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Photosynthesis and chlorophyll fluorescence of infertile and fertile stalks of paired near-isogenic lines in maize (*Zea mays* L.) under shade conditions

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Abstract

The rainy season affects the development of maize in Liaoning Province in China. Continuous, rainy weather and scant sunlight result in poor pollination, bald tips, and in an abnormally high, barren stalk. Field studies were conducted at the kernel formation stage (3–11 d after silking). Paired, near-isogenic lines of nonbarren stalk (Shennong 98B) and barren stalk (Shennong 98A) were exposed to 38, 60, and 75% shading to investigate changes in photosynthesis and chlorophyll (Chl) fluorescence characteristics under different light intensities. Net photosynthetic rate (P_N), leaf maximum photochemical efficiency of PSII (F_v/F_m), photochemical quenching of Chl fluorescence (q_P), and actual photochemical efficiency of PSII (Φ_{PSII}) of Shennong 98B were always higher than those of Shennong 98A under natural light, contrary to nonphotochemical quenching (NPQ). F_v/F_m, Φ_{PSII}, and q_P increased, while P_N and electron transport rate (ETR) decreased after shading, and this was aggravated with increasing shade intensity. P_N, q_P, Φ_{PSII}, and ETR were lower than the values in natural light condition after seven days of shading. NPQ, F_v/F_m, Φ_{PSII}, q_P, and ETR recovered, when shading was removed. The P_N of two inbred lines returned soon to the control levels after 38% shade. Under shade and natural light conditions, the P_N and Chl fluorescence characteristics of Shennong 98A were both lower than those of Shennong 98B. We suggest that a poor adaptability to low light is an important physiological reason for inducing barren stalk in low light–sensitive maize.

Additional key words: inbred lines; light transfer; photosynthetic characteristics; weak illumination.

Introduction

Maize production is evaluated under natural conditions typical for a region. Changes in environmental condition in different regions and over different years usually include different light conditions. It can result in unfavorable effects on maize growth and development if plants experience a stress from weak illumination (Gmelig 1973, Gerakis 1980).

Liaoning Province in China is a main, representative, production area for spring maize, where the rainy season often coincides with the period when maize undergoes pollination, grain formation, and early grain-filling stages. During this time, limited sunlight with adverse weather often occurs when maize is in a growth and development stage. Continuous rainy weather and scant-sunlight days impact the vegetative growth of maize; it results in poor pollination, bald tips, and even abnormally high rate of barren stalks in individual varieties (Zhong *et al*. 2011). In 2010, some maize varieties grown in Liaoning Province showed a high rate of barren stalks; the rate of barren stalk was closer to 80%. Therefore, exploring the photosynthetic characteristics of abnormal, infertile, barren stalk under low light conditions has its important theoretical value and practical significance. The relationship between stress of weak illumination and barren stalk occurrence is still unknown. Many studies are focused on effects of shading and low light on crop growth (Early *et al*. 1967, Reed *et al*. 1988, Hamamoto *et al*. 2000, Fernando *et al*. 2008). Li *et al.* (2005) suggested that photosynthetic

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Abbreviations: CL – control; DAS – days after shading; DAT – days after transfer; DBS – days before shading; ETR – electron transport rate; F_v/F_m – maximum photochemical efficiency of PSII; NPQ – nonphotochemical quenching; NILs – near-isogenic lines; P_N – net photosynthetic rate; q_P – photochemical quenching; ShA – Shenong98A; ShB – Shenong 98B; Φ_{PSII} – actual photochemical efficiency of PSII.
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rates and fluorescence parameters of various varieties (Danyu 13 and Yedan 22) differed in responses to light intensity. Li (1998) showed a decreasing trend in leaf P_N of different maize genotypes due to short-term light shading. Leaf P_N increased when plants returned to natural light conditions after shading for two weeks; the increasing trend was more apparent in inbred lines than in hybrids. Liu *et al.* (2007) found that light-related, ecological adaptabilities and light sensitivities of different tobacco varieties were different; plants with high photosynthetic efficiency under natural light conditions can take full advantage of weak light when switched to a shade environment. Mou *et al.* (2008) showed that low leaf Φ_{PSII} and q_P caused by shading result in a reduction in leaf P_N and in the accumulation of dry matter in wheat. High sensitivity to weak light is an important reason for yield reduction in shade-intolerant maize varieties. Previous studies of weak light stress were generally conducted in the pots. However, experiments with potted maize can lead to a series of distortion problems (Li *et al.* 2005, Zhao *et al*. 2003).

