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Effect of Rapid Dehydration on Photosynthetic and Fluorescent Properties of Cucumber Leaves Detached from Low Light Treated Seedlings

W. Li[1,2)], X.L. Sui[1)], L.H. Gao[1)], H.Z. Ren[1)] and Z.X. Zhang[1)]
([1)]College of Agronomy and Biotechnology, China Agricultural University, Beijing, China and [2)]College of Agronomy, Guizhou University, Guiyang, China)

Summary

Two cucumber (*Cucumis sativus* L.) cultivars, including the shade-susceptible cv. 'Jingyan 2' and shade-tolerant cv. 'Deltastar', were compared for the changes in gas exchange and chlorophyll a fluorescent parameters during rapid dehydration of mature leaves detached from seedlings grown for 20 days under low light (PFD: 75–85 μmol m^{-2} s^{-1}). During the continuous water loss process after separation from plants, leaf net photosynthesis rate (Pn), transpiration rate (Tr), efficiency of excitation energy captured by open photosystem II (PSII) reaction centre (Fv′/Fm′), quantum efficiency of PSII photochemistry (ΦPSII) and partitioning proportion for photochemical reaction of light energy absorbed by PSII (P) gradually decreased, the antennae heat dissipation (D) and reaction centres dissipation of light energy absorbed by PSII (Ex) gradually increased, and the maximal photochemical efficiency of PSII (Fv/Fm) remained largely stable. The declining of the photosynthetic parameters was faster and lasted shorter period than the fluorescent parameters. The impact of dehydration was much more severe in the control plants grown under normal light intensity, which indicates that plants grown under low light had improved tolerance to subsequent water deficient stress. Between the two cultivars both exposed to low light, cv. 'Deltastar' was able to maintain more stable chl fluorescence, photosynthetic parameters and the critical water content during rapid dehydration process. These characteristics may account for the better tolerance to shade and drought condition of 'Deltastar' compared to 'Jingyan 2'.

Key words. *Cucumis sativus* – 1ow light – relative leaf water content – gas exchange parameters – chlorophyll a fluorescence – photosynthetic critical water content

Introduction

Low light is a major limiting factor for greenhouse cucumber production in the spring season. Insufficient light intensity reduces photosynthetic activities, and affects plant growth and development. Crop production also depends on appropriate water supply; drought stress causes reduction in net photosynthesis (Pn), apparent quantum yield (AQY), transpiration (Tr), photosynthetic saturation light intensity, and CO_2 saturation point. Concurrently, light and CO_2 compensation points become higher (Zhu et al. 2005; Ke and Yang 2007).

The reduction of the fluorescent light parameters (such as Fo, Fm, Fv, and Fv/Fm) suggests that photochemical conversion of harvested light energy in the PSII system is inhibited by drought stress. The lower $T_{1/2}$ and PQ value represents a decline of photosynthetic potential activity in PSII (Fv/Fo). In plant leaves, inhibition of photosynthetic electron transmission and photosynthetic phosphorylation can directly cause damages to the light emission complexes, such as the PSII oxygen-evolving complex, PSII light-harvesting pigment-protein complex, which eventually affects photosynthetic activities (Lu et al. 1993, 1999).

Desiccation stress activates production of reactive oxygen species (ROS). The subsequent physiological responses include marked concentration of malondialchehyche (MDA) due to membrane lipid peroxidation, reduced membrane lipid fluidity with lower unsaturated fatty acid content, and structural deformation of chloroplast and mitochondria in the mesophyll cells (Li et al. 2005). Leaves experience natural water loss after being separated from plants, meanwhile, their chlorophyll fluorescent parameter qN increases, and the xanthophyll cycle is activated to dissipate excessive light energy in order to alleviate or avoid damage to the photosynthetic apparatus (Feng et al. 2002).

Those plant responses are incurred when they are exposed to either water or light stress. No relevant studies have been conducted to understand the combined impact of water and low light stresses on photosynthesis, such as the physiological response of leaves grown under low light conditions to the ensuing dehydration condition. In this research, cucumber seedlings were treated with low

light first, the leaves were then exposed to rapid water loss stress by detaching from plants. The relationship between water status and photosynthesis was established by comparing the corresponding changes in photosynthetic and fluorescent parameters in two cultivars with different levels of shade tolerance. Integration of such information in the water management strategy will improve cucumber production in the solar greenhouse where low light is a major stress factor.

Materials and Methods

Plant material

Cucumis sativus L. cv. 'Jingyan 2' is a field-grown shade-susceptible cultivar. The shade tolerant greenhouse cv. 'Deltastar' was bred by Rijk Zwaan, Netherland. Seeds of the two cultivars were provided by Dr Wang Yongjian at Beijing Vegetable Research Center, Beijing, China.

