor (gs) (mmol m^{-2} s^{-1}), transpiration rate (E) (mmol m^{-2} s^{-1}), intercellular CO_2 concentration (Ci) (μmol mol^{-1}), stomatal limitation (Ls), and water use efficiency (WUE) (μmol CO_2/mmol H_2O) least squares means computed from the time-repeated measures analysis for the entire reproductive stage of tomato plants.

Treatments	P_N	gs	Ci	E	Ls	WUE
WlFl	14.6 a	0.230 b	239.7 b	5.92 b	0.396 d	2.57 c
WlFh	13.1 d	0.174 e	224.5 c	4.80 e	0.438 a	2.93 a
WmFl	14.8 a	0.249 a	252.9 a	6.35 a	0.360 e	2.41 d
WmFh	14.4 ab	0.201 c	240.5 b	5.65 c	0.392 d	2.70 b
WhFl	13.8 c	0.202 c	228.3 c	5.52 d	0.425 b	2.59 c
WhFh	14.1 bc	0.187 d	236.0 b	5.51 d	0.408 c	2.72 b
SWC	***	***	***	***	***	***
F rates	***	***	***	***	***	***
SWC × F	***	***	***	***	***	***
time	***	***	***	***	***	***
SWC × time	***	***	***	***	***	***
F × time	***	***	***	***	***	***
SWC × F × time	***	***	***	***	***	***
SWC at Fl	***	***	***	***	***	***
SWC at Fh	***	***	***	***	***	***
F rates at Wl	***	***	***	***	***	***
F rates at Wm	*	***	***	***	***	***
F rates at Wh	ns	***	***	ns	***	***

The different letters indicate significant difference among treatments at $p \leq 0.05$ level; SWC, soil water content; F, fertilizer; time, different sampling dates; the *, **, and *** significant at $p \leq 0.05$, 0.01, and 0.001 levels, respectively; NS, not significant.



The horizontal different letters indicate significant difference among treatments at $p \leq 0.05$ level.

Fig2. The relative amounts of light absorbed by PS II that were used in photochemistry (P), dissipated thermally (D), and not used in photochemistry or dissipated by the PSII antenna (X) least squares means computed from the time-repeated measures analysis for the entire reproductive stage of tomato plants.

er significantly influenced ERT and qP in every SWC (Table 3). Fh had strongly negative impacts on ETR and qP in the Wl and Wm treatments (WlFl *vs.* WlFh and WmFl *vs.* WmFh) but had positive effects in the Wh treatment (WhFl *vs.* WhFh). Regardless of SWC, Fh strongly increased NQP during the entire reproductive season (WlFl *vs.* WlFh, WmFl *vs.* WmFh, and WhFl *vs.* WhFh). On average, the Chl fluorescence was high in WmFl treatment and low in WlFh and WhFl treatments. Some linear correlations between Chl fluorescence and photosynthetic pigment parameters were significant (Fig 4). Fv/Fm was positively related to Chl a contents and Chl/Car ratios, but Φ_{PSII}/Φ_{CO2} was negatively related to TChl contents and Chl/Car ratios. These relationships suggested that the high Chl and Chl/Car ratio led to a high maximum quantum yield of PSII (Fv/Fm) and a low rate of photosynthetic electron transport to alternative electron sinks such as nitrate reduction and the Mehler reaction (Shi et al., 2008). P_N was positively correlated with Fv′/Fm′ (r = 0.45), Φ_{PSII} (r = 0.47), Φ_{PSII}/Φ_{CO2} (r = 0.51), and ETR (r =0.33) (Fig. 5a-d), suggesting that these parameters react in parallel to soil moisture and fertilizer application rates. In contrast, there was a significant negative relationship between P_N and Fv/Fm (r = -0.39) (Fig. 5e), contradicting Cha-um and Kirdmanee (2009) and Cha-um et al. (2010). However, Boughalleb et al. (2009) reported that the relationship between P_N and Fv/Fm was different in different plants. That study demonstrated that soil moisture, fertilizer application rates, and tomato plant factors interact strongly to influence P_N and Fv/Fm. Variation in Fv/Fm was slightly inversely associated with variation in P_N.

