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Effects of chilling and high temperatures on photosynthesis and chlorophyll fluorescence in leaves of watermelon seedlings

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Abstract

The effects of chilling (CT, day/night temperatures of 12/10 °C, an irradiance of 250 μmol m^{-2} s^{-1}), chilling combined with a low irradiance (CL, 12/10 °C, 80 μmol m^{-2} s^{-1}), and a high temperature (HT, 42/40 °C, 250 μmol m^{-2} s^{-1}) on chlorophyll content, chlorophyll fluorescence, and gas exchange were studied in two watermelon cultivars, ZJ8424 and YS01, differing in their resistance. The chlorophyll content, net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) decreased substantially, whereas the intercellular CO_2 concentration (c_i) increased when the two watermelon cultivars were grown under these stresses. The photosynthetic parameters showed greater changes at chilling than at the high temperature, and the CL caused a more pronounced inhibition in P_N compared with the CT. After 2 d exposure to the CT, YS01 had higher P_N, g_s, and E, but a lower c_i compared with ZJ8424. The maximum efficiency of photosystem (PS) II photochemistry (F_v/F_m), effective quantum yield of PS II photochemistry (Φ_{PSII}), photochemical quenching (qP), and electron transport rate (ETR) decreased under the CT and CL but showed only a slight drop under the HT. All these stresses significantly increased non-photochemical quenching (NPQ). The CT brought more damage to the photosynthetic apparatus of leaves compared with the CL. In addition, after returning to normal conditions (25/15 °C, 250 μmol m^{-2} s^{-1}) for 3 d, the photosynthetic parameters recovered to pre-stress levels in HT treated seedlings but not in CT treated seedlings. In conclusion, the low irradiance could help to alleviate the extent of photoinhibition of PS II photochemistry caused by chilling and cv. ZJ8424 was more sensitive to the extreme temperatures than cv. YS01.

Additional key words: chlorophyll content, *Citrullus lanatus*, irradiance, stomatal conductance, transpiration rate.

Introduction

Temperature and radiation are two important factors that affect plant growth and photosynthesis (Taylor and Rowley 1971, Greer *et al.* 1986). In natural environments, low or high temperatures usually have damaging impacts on plant photosynthesis (Berry and Björkman 1980, Zinn *et al.* 2010). They significantly reduce the photosynthetic efficiency, CO_2 assimilation, and activity of photosystem (PS) II (Murata *et al.* 2007, Ruelland and Zachowski 2010). At high temperatures, photochemical reactions in thylakoid membranes and carbon metabolism in the stroma of chloroplasts have been reported to be the primary sites of an injury (Yamori *et al.* 2008). However, low temperatures can disrupt essentially all major components of photosynthesis including thylakoid electron transport, carbon reduction cycle, and control of stomatal conductance (Allen and Ort 2001), thus photoinhibition usually happens when plants are exposed to low temperatures (Du *et al.* 1999). The negative effect

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Abbreviations: c_i - intercellular CO_2 concentration; CL - chilling at low irradiance; CT - chilling at normal irradiance; E - transpiration rate; ETR - electron transport rate; F_0 - minimal fluorescence; F_v/F_m - maximum efficiency of PS II photochemistry; g_s - stomatal conductance; HT - high temperature; NPQ - non-photochemical quenching; PS - photosystem; qP - photochemical quenching; P_N - net photosynthetic rate; SE - standard error; Φ_{PSII} - effective quantum yield of PS II photochemistry.