Experimental design

The experiment was conducted in the solar-greenhouse and phytotron at the Scientific Park of China Agricultural University. Seeds were sown individually into plastic pot (12×12 cm) containing a mixture of garden soil, vermiculite and peat moss (1: 2: 7, v/v/v). The seedlings were started in the solar greenhouses which were managed following routine practice. When the first two true leaves were fully expanded and the shoot began to elongate, the healthy and uniform seedlings were transferred into the artificial greenhouse. Low light stress was applied by shading the greenhouse to a light intensity of 75–85 μmol m^{-2} s^{-1} PFD, while the control area was provided with 500–600 μmol m^{-2} s^{-1} PFD. A 9/15-h light-dark cycle at 25/18 °C (d/n) temperature was maintained during the treatment period. After 20 d, measurements were taken utilizing the newly developed mature green leaves.

Measurement of leaf gas exchange parameters

In the artificial greenhouse, the plants were irradiated to induce photosynthesis. After 2 h, 3 leaves of similar size at identical shoot positions were selected from four plants from the treated and control of both cultivars. Leaf blades were dissected at the petiole/leaf blade junction and immediately placed into the leaf chamber of a Li-6400 portable photosynthesis system (Li-COR, USA).The PFD was set at 500 μmol m^{-2} s^{-1} for control and 100 μmol m^{-2} s^{-1} for shade-treated. The CO_2 concentration was 400±1 μmol m^{-2} s^{-1}, and temperature was 25±1 °C. Readings of gas exchange parameters was monitored continuously, including Pn, stomatal conductance (Gs), intercellular CO_2 mole fraction (Ci) and Tr. The following equations were used for the calculations: stomatal conductance: Ls = 1−Ci/Co, where Co is air CO_2 concentration; Water usage efficiency: WUE = Pn/Tr.

A single measurement was taken every 5 min, and the leaf tissues were immediately weighed on a balance (0.1 mg accuracy) to measure fresh weight (FW). The same procedure was repeated until Pn dropped to near zero. Next, the leaf blades were rehydrated to saturation by soaking in ddH_2O for 8 h in order to obtain the water saturated FW. Dry weight (DW) was determined by snap-killing the leaf tissues in an oven at 105 °C for 30 min followed by drying at 80 °C for about 30 h until constant weight.

The relative leaf water content (RLWC) was calculated for each time point when the photosynthetic parameters were measured using the equation: RLWC = (leaf fresh weight−leaf dry weight)/(leaf water saturated fresh weight−leaf dry weight)×100 %. A curve of RLWC versus each parameter was plotted in order to identify the correlation between leaf photosynthesis and RLWC.

Determination of leaf chlorophyll a fluorescent parameters

The experimental design and sample preparation of leaf chlorophyll a fluorescent parameters followed the same procedure described above in measurement of leaf gas exchange parameters. Prior to measurements, leaf blades were dark adapted in the PAM-2100 (Walz, Germany) leaf disk chamber for 20 min before dissected. First, the Run 2 program was started to measure the minimal and maximal chlorophyll fluorescence yields (Fo and Fm, respectively). The Run 1 program (plus the Fo′ function) was subsequently initiated to measure the maximum fluorescence (Fm′), initial fluorescence (Fo′), and stable fluorescence yield (Fs) in light adapted state.

The following equations were used for calculation of the relevant parameters: the optimum quantum yield of open PSII reaction centres (Fv′/Fm′) = (Fm′−Fo′)/Fm′; potential photochemical efficiency (Fv/Fo) = (Fm−Fo)/Fo; The maximum quantum efficiency of PSII (Fv/Fm) = (Fm−Fo)/Fm; The actual photochemical efficiency of PSII reaction centres in light (ΦPSII) = (Fm′−Fs)/Fm′; photochemical reaction rate (Prate) = (Fm′−Fs)/Fm′×PPFD; photosynthetic non-cyclic electron transport rate (J) = (Fm′−Fs)/Fm′×PPFD×f×α_{leaf}, where f is the excitation-energy distribution index, a value of 0.5 is normally used for C_3 plants, α_{leaf} is the light energy absorption coefficient of leaves, it is normally at 0.84; PSII partitioning of absorbed light energy for photochemical reaction (P) = Fv′/Fm′×qP, where photochemical quenching coefficient (qP) = (Fm′−Fs)/(Fm′−Fo′); PSII partitioning of absorbed light energy between antenna heat dissipation and photochemical reaction (D) = 1−Fv′/Fm′; PSII partitioning of absorbed light energy for P680 reaction center energy dissipation (Ex) = Fv′/Fm′×(1−qP) (Demmig-Adams and Adams 1996; Li et al. 2003).

For each leaf blade, both halves were monitored each for a 5-min period by alternatively placing the leaf clip at the same position across the main vein. Immediately after each measurement of fluorescent parameters, the FW of the tissues was taken on a balance (at 0.1 mg accuracy). The same procedure was repeated for each leaf until ΦPS II dropped to near 0. The saturated FW and DW of four individual leaves from each treated/control were measured, and the average of the corresponding RLWC was plotted against each fluorescent parameters.