Table 3. Chlorophyll fluorescence parameters least squares means computed from the time-repeated measures analysis for the entire reproductive stage of tomato plants.

Treatments	Fv/Fm	Fv'/Fm'	Φ_{PSII}	Φ_{PSII}/Φ_{CO2}	ETR	qP	NQP
WlFl	0.802 bc	0.517 c	0.355 b	10.9 ab	120.9 a	0.671 bc	1.32 c
WlFh	0.807 ab	0.521 c	0.341 c	10.9 ab	113.5 c	0.640 d	1.43 a
WmFl	0.810 a	0.539 ab	0.374 a	12.0 a	125.9 a	0.679 a	1.22 e
WmFh	0.808 ab	0.544 a	0.371 a	12.2 a	120.7 b	0.668 c	1.26 d
WhFl	0.799 c	0.521 c	0.341 c	9.9 b	114.9 c	0.635 d	1.24 b
WhFh	0.803 abc	0.537 b	0.373 a	11.6 a	125.6 a	0.677 ab	1.30 c
SWC	***	***	***	**	***	***	***
F rates	ns	***	***	ns	ns	ns	***
SWC × F	ns	***	***	*	***	***	***
time	***	***	***	***	***	***	***
SWC × time	*	***	***	**	***	***	***
F × time	***	***	***	*	***	***	***
SWC × F × time	***	***	***	***	***	***	***
SWC at Fl	**	***	***	*	***	***	***
SWC at Fh	ns	***	***	*	***	***	***
F rates at Wl	*	ns	***	ns	***	***	***
F rates at Wm	ns	ns	ns	ns	**	***	***
F rates at Wh	ns	***	***	*	***	***	***

The different letters indicate significant difference among treatments at $p \leq 0.05$ level; SWC, soil water content; F, fertilizer; time, different sampling dates; the *, **, and *** significant at $p \leq 0.05$, 0.01, and 0.001 levels, respectively; NS, not significant.

Sustainability index (SI) of photosynthetic parameters

Horton (2000) proposed that prolonging the duration of photosynthesis offered an opportunity to increase the total amount of carbon fixed by a crop plant, and that delaying leaf senescence would be a prime target for crop improvement. The sustainability indexes (SI) of photosynthetic parameters under different soil moisture and fertilizer conditions are shown in Table 4. This indicates the degree of duration of parameters throughout fruit growth. SWC and the SWC×F interaction had greater effects on SIs of photosynthetic parameters than did fertilizer application rates alone. The SIs of Ci, E, and ETR were significantly influenced by fertilizer. Of all the measured parameters, only the SIs of Fv/Fm and Φ_{PSII}/Φ_{CO2} were not affected by any factors tested in the current experiment (Table 4). On average, the SIs of interested parameters were high in the Wl treatment, regardless of fertilizer application rates. Throughout the fruit growing season in tomato, the linear correlations between SIs of Chl a, TChl, Car, Fv/Fm, Φ_{PSII}/Φ_{CO2}, and ETR, on the one hand, and the SI of P_N, on the other hand, were significant (Fig. 6). Positive correlations (negative for Fv/Fm) were found for these parameters. This indicated that the sustainability of photosynthesis in the tomato leaves was due primarily to the sustainability of photosynthetic pigment contents and PS II electron transport.

Fruit yields and plant dry biomass

Fruit yield per plant and plant biomass were significantly different among combined treatments. Like Chl fluorescence, soil moisture had a greater influence on fruit yield, plant biomass, and root/shoot ratio than did fertilizer rates (Table 5). Fertilizer rates had no influences on fruit yield, leaf biomass, root biomass, or root/shoot ratio but significantly increased stem and total biomass, particular in the Wm treatment ($p \leq 0.01$). Although SWC strongly affected stem biomass, based on a two-way ANOVA, no significant influence was found in the Fh treatment ($p > 0.05$). There were no effects of SWC×F interactions on fruit yield, plant biomass, or root/shoot ratio. On average, fruit yield increased gradually with SWC (WlFl+WlFh *vs.* WmFl+WmFh *vs.* WhFl+WhFh). The total biomass and root/shoot ratio were higher in the WmFh and WhFl treatments than in other combined treatments.