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of low temperature on photochemical efficiency is more pronounced when combined with a high irradiance (Groom *et al.* 1992, Oquist *et al.* 1993). Excess of radiation is one of the most common sources of oxidative stress in plants, and exposure of photosynthetic organisms to a strong radiation usually causes an imbalance between energy supply and energy consumption, which generally leads to the photoinhibition (Demmig-Adams and Adams 1992, Dat *et al.* 2000). In addition, a strong radiation has an inhibitory effect on repair due to production of reactive oxygen species. Photosynthetic organisms are often exposed to abiotic stresses which lead to photoinhibition (Huner *et al.* 1998). However, plans can reduce energy transfer efficiency to PS II either by diverting energy from PS II to PS I through state transitions or by dissipating excess energy as heat by non-photochemical quenching (NPQ). The extent of photoinhibition depends on the balance between photodamage to PS II and the repair of such a damage (Aro *et al.* 1993).

Watermelon (*Citrullus lanatus*) is an important crop belonging to the family of *Cucurbitaceae* and native to southern Africa. It has become one of the most important economic crops in China but its germination and seedling growth suffers from abiotic stresses (Yan *et al.* 2013). Up to now, only a few reports have shown negative impacts of a low or high temperature on photosynthesis and chlorophyll fluorescence in watermelon seedlings (Wang *et al.* 2010, Hou *et al.* 2014). The aim of this research was to investigate the interacting effect of extreme temperatures and radiation on the watermelon seedlings. For this purpose, the chlorophyll content, photosynthetic gas exchange, and chlorophyll fluorescence were measured.

Materials and methods

The seeds of watermelon (*Citrullus lanatus* Matsum. & Nakai cvs. ZJ8424 and YS01) were obtained from the Chinese Academy of Tropical Agriculture Sciences, Dan Zhou, China in 2014. The seeds were germinated on filter paper in Petri dishes containing distilled water in the dark and at a temperature of 25 °C for 3 d and then planted in plastic pots (one seedling per pot) containing rice chaff and grown in a greenhouse at a 12-h photoperiod, day/night temperatures of 28/20 °C, a photosynthetic photon flux density (PPFD) of 310 µmol m^{-2} s^{-1}, and a relative humidity of 68 % for about 13 d. The seedlings reaching the stage of three fully expanded leaves were subjected to chilling or high temperature stresses. They were placed in a growth chamber at 12/10 °C + a PPFD of 250 µmol m^{-2} s^{-1} as chilling temperature stress (CT), 12/10 °C + a PPFD of 80 µmol m^{-2} s^{-1} as chilling temperature combined with low irradiance (CL), or 42/40 °C + a PPFD of 250 µmol m^{-2} s^{-1} as high temperature stress (HT). The control seedlings grew at 25/15 °C + a PPFD of 250 µmol m^{-2} s^{-1}. After 2 d of the treatments, all the seedlings were returned to normal growth conditions at 25/15 °C + a PPFD of 250 µmol m^{-2} s^{-1} for 3 d. The 12-h photoperiod was maintained and a relative humidity of 70 %. Acclimation periods of 8 h at 15/12 °C and 10 h at 32/30 °C were allowed before imposition of chilling and high temperature treatments, respectively. The second fully expanded leaves were used for the measurements, and all experiments were repeated at least three times.

A portable chlorophyll meter (*SPAD-502*, *Minolta*, Osaka, Japan) was used to measure greenness or a relative chlorophyll content. The measurements were performed on five parts of the middle section of leaves of three randomly selected plants per each treatment.

Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (c_i), and transpiration rate (E) of intact leaves were measured with a portable photosynthesis system (*Li-6400*, *Li-COR*, Lincoln, USA) at a temperature of 25 °C, a PPFD of 800 µmol m^{-2} s^{-1}, a relative humidity of 70 - 75 %, and a CO_2 concentration ranging from 380 to 390 µmol mol^{-1}. The measurements were carried out at 09:00 - 11:00 to avoid a midday depression of photosynthesis and respective changes in stomatal conductance.