Results

Dehydration-induced changes in photosynthetic parameters of the detached cucumber leaves after treated with low light

After separated from the seedlings, RLWC dropped slowly for leaves grown under both low light and control condi-

tions. During the continuous dehydration process, Pn and Gs rapidly declined, Ci fluctuated up and then down, and Ls decreased initially followed by a rapid rise (Fig. 1a–d). Compared to control (Fig. 1a, c), low light treated leaves (Fig. 1b, d) had lower Pn and Gs shortly after detachment from the plants, and both parameters declined more slightly and smoothly. The corresponding RLWC level when Pn dropped to 0 depends on both the genetic traits and the light conditions. For low light treated seedlings, the Pn of 'Jingyan 2' dropped to near 0 at 67 % RLWC (Fig. 1b), but it maintained above 0 at <60 % RLWC in 'Deltastar' (Fig. 1d). When only the light condition was considered, Pn of 'Jingyan 2' dropped to near 0 at 67 % RLWC in low light treated tissues (Fig. 1b), and 77 % RLWC for the untreated leaves (Fig. 1a). Similar difference also appeared in 'Deltastar' (Fig. 1c, d).

Response of WUE, Tr and Rs to rapid dehydration in the detached cucumber leaves treated with low light

During the continued dehydration process, RLWC gradually dropped. Concurrently, Tr and WUE rapidly decreased, but Rs greatly increased (Fig. 2). Compared to the control (Fig. 2a, c), the low-light treated leaves started with lower Tr and WUE, and also experienced less dramatic changes in Tr, WUE and Rs during the dehydration process (Fig. 2b, d). The three parameters (Tr, WUE and Rs) (Fig. 2b) were > 0 at the lowest 67 % RLWC compared to 77 % RLWC in the untreated control plants. Both exposed to low-light condition (Fig. 2b, d), 'Deltastar' showed significantly higher tolerance to subsequent dehydration than 'Jingyan 2' (Fig. 2b). At 57 % RLWC, 'Deltastar' (Fig. 2d) maintained higher Tr level, which declined to near 0 in 'Jingyan 2' at 67 % RLWC (Fig. 2b).

Response of Fv/Fm, Fv/Fo and Fv′/Fm′ to dehydration in detached cucumber leaves after low light treatment

Changes in the chlorophyll fluorescent parameters during dehydration process were similar between the low light treated and the control leaves. In general, Fv/Fm remained similar, Fv/Fo decreased slightly, and Fv′/Fm′ declined significantly. Fv/Fm of 'Deltastar' (>0.8) was higher than 'Jingyan 2' (<0.8). The overall Fv/Fo was higher in 'Deltastar' than 'Jingyan 2', and different patterns were found in the two cultivars. During dehydration process, Fv/Fo increased initially to reach a small peak (4.50) followed by declining in 'Jingyan 2', while the peak was much less pronounced in 'Deltastar'.

In the low light treated leaves, the declining Fv′/Fm′ had different impact on Pn of the two cultivars. When Fv′/Fm′ was lowered to 0.2, Pn dropped to near 0 in 'Jingyan 2', but maintained above 0 in 'Deltastar'. The untreated control leaves had a much higher Fv′/Fm′ (0.35–0.55) than the low light treated tissues (0.1–0.25) when Pn was near 0 (Fig. 3, 1). In Conclusion, these results indicate that water loss of the detached leaves had no significant impact on maximum photochemical efficiency of PSII reaction centre, but, it could cause significant reduction in the potential photochemical efficiency and capturing excit-