Photosynthesis is the foundation of crop yield production (Zou et al., 2007). A positive correlation between grain yield and photosynthetic rate was observed in asparagus (Faville et al., 1999), rice (Lin et al., 2005; Hubbart et al., 2007), and blue panicgrass (*Panicum antidotale Retz.*) (Ashraf, 2003). However, Ahmadzadeh et al. (2004) illustrated that the maintenance of leaf CO_2 exchange rate, not potential leaf CO_2 exchange rate, was positively associated with dry matter accumulation and grain yield. Sinclair et al. (2004) illustrated that a 33% increase in leaf photosynthesis could translate into an 18% increase in biomass but only a 5% increase in grain yield or a 6% decrease in grain yield in the absence of additional nitrogen. There were no significant linear correlations between fruit yield and photosynthetic parameters and their SIs (data not shown), but a significantly quadratic correlation existed between P_N and fruit yield (Fig. 7). This was likely due to the fact that more photosynthates were allocated to vegetative organs than to reproductive organs, leading to low fruit yield when P_N was higher than a certain value.

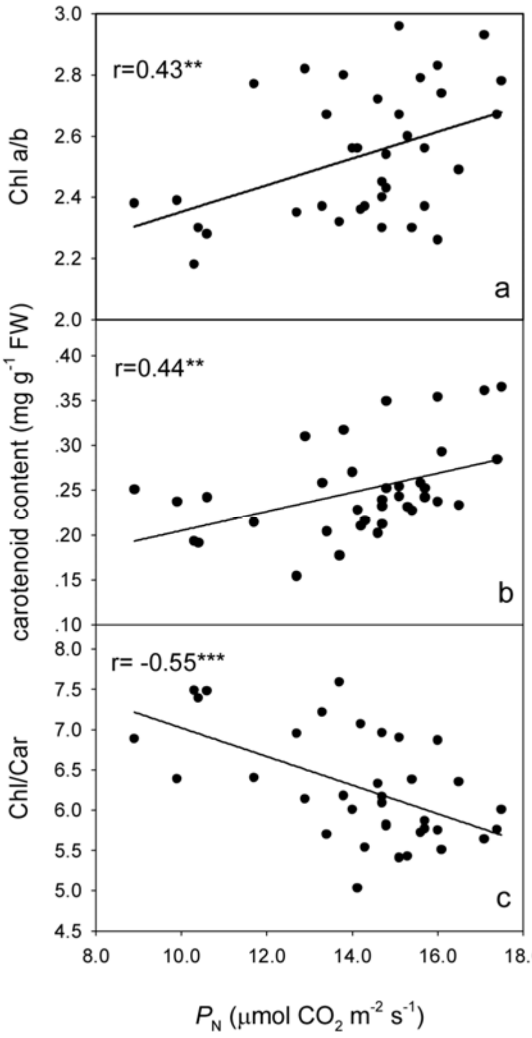
Materials and methods

Experimental site

The greenhouse experiment was carried out at the Institute of Soil and Water Conservation (ISWC), Northwest A&F University in Yangling (34°12′-34°20′ N; 108°-108°7′ E, elevation 560 m), Shaanxi, China, from May to October in 2010. The soil used in this trial was obtained from the Ansai experimental station (0-30 cm layer) in Shaanxi, China and was sieved through a 1-cm mesh.

Plant materials and soil conditions

Tomato plants (*Lycopersicon esculentum* Mill., cultivar Tianfu



The asterisks indicate significant differences at the 1% (**) and 0.1% (***) probability levels, respectively.

Fig 3. Correlations of P_N with Chl a/b (a), Car (b), and Chl/Car (c) for the entire fruit growing season.

501) with three leaves were transplanted on 6th May in 2010 into plastic pots (outer diameter, 30 cm; height, 25 cm). One plant was transplanted into each plastic pot containing 9.0 kg of air-dried soil. The surface of the soil was covered with perlite to reduce evaporation. The soil was loessial, and soil water holding capacity was 22% (mass basis). The soil bulk density was 1.15 g cm^{-3} and the pre-sowing soil test indicated that the mean organic matter content was 12.6 g kg^{-1}, available N (1 mol L^{-1} NaOH hydrolysis) was 16.5 mg kg^{-1}, available P (0.5 mol L^{-1} $NaHCO_3$) was 26.9 mg kg^{-1}, available K (1 mol L^{-1} neutral NH_4OAc) was 221.9 mg kg^{-1}, total N content was 0.723 g kg^{-1}, pH was 7.9, and electrical conduction was 0.35 ms cm^{-1}.