Chlorophyll fluorescence parameters were measured with a *PAM-2500* portable fluorometer (*Walz*, Effeltrich, Germany) connected to a computer with the data acquisition software *Pam-Win3* after dark adaptation of leaves at room temperature of 25 °C for 20 min. Then, the seedlings were exposed to a sufficiently low irradiance for the measurement of the minimal fluorescence (F_0). The maximum fluorescence (F_m) was measured after a saturation pulse (SP, 3 000 µmol m^{-2} s^{-1}) and the maximal quantum yield $F_v/F_m = (F_m-F_0)/F_m$ was calculated (Krause and Weis 1991). After a time delay of 40 s, actinic irradiance was turned on and superimposed with an SP, followed by repetitive SPs at every 20 s for 5 min. The effective quantum yield of PS II photochemistry (Φ_{PSII}), photochemical quenching (qP), electron transport rate (ETR), and nonphotochemical quenching (NPQ) were determined by the last SP given when a steady-state chlorophyll fluorescence was reached after 5 min of the actinic irradiance (Genty *et al.* 1989).

All figures were drawn by the origin data analysis and graphing software *OriginPro 8.6* (*OriginLab Corporation*, Massachusetts, USA). All the measurements were performed for three times, and means and stand errors (SEs) are reported.

Results

The relative chlorophyll content (the SPAD value) was measured on the second leaves of the watermelon seedlings in this experiment (Fig. 1). After 2 d of the chilling temperature, the chlorophyll content decreased by 10.3 and 11.6 % in YS01 under the CT and CL, respectively. However, the HT had a weak effect on chlorophyll content and showed only a slight decrease of 5.4 %. In contrast, the chlorophyll content in leaves of ZJ8424 decreased by 17.3 and 23.1 % after exposure to the CT and CL, respectively. Therefore, a difference was found in chlorophyll content between the YS01 and ZJ8424 cultivars under the temperature stress. After returning the seedlings to the normal growth conditions, the chlorophyll content in the two cultivars exposed to the HT were almost fully restored 3 d after recovery, but it did not fully recover in the seedlings exposed to the CT. The cultivar YS01 showed a better recovery than ZJ8424.

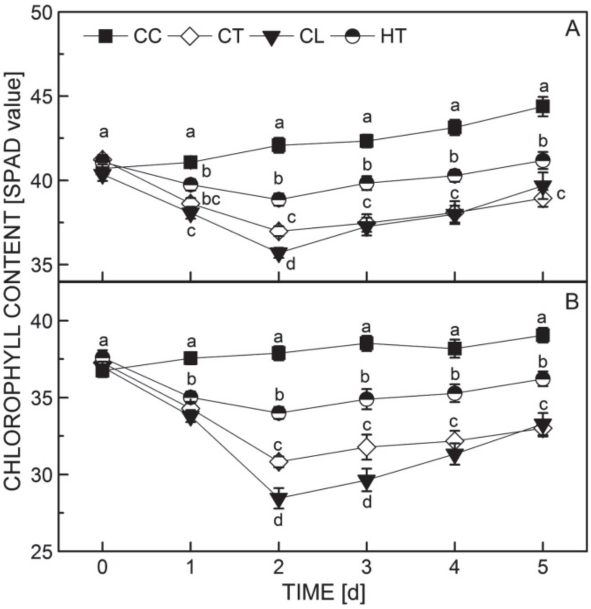

Fig. 1. Effects of high temperature (HT), chilling temperature (CT), and chilling temperature combined with low irradiance (CL) on chlorophyll content in leaves of YS01 (*A*) and ZJ8424 (*B*). CC - control. Time 0 d indicates data obtained before the stresses; 1 and 2 d indicate seedlings for 1 and 2 d at the respective stress; 3, 4, and 5 d indicate seedlings after 1, 2, and 3 d of recovery. Means ± SEs, $n = 3$. Different letters indicate significant differences ($P \leq 0.05$) among the various treatments in the same period.