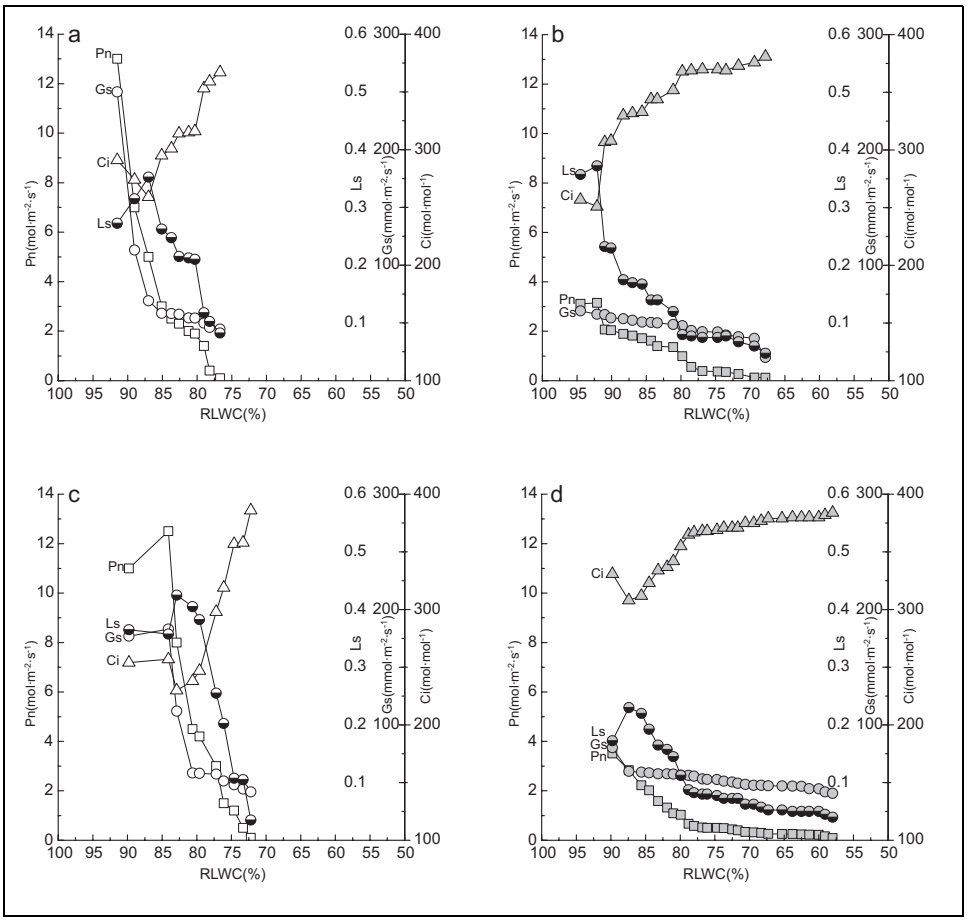


Fig. 1. Effect of relative leaf water content (RLWC) on photosynthetic characteristics in detached cucumber leaf after treated under low light. (a): 'Jingyan 2', control; (b): 'Jingyan 2', low light treated; (c): 'Deltastar', control; (d): 'Deltastar', low light treated.

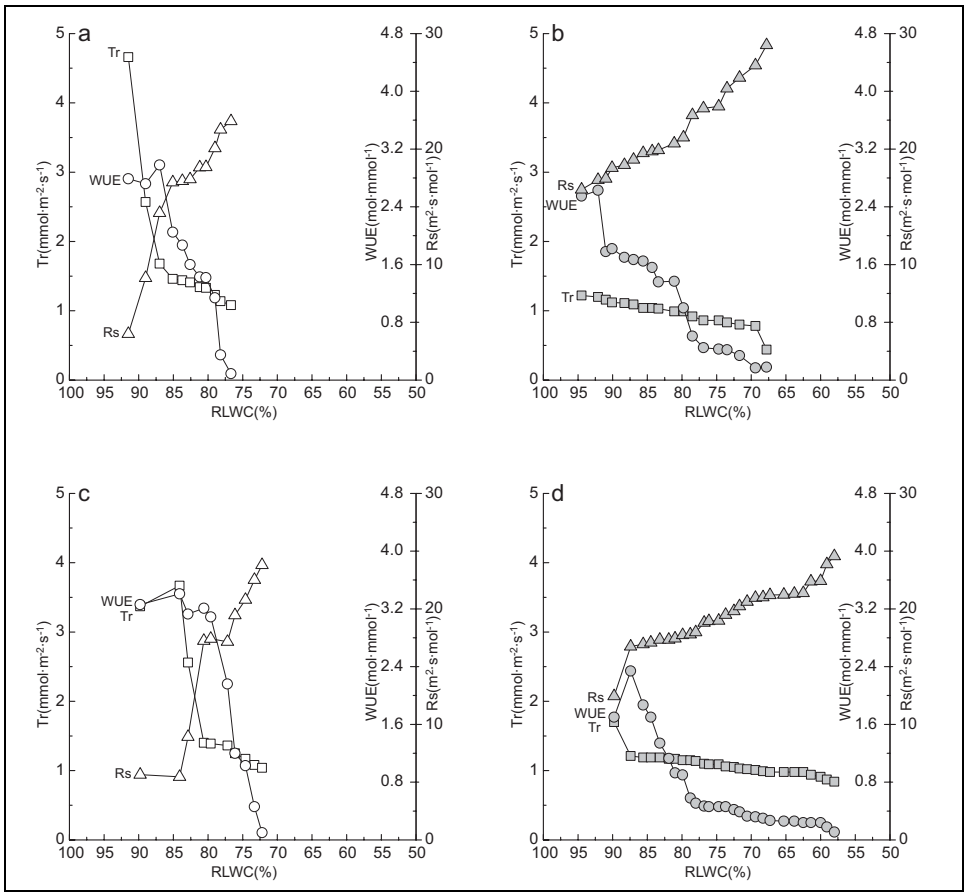


Fig. 2. Effect of relative leaf water content (RLWC) on water usage efficiency, transpiration rate and stomatal resistance in detached cucumber leaf after treated under low light. (a): 'Jingyan 2', control; (b): 'Jingyan 2', low light treated; (c): 'Deltastar', control; (d): 'Deltastar', low light treated.