In addition, the response of low light–sensitive varieties to light transfer may be stronger than in the insensitive varieties, and it requires a further study. We investigated the effects of shade on the net photosynthetic rate and fluorescence characteristics in paired near-isogenic lines (NILs) of vulnerable and unvulnerable, barren stalk inbred lines of Shennong 98A and Shennong 98B in order to exclude interference of trail results caused by genetic background differences. Differences in low-light sensitivity of the shade-tolerant lines were compared to find explicitly the key stress period affecting photosynthetic performance, to explore dynamic adaptive changes in the photosynthesis and in fluorescence characteristics to shading and after transfer from different light intensity. We also aimed to investigate the photosynthetic characteristics of barren stalk in low light–sensitive inbred lines when exposed to limited light conditions.

Materials and methods

Experimental design: The experiment was carried out at the south farm of Shenyang Agricultural University (41°49'N, 123°34'E), which is classified as a north temperate climate, with a semihumid, continental climate often affected by monsoons. The annual average temperature is 8ºC, with an annual average rainfall of 628 mm and a frost-free period of about 150–170 d. The experiment applied a split-plot experimental design with inbred lines as the main plots and shading intensities as subplots. The row length of a plot was 7.5 m, and row width was 0.6 m. There were seven rows in each plot and 31.5 m^2 for each plot. The basic physical and chemical properties of the experimental soil was 26.59 g kg^{-1} of organic matter, 2.35 g kg^{-1} of total nitrogen, 108.75 mg kg^{-1} of alkaline hydrolysed nitrogen, 11.19 mg kg^{-1} of available phosphorus, and 102.83 mg kg^{-1} of available potassium. Pairs of near-isogenic lines of maize Shennong 98A (ShA) and Shennong 98B (ShB) were developed by the Institute of Specialty Corn of Shenyang Agricultural University. ShA is a barren-stalk defective inbred line, with barren stalk growing under weak light conditions. ShB spikes grow well as evidenced by previous field-based investigation. Sowing, seedling emergence, jointing, tasseling, and silking days were on May 10, May 20, June 19, July 21, and July 26 during 2012, respectively.

Shading intensity: The shading treatment was applied three days after onset of silking by using several light-transmitting, black, sun shelters. Three shading intensities were set as 38 (S1), 60 (S2), and 75% shading (S3), with natural light (0%) as a control (CL). The treatments were applied in the field and the sun shelters were installed above (at a height of 1 m) in order to avoid high ambient air and soil temperatures and to ensure the microclimate under the sun shelter was the same as the ambient air temperature (Table 1). Field studies were carried out at the kernel formation stage (3–11 d after silking). And the shade treatment lasted for 8 d. Then plants were exposed to natural light conditions.

Field microclimate: The intensity of illumination and CO_2 concentration with relative humidity was measured at 10:00 h with the *LAI-2200C* plant canopy analyzer (*LI-COR Biosciences* Inc., Lincoln, NE, USA) and

Table 1. Effects of different shading on microclimate of a maize population. The means ± SE (n = 5) followed by *different letters* in the same parameter that differ significantly at $p \leq 0.05$, according to one-way *ANOVA* and *t*-test. CL – control; S1, S2, S3 – 38, 60, and 75% shading, respectively; PPFD – photosynthetic photon flux density.

Shading intensity	PPFD [μmol m^{-2} s^{-1}]	CO_2 concentration [μmol mol^{-1}]	Relative humidity [%]	Temperature at different positions [K] Top canopy	Surface	Ground
CL	1,379.47 ± 2.00[a]	368.28 ± 1.03[a]	69.18 ± 0.56[a]	302.20 ± 0.45[ab]	299.55 ± 0.07[a]	295.82 ± 0.47[a]
S1	855.27 ± 1.23[b]	368.52 ± 1.05[a]	67.84 ± 0.53[a]	302.47 ± 0.37[ab]	298.28 ± 0.13[ab]	295.25 ± 0.43[a]
S2	551.79 ± 1.00[c]	368.59 ± 0.65[a]	68.40 ± 0.49[a]	302.60 ± 0.37[a]	298.42 ± 0.25[ab]	294.75 ± 0.52[a]
S3	344.87 ± 0.79[d]	368.63 ± 0.57[a]	73.00 ± 0.49[a]	302.00 ± 0.42[b]	296.85 ± 0.17[b]	294.72 ± 0.39[a]

a *Li-6400* portable photosynthetic apparatus (*LI-COR Biosciences* Inc., Lincoln, NE, USA), respectively. The temperature of the canopy, surface, and 20 cm below the surface were detected for each treatment by using a normal thermometer and geothermometer (*HG04-2, Tuopu Inc*., Zhejiang, China) at 8:00, 12:00, and 17:00 h.