Soil water content and fertilizer treatments

Two fertilizer levels were studied (low [Fl]: N 0.187g kg^{-1} dry soil + P_2O_5 0.131 g kg^{-1} dry soil + K_2O 0.224 g kg^{-1} dry soil and high [Fh]: N 0.267 g kg^{-1} dry soil + P_2O_5 0.187 g kg^{-1} dry soil + K_2O 0.320 g kg^{-1} dry soil) in combination with three soil water contents (low [Wl]: 55%±5% of field water holding capacity [FC]；moderate [Wm]: 75%±5% FC；and high [Wh]: 95%±5% FC) (Hosseini et al., 2009; Liu et al., 2009). Prior to transplanting, 20% of the N, 100% of the P_2O_5, and 50% of the K_2O were applied for each fertilizer treatment using urea, diammonium phosphate, and potassium sulfate, respectively. All fertilizers were applied with analytical reagents and mixed into the soil in powdered form. The remaining 80% of the N was dissolved into water and applied in equal portions on 6th June (30 days after transplanting [DAT]), 6th July (60 DAT), 6th August (90 DAT), and 6th September (120 DAT). The remaining 50% of the K_2O was applied on 27th July (80 DAT) as an aqueous solution. The soil water contents (SWC) were established on 26th May and measured gravimetrically every day. In order to control SWC treatments carefully, movable sheds were used during rainfall.

Leaf gas exchange and chlorophyll fluorescence measurements

Leaf gas exchange measurements were coupled with chlorophyll fluorescence measurements using an open gas exchange system (LI-6400; LI-COR, Inc., Lincoln, NE, USA) with an integrated fluorescence chamber head (LI-6400-40 leaf chamber fluorometer; LI-COR, Inc.) on fully developed leaves between the sixth and seventh nodes throughout the reproductive season. The LI-6400 was operated as an open system. The gas exchange rates were recorded at 27°C leaf temperature, 500 μmol s^{-1} flow rate, 400 mL L^{-1} CO_2 (reference CO_2), and 1000 μmol m^{-2} s^{-1} incident PPFD. The water use efficiency (WUE) and stomatal limitation (Ls) were calculated as net CO_2 assimilation rates (P_N)/transpiration rates (E) and 1-intercellular CO_2 concentration (Ci)/ambient CO_2 concentration (Ca). The quantum efficiency of CO_2 fixation (Φ_{CO2}) was determined under non-photorespiratory conditions (2% O_2) by dividing the rate of net CO_2 assimilation (P_N) by the rate at which quanta were absorbed (Fryer et al., 1998). Fluorescence parameters were set following the recommended values published in the LI-COR 6400 manual. Before measurement, the sample leaves were dark-adapted for 30 min with dark adapting clips and the initial fluorescence (Fo) and maximal fluorescence (Fm) were measured. The steady state value of fluorescence (Fs), maximal fluorescence in a light-adapted state (Fm′), and basal fluorescence (Fo′) were determined after far-red illumination. The photochemical quenching coefficient (qP), non-photochemical quenching coefficient (NQP), maximal PSII photochemical efficiency in a light-adapted state (Fv′/Fm′), maximal PSII photochemical efficiency in a dark-adapted state (Fv/Fm), and actual PSII efficiency (Φ_{PSII}) were calculated as follows: (Fm′-Fs)/(Fm′-Fo′), (Fm-Fm′)/(Fm-Fo′), (Fm′-Fo′)/Fm′, (Fm-Fo)/Fm, and (Fm′-Fs)/Fm′, respectively (Genty et al., 1989; van Kooten and Snel, 1990). The relative amounts of light absorbed by PSII that were used in photochemistry (P) and dissipated thermally (D) were calculated by (Fv′/Fm′) ([Fm′–Fs]/Fv′), equivalent to Φ_{PSII}, and 1-(Fv′/Fm′), respectively. The fraction of light absorbed by PSII that was neither used in photochemistry nor dissipated by the PSII antennae (X) was calculated as (Fv′/Fm′) (1-[Fm′–Fs]/Fv′) (Abadía et al., 1999).Leaf gas exchange parameters and chlorophyll fluorescence were measured six times: 30 days after flowering (DAF) (10th July), 49 DAF (23rd July), 56 DAF (4th August), 68 DAF (16th August), 80 DAF (27th August), and 96 DAF (13th September), throughout the reproductive stage. The sustainability indexes (SI) of the investigated parameters were calculated by dividing the values at the next sampling date by the values at the last sampling date (Kumagai et al., 2009).