The high and especially chilling temperatures clearly reduced P_N, g_s, and E, whereas increased ci, although the effect was more pronounced in the latter. After 2 d, P_N in leaves of YS01 exposed to the CT, CL, and HT decreased by 50.8, 62.2, and 21.7 %, respectively. However, P_N in leaves of ZJ8424 under the same treatments decreased by 70.2, 81.1, and 31.5 %, respectively. When the seedlings were returned to the normal growth conditions, P_N rapidly recovered to the untreated levels after the HT in both the cultivars but slowly recovered after the CT and CL. Net photosynthetic rate in YS01 had higher recovery ratios compared with ZJ8424.

The cultivar ZJ8424 showed greater declines in P_N, g_s, and E after 2 d of the CT, CL, and HT and a lesser recovery after 3 d compared to YS01 indicating that ZJ8424 was more sensitive to the temperature stress than YS01. In addition, the high temperature had relatively weak effects on photosynthesis of the watermelon seedlings compared to the chilling temperature.

Under the normal growth conditions, the chlorophyll fluorescence parameters were constant for 6 d. However, the CT, CL, or HT significantly reduced F_v/F_m in both the cultivars. For example, F_v/F_m in the leaves of YS01 under the CT, CL, and HT decreased by 5.7, 3.6, and 2.3 %, respectively (Fig. 3). The CT and CL caused a lower F_v/F_m compared with the HT, whereas F_v/F_m was higher under the CL than CT. In the leaves of YS01, F_v/F_m was higher compared with ZJ8424 under these stresses. Also Φ_{PSII}, qP, and ETR were reduced by the HT and especially by the CT and CL. The cultivar YS01 showed a relatively higher Φ_{PSII}, qP, and ETR compared with ZJ8424 indicating that ZJ8424 was more sensitive to the temperature stress compared with YS01. The temperature stress gradually increased NPQ with a peak on the second day of the treatment. When the seedlings were moved to the normal growth conditions, the fluorescence parameters recovered fully within 3 d after the HT, but recovered partially after CT and CL. In addition, YS01 showed higher recovery ratios than ZJ8424, which could reflect the different tolerance of the two cultivars.