***P*N and Chl fluorescence parameters**: The P_N of leaves were measured on a sunny morning from 9:30 to 11:30 h using the *Li-6400* portable photosynthesis system (*LI-COR Biosciences* Inc., Lincoln, NE, USA) equipped with an artificial irradiance source *6400-02B* RedBlue. The light intensities for the measurement were adjusted to actual light intensities for different treatments. CO_2 flux was adjusted to maintain a concentration of 380 μmol mol^{-1} inside the chamber and the leaf chamber temperature was maintained at 27ºC. The basic fluorescence after the dark adaptation (F_0), maximum fluorescence (F_m), and the Φ_{PSII} and F_v/F_m of ear leaves were determined by using the *Li-6400* portable photosynthesis system at 1, 3, 5, and 7 d after shading (DAS) and it was followed by light recovery at 1, 3, and 5 d (DAT). Φ_{PSII}, ETR, q_P, and NPQ were calculated by the following formulas: $(F_m' - F_s)/F_m'$, $\Phi_{PSII} \times PAR \times 0.5 \times 0.84$, $(F_m' - F_s)/(F_m' - F_0')$, and $F_m/F_m' - 1$, respectively. Both lines of each treatment were determined from three plants. The leaves were placed under a dark for 30 min using light exclusion clips before measurement. Clips were randomly sampled at the centre of the leaves except for the nervure.

Data analysis: *Microsoft Excel* software was used for data processing and mapping and *SPSS12.0* software was used to analyze significance. *P*<0.05 was considered as statistically significant.

Results

P_N differed in the different inbred lines. Our experiment showed that the ear leaf P_N decreased in both inbred lines with progress in the reproductive process and the declining rate became the fastest on the 1 DAS (Fig. 1). The P_N of the shade-tolerant line, Sh 98B, was higher than that of the shade-intolerant, inbred line, ShA, which indicated that the photosynthetic capacity of ShB was better than Sh 98A under normal light conditions. Compared with natural light conditions, the P_N of ShB was less reduced under S1, while the P_N in the other shade treatments decreased significantly and the degree of their decline increased with an increase in shade intensity. Comparing the P_N of both lines, ShA showed P_N always lower than ShB and the declining rate of ShA was significantly higher than that of ShB with the increasing shade intensity. Under shade conditions, the decrease of P_N occurred mainly due to the lower light intensity, while the changing values of P_N was determined by the difference in photosensitivity between the inbred lines.

When the maize was transferred from the shade to the CL condition, the P_N recovered gradually in both lines with some differences in a recovery speed. The S1 treatment showed a faster change and both lines were able to return quickly to the control level after removal of the