Measurement of photosynthetic pigments

After the measurements of gas exchange and chlorophyll

Table 4. The sustainability index (SI) of photosynthetic parameters least squares means computed from the time-repeated measures analysis for the entire reproductive stage of tomato plants.

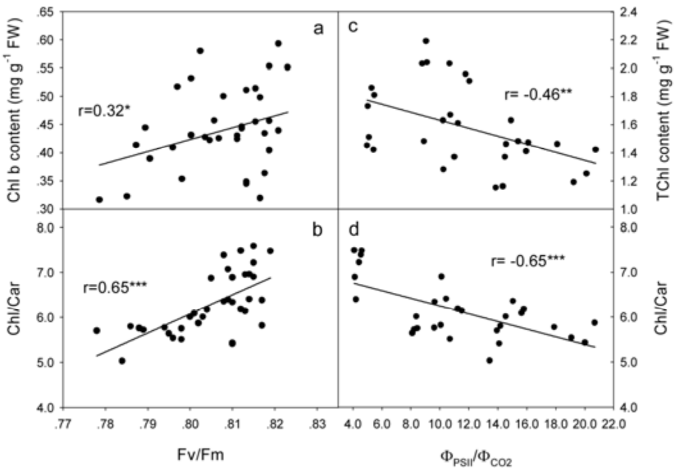
Treatments	Chl a	Chl b	TChl	Car	P_N	gs	Ci	E	Fv/Fm	Fv'/Fm'	Φ_{PSII}	Φ_{PSII}/Φ_{CO2}	ETR
WlFl	1.087 ab	1.107 a	1.089 ab	1.092 ab	0.992 a	1.117 a	1.095 a	1.023 cd	1.001 a	0.992 a	0.960 a	0.766 a	1.076 a
WlFh	1.143 a	1.112 a	1.132 a	1.160 a	0.965 ab	1.051 ab	1.101 a	1.111 a	1.000 a	0.998 a	0.952 a	0.844 a	1.060 ab
WmFl	1.024 cd	1.016 cd	1.021 cd	1.017 c	0.933 b	0.989 b	1.001 d	0.998 d	0.998 a	0.970 b	0.922 b	0.812 a	1.005 d
WmFh	1.059 bc	1.050 b	1.055 bc	1.055 bc	0.971 ab	1.053 ab	1.064 b	1.091 a	1.003 a	0.988 ab	0.936 ab	0.876 a	1.039 bc
WhFl	1.023 cd	1.034 bc	1.025 cd	1.048 bc	0.959 ab	1.035 b	1.027 cd	1.046 bc	0.999 a	0.987 ab	0.947 ab	0.798 a	1.021 cd
WhFh	0.987 d	0.986 d	0.984 d	0.983 c	0.959 ab	1.018 b	1.044 bc	1.057 b	1.001 a	0.987 ab	0.948 ab	0.847 a	1.076 a
SWC	***	***	***	***	ns	***	***	*	ns	**	***	ns	***
F rates	ns	ns	ns	ns	ns	ns	***	***	ns	ns	ns	ns	***
SWC × F	**	***	***	***	*	***	***	***	ns	ns	ns	ns	***
SWC at Fl	ns	***	***	**	**	***	***	***	ns	*	*	ns	***
SWC at Fh	***	***	***	***	ns	ns	***	***	ns	ns	**	ns	***
F rates at Wl	***	ns	***	*	ns	**	ns	***	ns	ns	ns	ns	ns
F rates at Wm	*	**	*	ns	*	*	***	***	ns	*	ns	ns	***
F rates at Wh	ns	**	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	**

The different letters indicate significant difference among treatments at p ≤ 0.05 level; SWC, soil water content; F, fertilizer; the *, **, and *** significant at p ≤ 0.05, 0.01, and 0.001 levels, respectively; NS, not significant.