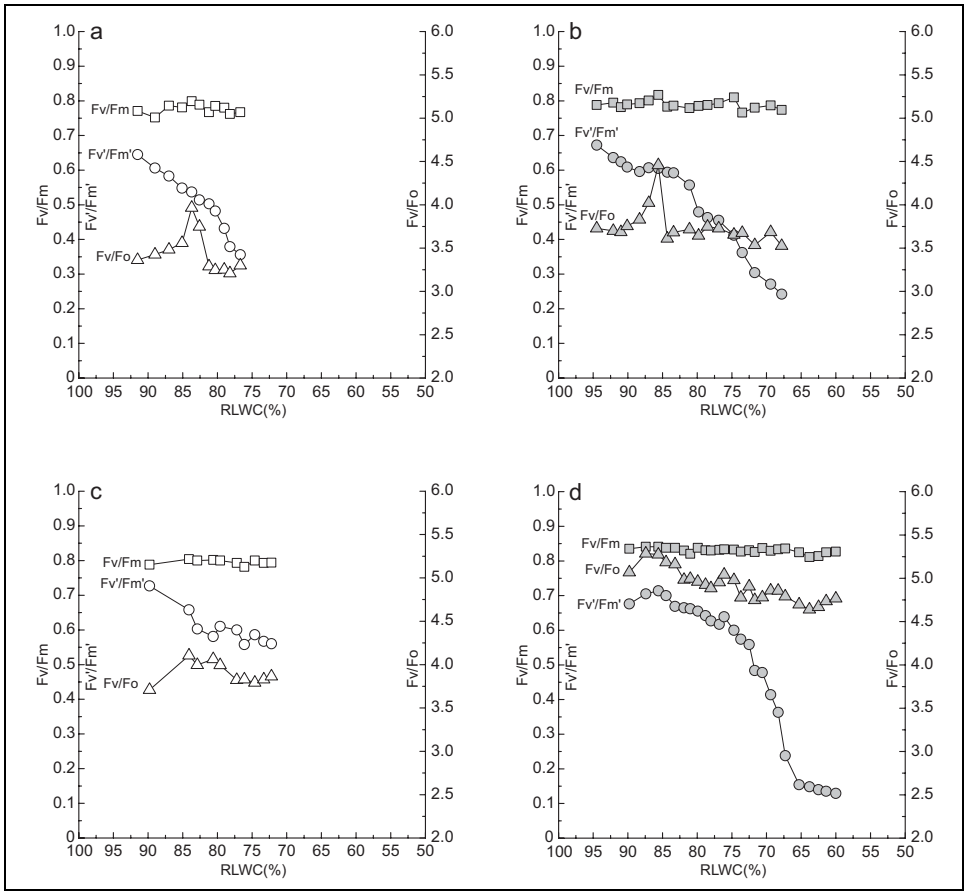


Fig. 3. Effect of relative leaf water content (RLWC) on Fv/Fm, Fv/Fo and Fv′/Fm′ in detached cucumber leaf after treated under low light. (a): 'Jingyan 2', control; (b): 'Jingyan 2', low light treated; (c): 'Deltastar', control; (d): 'Deltastar', low light treated.

ed energy efficiency of open reaction centre. Such effect became more serious at later stage of dehydration, and tolerance of photosynthetic capacity to dehydration and low light stresses varied between the two cucumber cultivars.

Changes in ΦPSII, Prate and J in detached cucumber leaves after low light treatment

During the dehydration process of the detached leaves, ΦPSII, Prate and J all decreased as RLWC declined (Fig. 4). Compared to the control, ΦPSII was lower and declined more rapidly, and Prate and J were also lower, but decreased more smoothly in the low light treated leaves. The two cultivars differed in the dehydration-induced changes of ΦPSII, Prate and J. In the low light treated leaves, the ΦPSII value was <0.3 for 'Jingyan 2', but it was <0.2 for 'Deltastar' when Pn was near 0. Such inter-cultivar difference was minimal for the leaves grown under control light condition although their Prate, J and ΦPSII also decreased during dehydration process. These results suggest that tolerance to low light of the photochemical reactions in the detached leaves was somehow enhanced by dehydration, and 'Deltastar' performed better than 'Jingyan 2'.