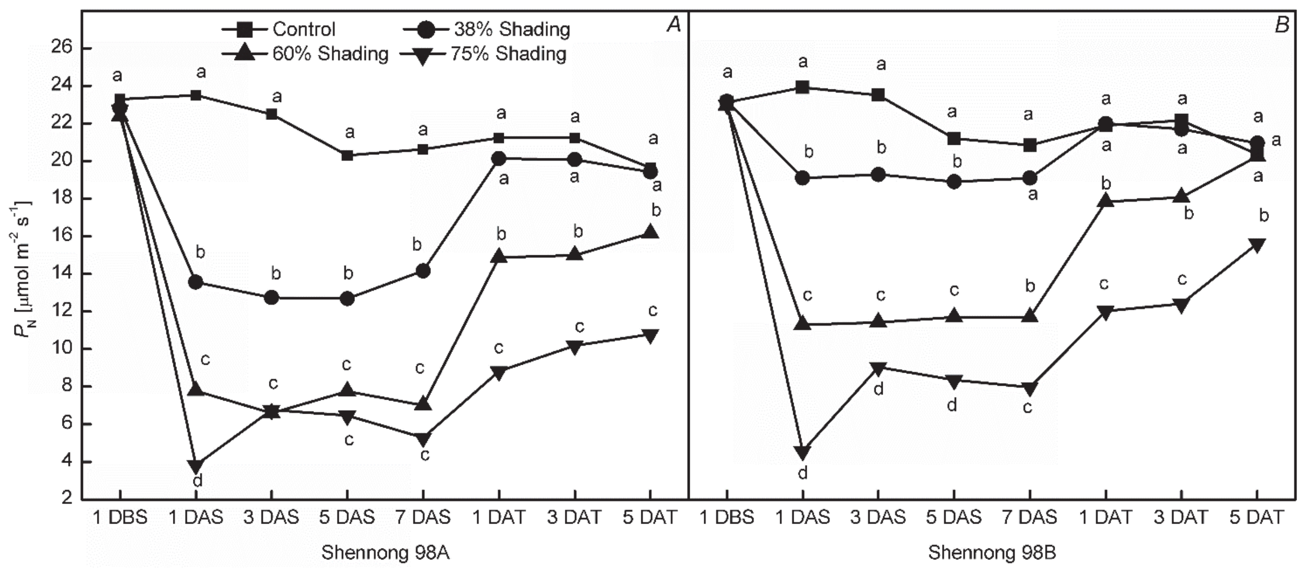

Fig. 1. Responses of net photosynthetic rate (P_N) to shading and transfer to natural light in Shennong 98A (*A*) and Shennong 98B (*B*). *Vertical bars* denote the SE (*n* = 5). *Small letters* represent a difference under different shading stresses (*p*<0.05) according to a least significant difference (LSD) test. DBS – days before shading; DAS – days after shading; DAT – days after transfer from shading to natural light.

shading. The reduction of the P_N under the shade was temporary and the photosynthetic apparatus was not damaged irreversibly. After 5 DAT of the S2 treatment, the P_N of ShB was able to return to the control level, while ShA was only able to restore 77.1% of P_N under CL. At 5 DAT of the S2 treatment, the P_N of ShB was restored to 74.1% of that under CL, while ShA reached only 52.9% of that under CL (Fig. 1).

F_v/F_m is commonly used to measure intrinsic photochemical efficiency and the potential activity of the plant leaf; it is an important indicator for photoinhibition of photosynthesis. F_v/F_m of the shade-tolerant line ShB was higher than that of the shade-intolerant ShA under CL. The F_v/F_m was completely opposite under the shade and CL treatments. When the maize was transferred from a shade to a natural light condition, F_v/F_m was higher than that in control. When the maize was transferred from a shade to a natural light condition, F_v/F_m was higher than that in control. F_v/F_m declined rapidly at the beginning and began to rise after one day. However, F_v/F_m was still lower than that of CL after five days without shade. Short-term shade did not decrease F_v/F_m and the ratio was higher than that of the control, which could represent the physiological adaptive response of maize to weak light stress. As a result, the effects of a sudden exposure in natural light on the photosynthetic organs were more serious than the effects of the shade treatment. The trends of F_v/F_m were similar in both inbred lines, but the changing values were quite different in comparison with the highest F_v/F_m of ShA and ShB. The F_v/F_m of ShB tended to be higher than that of ShA. The F_v/F_m responses to shade and light transfer were different in both inbred lines; ShB showed the higher F_v/F_m with a better adaptation ability to light transfer (Fig. 2).

Chl fluorescence: The q_P is used to represent the openness of the PSII reaction center, which reflects the efficiency of light energy captured by PSII antenna pigments. NPQ is the part of light energy dissipated in the form of heat, which reflects the capacity to dissipate excessive light energy in the photosynthetic system (Krause and Weise 1991). The conversion efficiency for solar radiation energy in ShB was always higher than that of ShA under a natural light condition. The NPQ showed exactly the opposite trend. The responses of both fluorescence parameters to shade stress were different. When the maize was shifted to a shade environment from a natural light condition, q_P initially increased and then started decreasing. After 1 DAS, S3 showed a higher increase of q_P than S2, while S1 reached a maximum value at 3 DAS. Leaf was able to improve the utilization efficiency of light energy through self-regulation under weak light conditions, but the better light utilization efficiency could not fully compensate for the photoinhibition caused by the lack of light and the q_P was lower than the control after 7 DAS and eventually showed a downward trend. When the maize under the shade was suddenly exposed to bright light, q_P and NPQ increased, and values of S1, S2, and S3 were all higher than that of the control (CL) except q_P in ShB. The q_P of the low light–sensitive ShA were lower than those of ShB, whether in natural light or under shade environment. Further, the differences between both inbred lines were