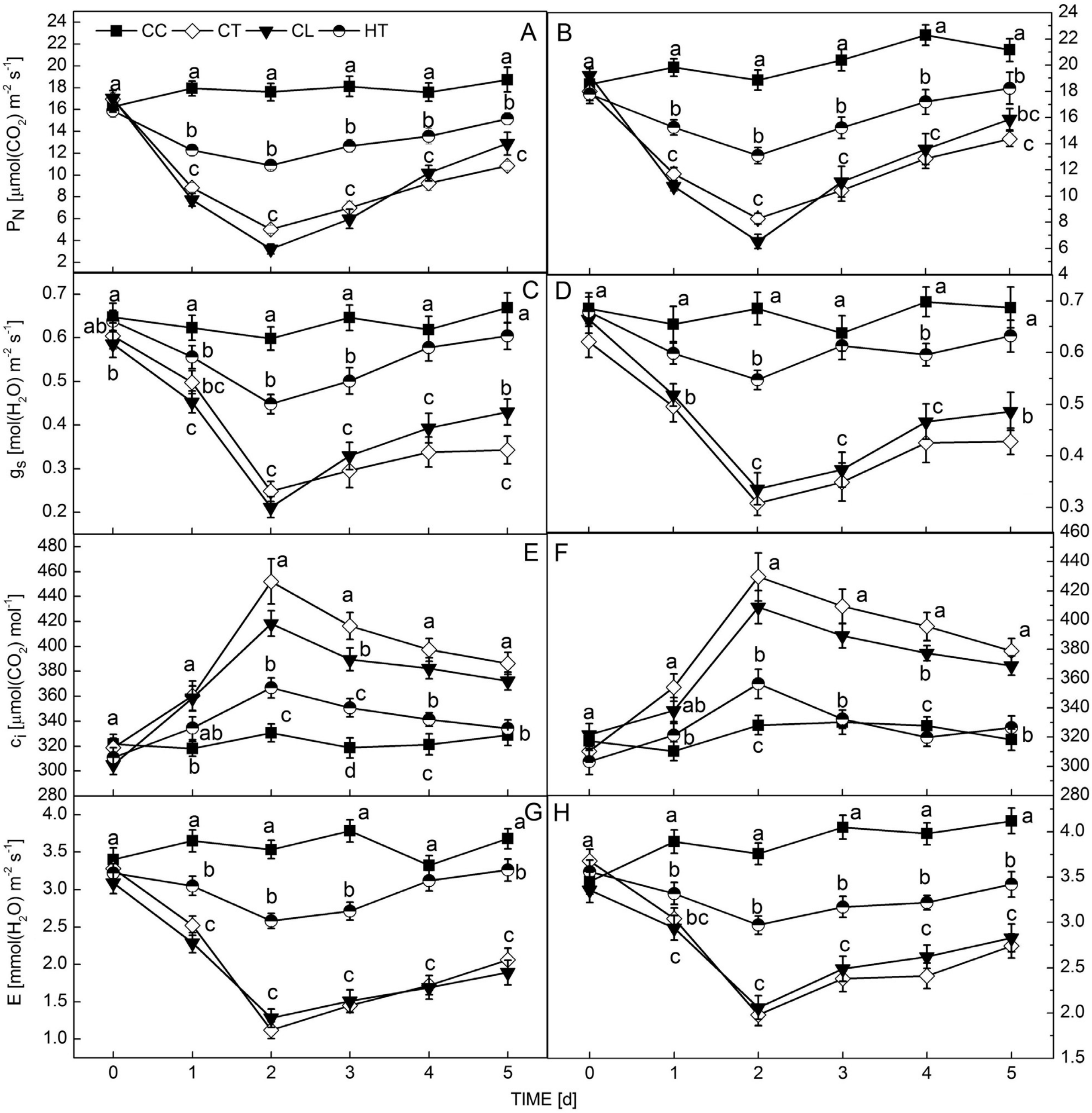

Fig. 2. Effects of high temperature (HT), chilling temperature (CT), and chilling temperature combined with low irradiance (CL) on net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (c_i), and transpiration rate (E) in leaves of ZJ8424 (*A*, *C*, *E*, *G*) and YS01 (*B*, *D*, *F*, *H*). For other details, see Fig. 1. Means ± SEs, *n* = 3. Different letters indicate significant differences ($P \leq 0.05$) among various treatments in the same period.

Discussion

Chlorophyll content provides valuable information about physiological status of plants, and can directly determine photosynthetic potential and primary production (Filella *et al.* 1995, Gitelson and Merzlyak 2003). It has been reported that chlorophyll content (the SPAD value) decreases when plants are subjected to low or high temperatures (Kudoh *et al.* 2002, Djanaguiraman *et al.* 2010, 2011). In our experiments, the chilling temperature brought a significant decrease in chlorophyll content, whereas the HT caused a slight decrease in chlorophyll content, which was in accordance with other scientists (Kudoh *et al.* 2002, Djanaguiraman *et al.* 2010, 2011).

Moreover, a difference in the change of chlorophyll content was found between the two cultivars, with ZJ8424 having a higher decline in chlorophyll content than YS01 under the CT, CL, or HT. These results indicate that the reduction of chlorophyll content in the two watermelon cultivars could be a typical symptom under environment stress. It has been reported that the reduction of chlorophyll content in plants due to increased activity of the chloroplast degrading enzyme, induced changes in ultrastructure of chloroplasts, and the chloroplasts could gradually lose its capacity to capture radiation energy (Kratsch and Wise 2000, Kudoh and Sonoike 2002).