Response of P, D and Ex to dehydration of detached cucumber leaves after low light treatment

As RLWC decreased during the dehydration process, P reduced gradually, but D and Ex tended to increase, especially D value became significant higher (Fig. 5a–d). The magnitude of changes in P and D+Ex was much bigger in the low light treated leaves than the controls, suggesting that the low light had enhanced photo-inhibition because less energy could be used in photochemical reaction while more dissipated through the antenna and reaction centers. After exposure to low-light stress, the scale of decreasing P and increasing D+Ex was larger in 'Deltastar' than in 'Jingyan 2'. When Pn dropped to 0, 'Deltastar' had P at 25 %, and D+Ex at 75 %, both are higher than the corresponding values (P at 10 %, and D+Ex at 90 %) in 'Jingyan 2'. Under control condition, the P was 50 % and D+Ex 50 % for both cultivars when Pn dropped to near 0. This analysis indicates that the detached cucumber leaves treated by low light still maintained some photosynthetic activities under dehydration condition when very low ratio of the absorbed solar energy was converted into photochemical reactions. 'Jingyan 2' was more sensitive to water loss compared to 'Deltastar' after low-light treatment.

Response of RLWC to rapid water loss in detached cucumber leaves after low light treatment

The critical RLWC during rapid dehydration process from the low light treated leaves was 69.9 % for 'Jingyan 2' and 62.7 % for 'Deltastar', these values were significantly lower than their respective control of 78.3 and 72.8 % (Fig. 6). The difference between the two cultivars was also significant. 'Deltastar' had lower critical RLWC val-

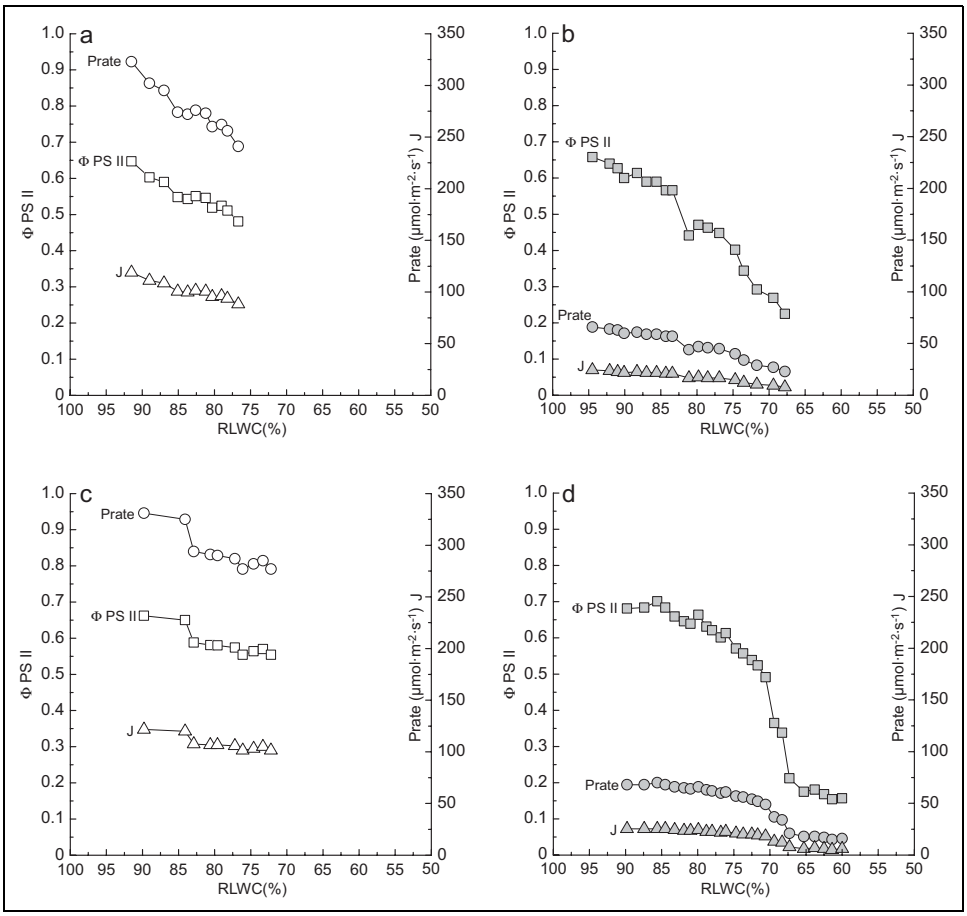


Fig. 4. Effect of relative leaf water content (RLWC) on ΦPSII, Prate and J in detached cucumber leaf after treated under low light. (a): 'Jingyan 2', control; (b): 'Jingyan 2', low light treated; (c): 'Deltastar', control; (d): 'Deltastar', low light treated.