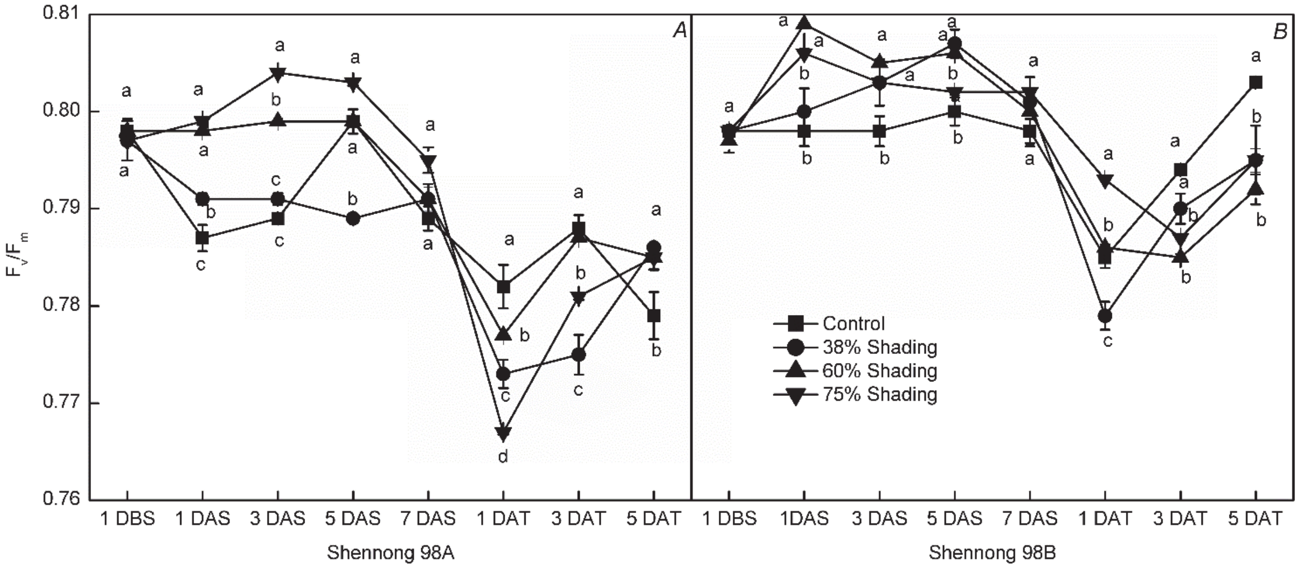

Fig. 2. Responses of maximum photochemical efficiency (F_v/F_m) to shading and transfer to natural light in Shennong 98A (*A*) and Shennong 98B (*B*). *Vertical bars* denote the SE ($n = 5$). *Small letters* represent a difference under different shading ($p<0.05$) according to a least significant difference (LSD) test. DBS – days before shading; DAS – days after shading; DAT – days after transfer from shading to natural light.