Table 5. Interaction effects of SWC and fertilizer rates on fruit yields (kg/plant) and plant dry weight (DW, g/plant) in tomato plants.

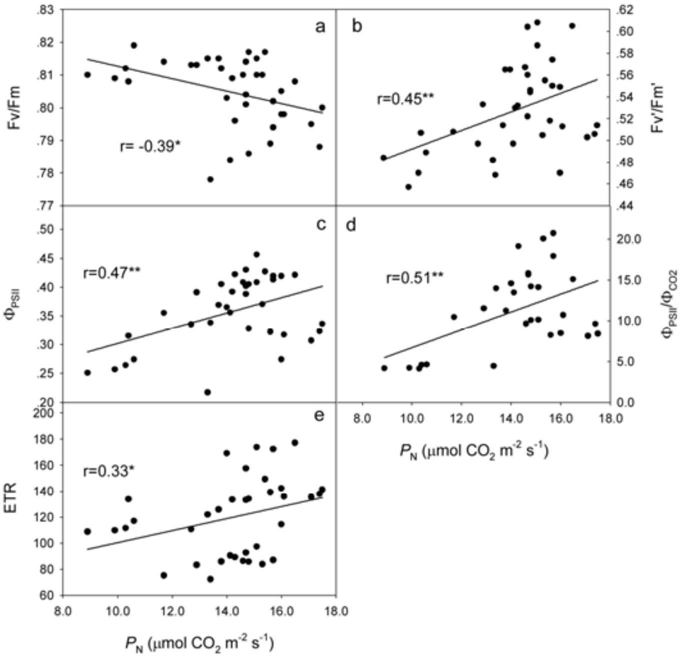
Treatments	Yield	leaf DW	stem DW	root DW	total DW	root/shoot
WlFl	0.77 c	25.0 b	17.6 b	9.2 b	51.7 c	0.215 b
WlFh	0.82 c	27.2 ab	22.9 ab	10.8 b	61.0 c	0.223 ab
WmFl	1.14 b	30.2 ab	21.0 ab	11.1 b	62.3 abc	0.217 b
WmFh	1.15 b	34.8 a	28.9 a	13.8 ab	77.5 a	0.218 b
WhFl	1.35 ab	29.7 ab	22.9 ab	22.5 a	75.1 ab	0.431 a
WhFh	1.46 a	26.8 ab	27.5 a	20.9 a	75.1 ab	0.386 ab
SWC	***	*	*	***	***	**
F rates	ns	ns	**	ns	**	ns
SWC × F	ns	ns	ns	ns	ns	ns
SWC at Fl	***	ns	**	*	*	*
SWC at Fh	***	ns	ns	**	**	*
F rates at Wl	ns	ns	ns	ns	ns	ns
F rates at Wm	ns	ns	**	ns	**	ns

The different letters indicate significant difference among treatments at p ≤ 0.05 level; SWC, soil water content; F, fertilizer; the *, **, and *** significant at p ≤ 0.05, 0.01, and 0.001 levels, respectively; NS, not significant.



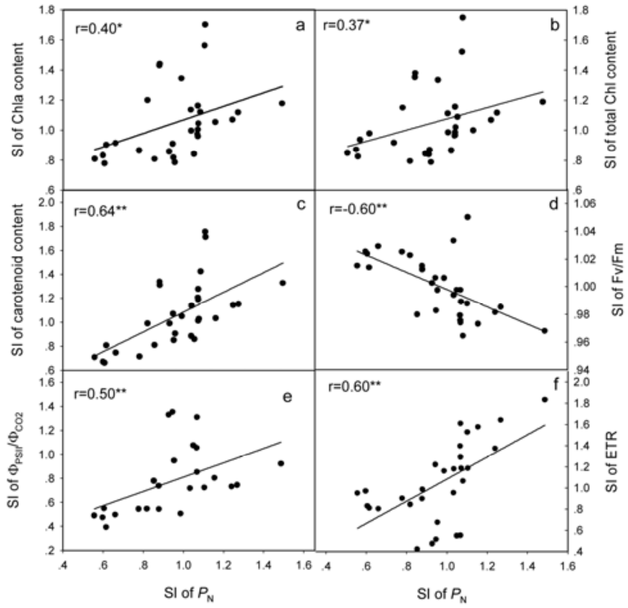
The asterisks indicate significant differences at the 5% (*), 1% (**), and 0.1% (***) probability levels, respectively.