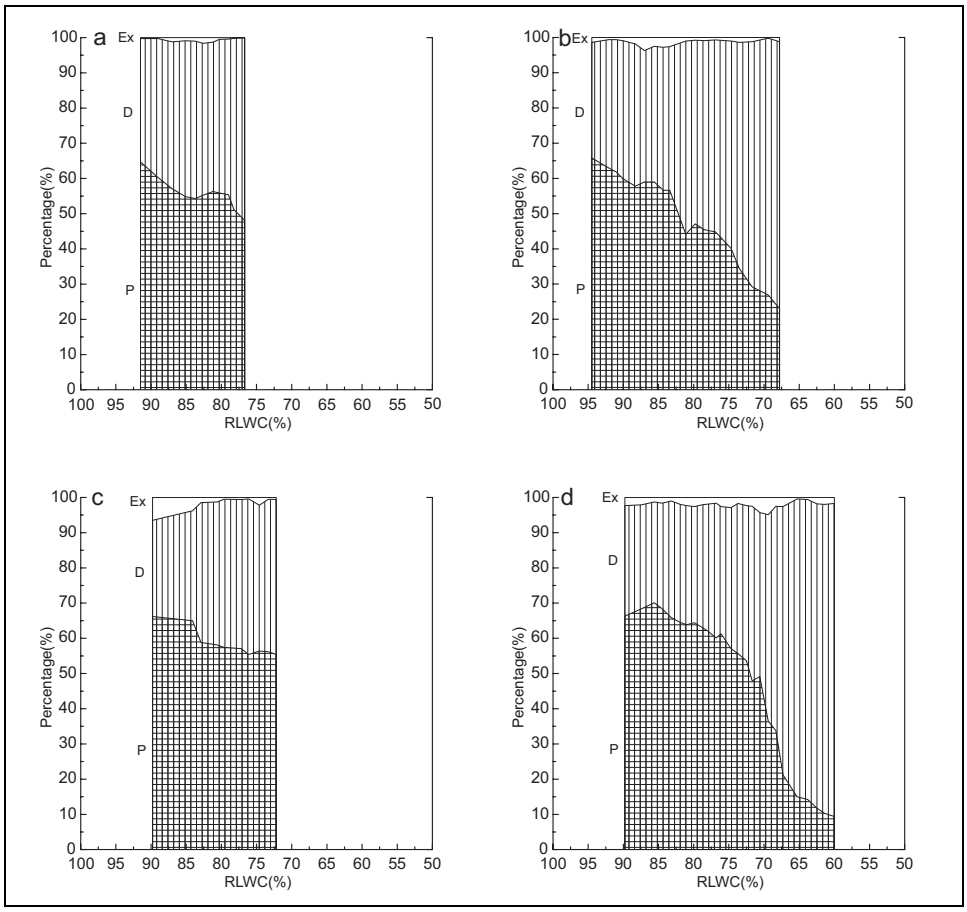


Fig. 5. Effect of relative leaf water content (RLWC) on P, D and Ex in detached cucumber leaf after treated under low light. (a): 'Jingyan 2', control; (b): 'Jingyan 2', low light treated; (c): 'Deltastar', control; (d): 'Deltastar', low light treated.

ues under both low light and control conditions compared to 'Jingyan 2'.

Discussion

Optimal plant growth and development require appropriate light and water conditions. Insufficient light resources cause reduction in the efficiency of capturing light energy and consequently the photosynthetic rate. Similarly, dehydration stress induces smaller stomatal aperture, which will lead to reduction of both photosynthesis and evaporation rate. Under slight dehydration stress, plant Pn reduction is mainly due to partial stomatal closure and the resultant higher resistance to CO_2 diffusion into leaf cells. This stage is characterized by stomatal limitation of photosynthesis, the plants experience greater reduction in evaporation than photosynthesis, and may have higher water usage efficiency initially. As dehydration progress, the mesophyll cells are damaged, and the plants face non-stomatal limitation of photosynthesis. Water loss will lead to higher ion concentration and acidic condition in the stroma, resulting in structural and functional damage to the thylakoid membranes, disturbance of the PSII oxidation and reduction reaction centres, and collapse in the multiple pigment-protein complexes in PSI and PSII. The declining in electron fluxes through both PSI and PSII will reduce ATP and NADPH productivity, and affect photoreaction. Meanwhile, the enzymes for dark reaction (carbon fixation) are also inhibited. Reduction in the activities of the enzymes, such as Rubisco, sucrose phosphate synthase, fructose 1, 6-bisphosphatase, PEP carboxylase, malate dehydrogenase and carbonic anhydrase, will eventually lead to sharp decline of photosynthesis.

The RLWC of the detached cucumber leaves dropped gradually concurrent with decreasing Pn, Gs and Tr. A similar pattern was observed on the seedlings of *Pinus sylvestris* L. var. 'Mongolica Litvin' growing in desert (Zhu et al. 2005). In this experiment with detached cucumber leaves, Pn reduction was mainly caused by stomatal limitation at the early stage. As the stress progressed into the mid-stage, both stomatal and non-stomatal limitations of photosynthesis appeared, the stomata closure became worse, and the mesophyll cells were dehydrated. The final stage ended with the non-stomatal-limitation resultant from serious damage of photosynthetic mesophyll cells. Within 0–10 min after detachment, the stomatal-limitation was predominant with a sharp reduction in Gs and Ci, and rapid rising of Rs and Ls. Due to a significant reduction in the quantity of CO_2 diffused into the photosynthetic mesophyll cells, the Pn value decreased dramatically.