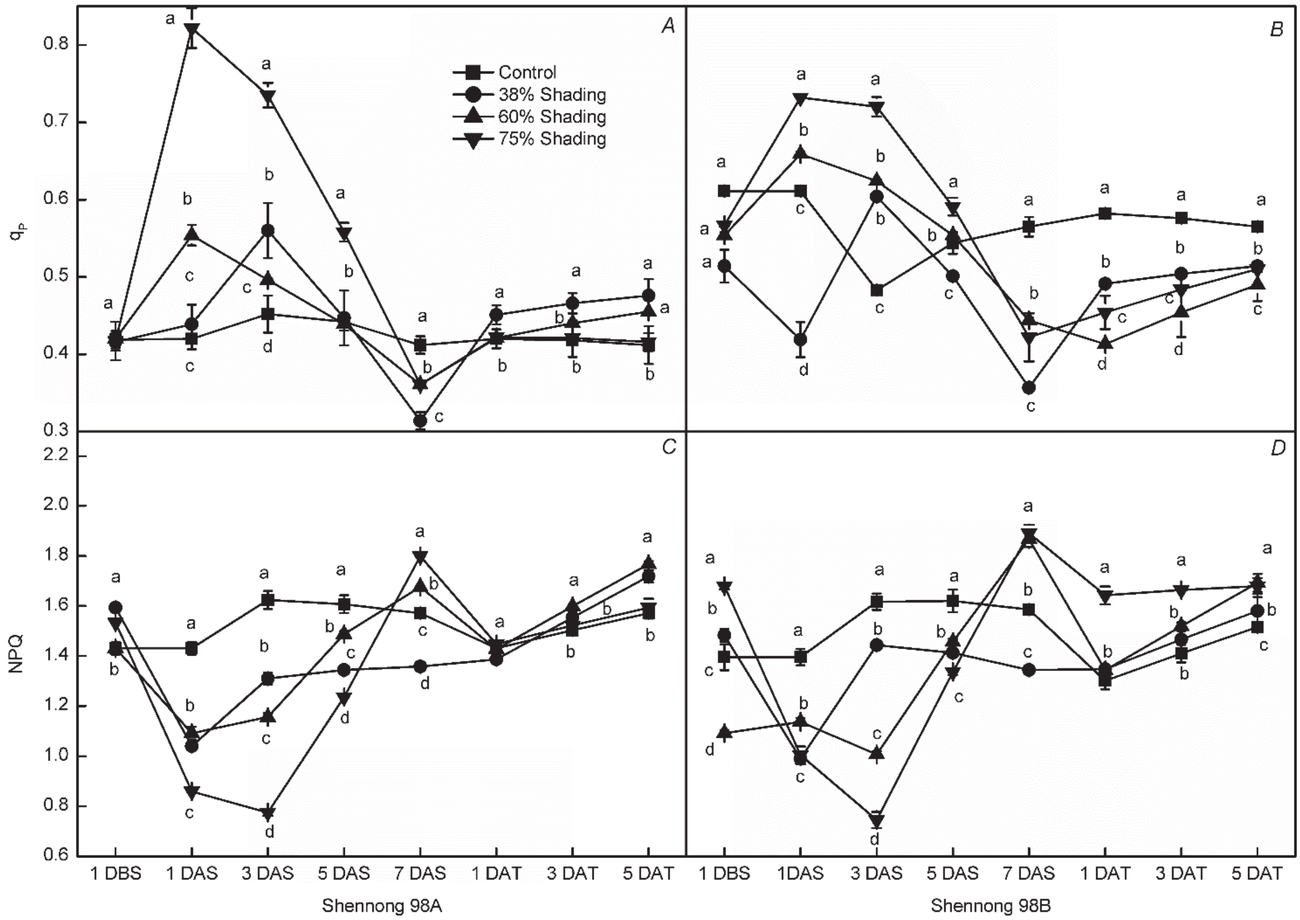

Fig. 3. Responses of chlorophyll fluorescence photochemical quenching (q_P) and nonphotochemical quenching (NPQ) to shading and transfer to natural light in Shennong 98A (*A*,*C*) and Shennong 98B (*B*,*D*). *Vertical bars* denote the SE ($n = 5$). *Small letters* represent a difference under different shading ($p<0.05$) according to a least significant difference (LSD) test. DBS – days before shading; DAS – days after shading; DAT – days after transfer from shading to natural light.

lesser after light exposure, which indicated that the degree of the PSII reaction center openness was lower in the low light–sensitive line than that of the insensitive line (Fig. 3).

Φ_{PSII} reflects primary light energy capture efficiency under actual circumstances, which shows the proportion of the energy consumed by the photochemical reaction (Govindjee 2002). Comparing Φ_{PSII} and ETR in two inbred lines under natural light, ShA showed always lower values than ShB. The Φ_{PSII} trends were different under the conditions of shade and CL. The Φ_{PSII} of both inbred lines showed an initial increase and then began to decrease after shading; it reached a maximum at 3 DAS and then began to decline. The Φ_{PSII} was lower than that of control at 7 DAS. The Φ_{PSII} trends were similar in both inbred lines, while the Φ_{PSII} of ShB was slightly higher than that of ShA under shade conditions. Under different shade intensities, the leaf Φ_{PSII} of S3 showed the highest increase, which indicated that the proportion of light energy absorbed by maize used for photosynthetic electron transport was significantly greater in S3. The Φ_{PSII} began to rise one day after the elimination of shade (1 DAT), but the trends were different in both lines. ShA began to rise on 1 DAT and remained stable from from 1 DAT until 5 DAT; ShB continued to rise between 1–5 DAT and returned to the control level on 5 DAT (Fig. 4).