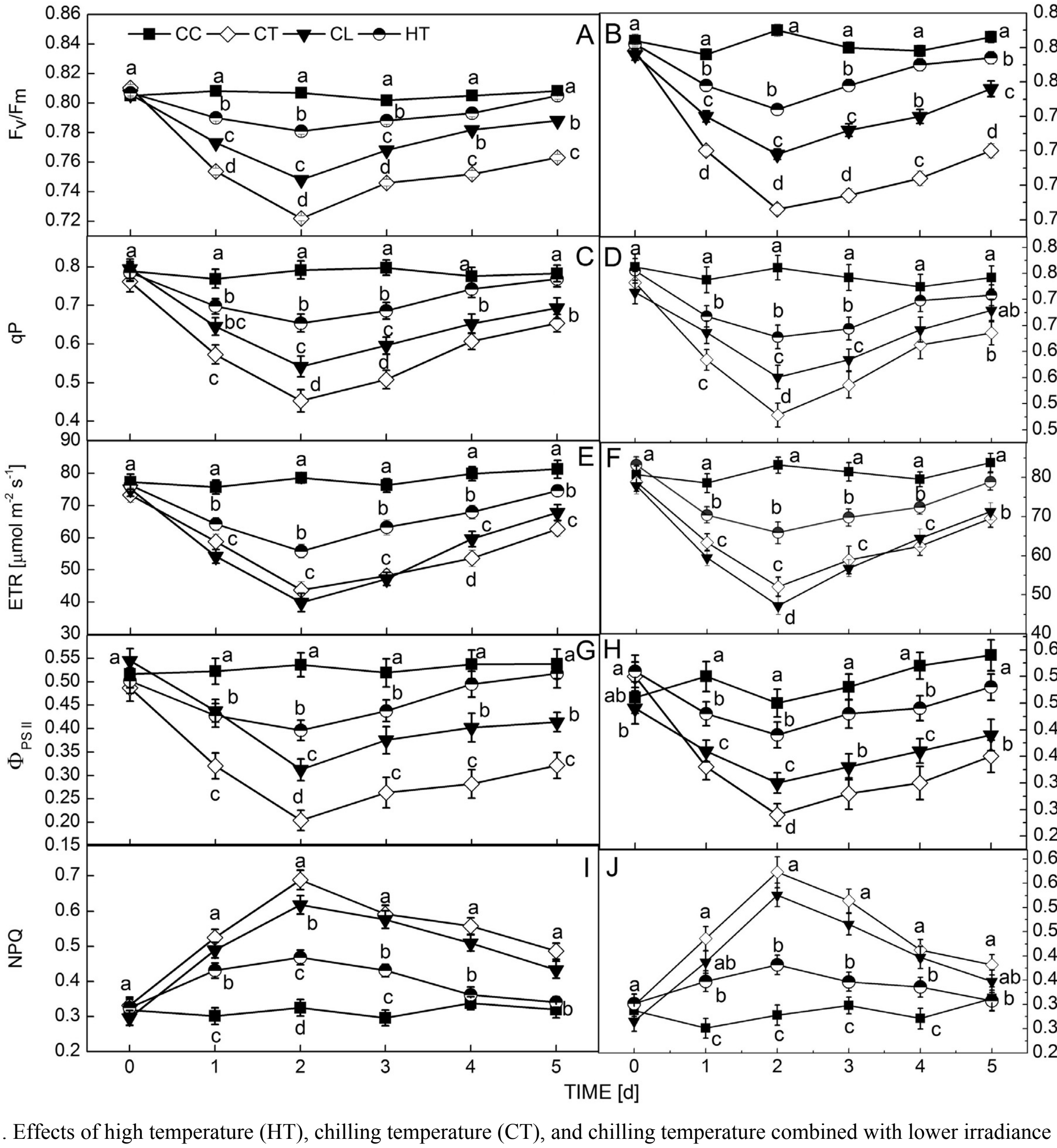

Fig. 3. Effects of high temperature (HT), chilling temperature (CT), and chilling temperature combined with lower irradiance (CL) on maximal quantum yield of PS II photochemistry (F_v/F_m), photochemical quenching (qP), electron transport rate (ETR), effective quantum yield of PS II photochemistry (Φ_{PSII}), and non-photochemical quenching (NPQ) in leaves of ZJ8424 (*A*, *C*, *E*, *G*, *I*) and YS01 (*B*, *D*, *F*, *H*, *J*). For other details see Fig. 1. Means ± SEs, $n = 3$. Different letters indicate significant differences ($P \leq 0.05$) among various treatments in the same period.