Fig4. Correlation of Chl fluorescence and photosynthetic pigment parameters for the entire fruit growing season.



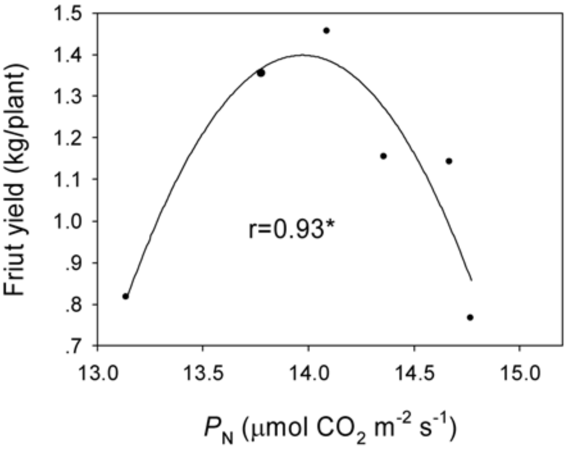
The asterisks indicate significant differences at the 5% (*) and 1% (**) probability levels, respectively.

Fig 5. Correlation of P_N with Fv/Fm (a), Fv′/Fm′ (b), Φ_{PSII} (c), Φ_{PSII}/Φ_{CO2} (d), and ETR (e) for the entire fruit growing season.



The asterisks indicate significant differences at the 5% (*) and 1% (**) probability levels, respectively.

Fig 6. Correlation of the sustainability indexes (SI) of P_N with Chl a content (a), total Chl content (b), carotenoid content (c), Fv/Fm (d), Φ_{PSII}/Φ_{CO2} (e), and ETR (f) for the entire fruit growing season.



The asterisk indicates significance at the 5% (*) probability levels.

Fig 7. Correlation of fruit yield with net photosynthetic rate (P_N).

fluorescence on each sampling date, the same leaves were cut and frozen in liquid nitrogen for the analysis of leaf Chl a, Chl b, and carotenoid contents in the laboratory. The Chl a, Chl b, and carotenoid contents were measured spectrophotometrically (Unicam UV-330, USA) and determined according to the equation of Lichtenthaler and Bushmann (2001).

Fruit yield and plant dry biomass measurements

The tomato fruits were harvested on 16th September and the total yield was determined. The leaves, stems, and roots of plants were separated and oven-dried at 70°C for 7 d, after which the dry biomasses were measured.

Statistical analysis

A complete randomized block design was used with twelve replications. The data set was subjected to analyses of variance (ANOVA) and correlation analysis using SAS software package 9.1 (SAS Institute, 2003). Comparison among treatments was performed using Tukey's multiple range tests at the 0.05 probability level. A time-repeated measurements analysis (repeated ANOVA) was used to determine the influences of soil water content, fertilizer, and their interaction on measured parameters throughout the observation period with the PROC MIXED procedure (Klaus and Oscar, 2008).

Conclusion

In general, high fertilizer rate had negative effects on photosynthetic parameters under low soil moisture (55% FC), irregular effects under moderate soil moisture (75% FC), and positive effects under high soil moisture (95% FC). Throughout the fruit growing season, soil moisture had a greater influence on fruit yield, plant biomass, and root/shoot ratio than did fertilizer rates. In addition, there was a quadratic correlation between P_N and fruit yield. This indicated that improvement of leaf photosynthesis would be possible in a suitable range for improving fruit yield potential, but the sustainability of leaf photosynthesis had little value for increasing fruit yield in tomato plants.

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