ETR reflects the apparent efficiency of electron transfer under actual light intensity. When the maize was shifted to a shade environment from a natural light condition, ETR was reduced significantly in both inbred lines. ETR of ShA was always lower than that of ShB, both in natural light or

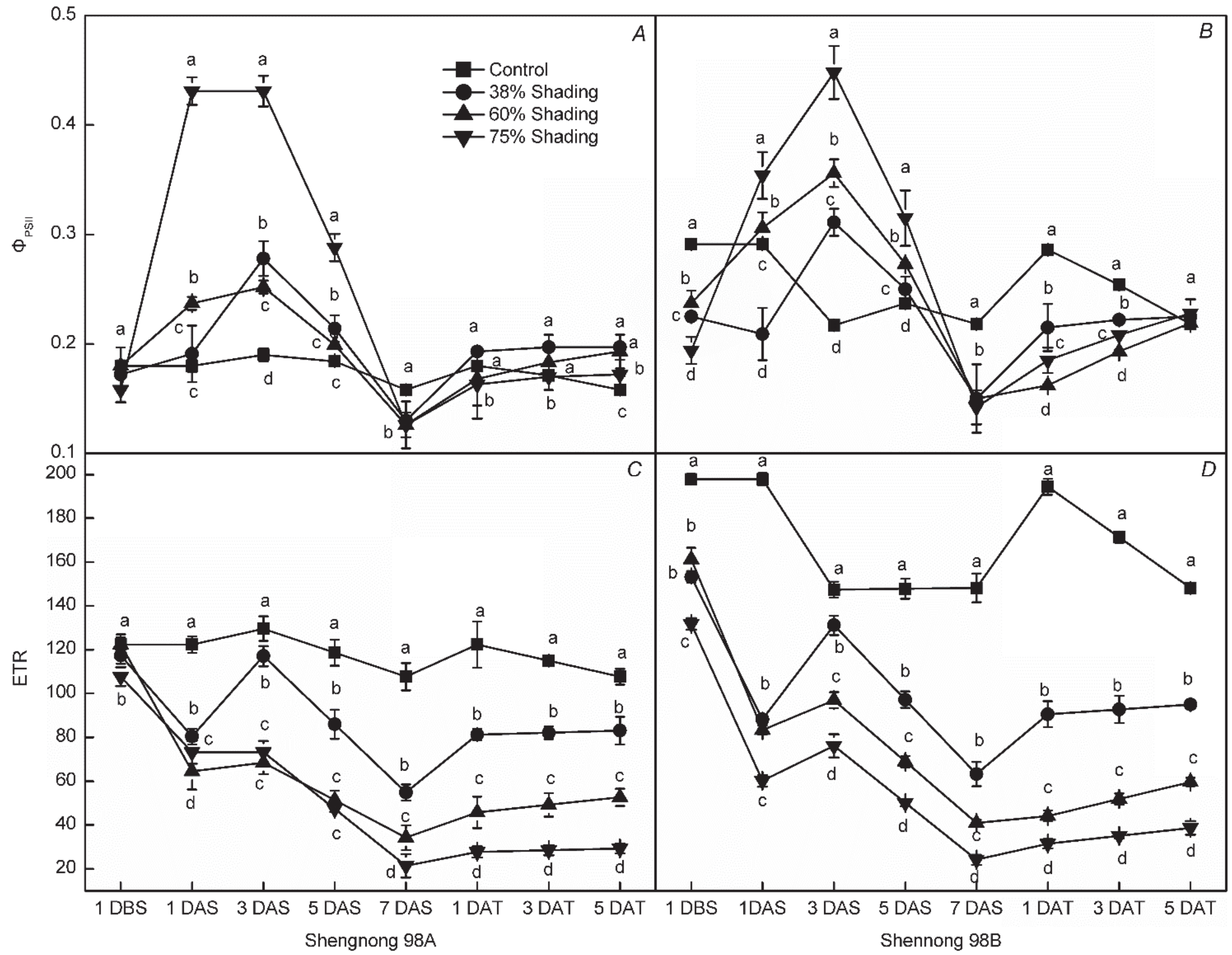

Fig. 4. Responses of actual photochemical efficiency (Φ_{PSII}) and electron transport rate (ETR) to shading and transfer to natural light in Shennong 98A (*A,C*) and Shennong 98B (*B,D*). *Vertical bars* denote the SE ($n = 5$). *Small letters* represent differences under different shading ($p<0.05$) according to a least significant difference (LSD) test. DBS – days before shading; DAS – days after shading; DAT – days after transfer from shading to natural light.