Further dehydration caused transition of photosynthesis into non-stomatal limitation stage. Two cultivars differed in the response to the rapid dehydration process. After 0–5 min, 'Jingyan 2' had lower Pn, Gs and Ci, but higher Ls. Opposite changes were found in 'Deltastar'. Such difference indicates that the leaves of 'Jingyan 2' are

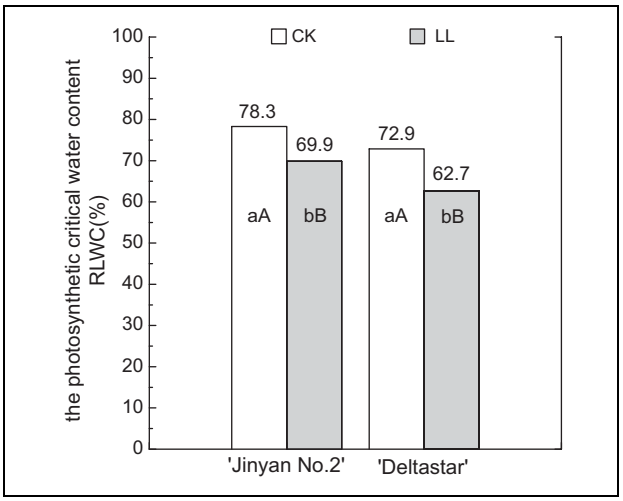


Fig. 6. Effect of low light on the photosynthetic critical water content in detached cucumber leaf. CK: the controls and LL: the low light treatments.

less tolerant to water loss at the early stage of detachment from the plants.

Chlorophyll fluorescent parameters of the detached cucumber leaves were also affected by the rapid dehydration. During the water loss process, P value gradually decreased while the D+Ex increased. Such changes suggest that photochemical quenching gradually diminished, but non-photochemical dissipation increased as dehydration progressed after detachment of the leaves from the plants. Leaves could have enhanced the Xanthophyll Cycle, which to some extent alleviates the damage to photosynthetic apparatus due to excessive light energy (Casper et al. 1993; Feng et al. 2002). After 15 min of detachment, the P value of the cucumber leaves reduced gradually. However, qP of the detached leaves from *Carya illinoensis* Koch did not have such obvious change after 2–4 h. The discrepancy was probably caused by the interspecific variation in drought tolerance. In the present study, the Fv/Fm of detached cucumber leaves remained basically stable compared to the up-then-down fluctuation of Fv/Fo. Conclusively, in the detached cucumber leaves, PSII maintained a similar maximum photochemical efficiency; the potential photochemical efficiency increased initially followed by reduction during the continued water loss process, and Fv/Fo was more susceptible to dehydration than Fv/Fm.

Results from this research show that response to dehydration of chlorophyll fluorescent parameters were delayed compared to the photosynthetic gas exchange. It is reasonable to assume that the rapid dehydration stress had bigger impact on photosynthetic gas exchange than on photochemical reaction. The underlying mechanism needs to be further studied. On the other hand, plant responses to *in vivo* gradual dehydration and *in vitro* rapid dehydration are basically the same. In this study, ΦPSII and J values of the detached cucumber leaves decreased gradually as extension of the detaching time period after the initial rapid water loss, which is similar to the results on rice (Lu et al. 1993), which may possibly be caused by the lower LHCPII polypeptide content. The swollen thylakoid membrane would expand the inner-membrane space, and the concurrent lower protein content would hinder electron flow. The metabolism of soluble matters such as stachyose and D-raffinose also affects tolerance to dehydration.

Leaf RLWC and turgor status can be used to measure drought tolerance (Patakas et al. 1997). When exposed to water stress, less reduction in RLWC often is associated with higher water holding capacity, and stronger drought tolerance. Low light treatment extended the time spent from leaf detachment until Pn dropped to near 0. It was 85 and 50 min for 'Jingyan 2' under low light and control conditions, respectively. The corresponding time for 'Deltastar' was 120 and 45 min. Apparent the difference for 'Deltastar' was much bigger than 'Jingyan 2'. The finding on the cucumber agrees with the observation on rice that drought tolerant winter cultivars have less reduction in fluorescent parameters, which may be associated with the transcription of the relevant genes (such as those encoding for LHCII proteins) (Liu et al. 2005). So, we should reduce the frequency and quantity of water during cucumber cultivation in existed low light stress solar-greenhouse in winter-spring season. This management method is advantageous to alleviate the labour capacity and to enhance the soil temperature, which mitigate the low light stress combined the low temperature.

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Addresses of authors: W. Li, College of Agronomy and Biotechnology, China Agricultural University, Beijing, China and College of Agronomy, Guizhou University, Guiyang, China, and X. L. Sui, L. H. Gao, H. Z. Ren and Z. X. Zhang (corresponding author), College of Agronomy and Biotechnology, China Agricultural University, Beijing, China, e-mail: Zhangzx@cau.edu.cn.