Plants grown under temperature stress usually show a decrease in photosynthesis due to stomatal closure, chloroplast impairment, or limitation of the carbon assimilation (Martin *et al.* 1981, Groom and Baker 1992, Pastenes and Horton 1996, Sonoike 1998, Wise and Olson 2004). In this study, the HT and especially CT and

CL caused decrease in P_N, g_s, and E, whereas the c_i value increased after 2 d of the stress treatments. These results indicate that chilling and the high temperature caused the reduction of P_N and this reduction was not determined only by the lower stomatal conductance because c_i was high under low g_s (Ploschuk *et al.* 2014). Moreover, photosynthetic parameters more likely exhibited greater changes in ZJ8424 than in YS01 under environmental stresses. Net photosynthetic rate in ZJ8424 had lower recovery ratios compared with YS01 indicating that ZJ8424 was more sensitive to the temperature stress than YS01.

It is clear that photoinhibition usually happens when plants are exposed to low or high temperatures. Short-term chilling temperatures can result in photoinhibition, and lead to inhibition of photosynthetic rate and electron transport (Powles *et al.* 1984). A high temperature affects photosynthetic functions of plants by its effect on the rate of CO_2 fixation, photophosphorylation, electron transport, and oxygen evolution (Sharkey *et al.* 2005, Allakhverdiev *et al.* 2008). Our results reveal that F_v/F_m under the CT was lower compared with the CL. It suggests that photoinhibition of photosynthesis in the seedlings occurred due to chilling under irradiance. However, the low irradiance might alleviate photochemical damage caused by chilling. The ratio F_v/F_m under the HT showed a slight decrease but recovered to 0.79 and 0.81 in ZJ8424 and YS01, respectively, indicating that this HT treatment did not cause a severe damage to the primary photochemical reactions in the photosynthetic apparatus. Also Φ_{PSII}, qP, and ETR decreased more under the CT and CL than under the HT. In contrast, NPQ increased with these treatments suggesting the heat dissipation in response to the chilling or high temperature stresses. It is well known that the quantum yield of electron transfer at PS II (Φ_{PSII}) is the product of the efficiency of the open PS II reaction centres and the photochemical quenching factor (qP; Genty *et al.* 1989).Therefore, the decrease of P_N and Φ_{PSII} under temperature stress is primarily due to the decrease in qP. This indicates that electron transport was inhibited under the temperatures stress, since qP is a proxy for the redox state of Q_A (the primary electron acceptor in PS II).

In this study, photoinhibition happened when the watermelon seedlings were exposed to the CT, whereas the HT did not cause any severe inhibition of photosynthesis. The CT caused a higher closure of reaction centres and a higher ETR compared with the CL. The cultivar YS01 exhibited a stronger tolerance against photoinhibition compared to ZJ8424; when the two watermelon cultivars returned to the normal conditions, they had the capacity for recovering from both the stresses. The fast phase of recovery is attributed to conformational changes in PS II and to regulatory mechanisms, whereas the slow phase of recovery is related to re-synthesis of photodamaged components of PS II and pigment-protein complexes (Matta and Maestri 1998).

In conclusion, the results suggest that the chilling temperature caused a more severe photoinhibition of photosynthesis compared with the high temperature in the watermelon seedlings. The low irradiance could help to alleviate the extent of photoinhibition of PS II photochemistry caused by the chilling temperature. In addition, cv. ZJ8424 was more sensitive to the extreme temperatures than cv. YS01.

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