shade conditions. These observations indicated that shade stress inhibited the electron transport. The ETR increased after light recovery in both lines, and the recovery rate and ETR of ShB were both higher than that of ShA (Fig. 4).

Discussion

Recently, extreme abiotic stress occurred frequently in Liaoning province of China, resulting in a greater impact on agricultural production. In 2010, large numbers of barren stalks were observed in some maize varieties. Shi *et al.* (2011) pointed out that a serious shortage of light could be the main reason for the occurrence of barren stalks in maize. Based on field production during different years and cultivation experiments from 2005 to 2011, we found that rainy weather, scant sunshine, and increase in plant density lead to a lack of sufficient sunlight. The response to insufficient light was dependent on maize variety. Several researchers used ordinary corns and inbred lines as experimental materials to study the issue (Zhao *et al*. 1999, Li *et al*. 2007). We found paired near-isogenic lines of barren stalk (ShA) and nonbarren stalk lines (ShB) in maize breeding. ShA showed a higher frequency of barren stalks, while ShB is nonbarren stalks under weak light conditions. The experimental stress treatment (38, 60, and 75% shade) was carried out under field conditions using the NILs as experimental materials, thus avoiding errors caused by pot conditions.

Our experiment showed that P_N, F_v/F_m, q_P, and the Φ_{PSII} of ShB were always higher than those of ShA under natural light, contrary to NPQ. The P_N of ShB under S1 was slightly lower than that of control, while the reduction of other treatments were all greater and enhanced with increasing stress. The P_N of the low light–sensitive ShA was always lower than that of ShB. Earlier studies indicated that photoinhibition and even light damage can easily occur when shifting from low-light conditions to sunshine, which is not conducive to the rapid recovery of plant photosynthetic capacity (Yang *et al*. 2008). This study found that the P_N of both lines recovered after shade was removed and the shade tolerant line was able to return to the control level soon after the S1 treatment. This indicated that the decline of P_N after short-term and mild shade was caused by the reduction of light intensity and did not cause irreversible damage to the photosynthetic apparatus. Changes in various Chl fluorescence parameters may reveal the adaptability of maize to weak light stress. Our study showed that the responses of maize photosynthesis and fluorescence parameters to shade were different. Light energy gained by maize was reduced after shading. In order to use the limited light energy fully, the degree of the PSII reaction center openness increased and energy conversion efficiency was improved, which was indicated by the increase of F_v/F_m, Φ_{PSII}, and q_P at the beginning of shading. NPQ showed the opposite trend. Excessive light energy was reduced and it resulted in the rapid decline of NPQ The photosynthetic electron transport efficiency decreased and ETR declined as well. However, the improved light utilization efficiency was not able to fully compensate for the effects of the reduction in light intensity, and it was indicated by lower Φ_{PSII} and q_P than that of the control. Further, the photosynthetic rates declined continuously after being in shade for seven days. With the removal of shade, NPQ increased and the F_v/F_m, Φ_{PSII}, q_P, and ETR were restored. This showed that maize was able to improve absorption of weak light and conversion efficiency through self-regulation and improvements in light-use efficiency. Based on our analysis, differences in weak light utilization efficiency was an important physiological reason for shade tolerance differences between ShA and ShB.

Conclusion: P_N, noncyclic ETR, and NPQ were significantly reduced in maize, while F_v/F_m, Φ_{PSII}, and q_P increased after shading. NPQ increased and F_v/F_m, Φ_{PSII}, q_P, and ETR were restored after exposure to natural light condition. Photosynthetic characteristics and their differences are important physiological indexes for identifying barren and nonbarren stalk lines. The P_N and fluorescence parameters were lower in the barren-stalk line ShA than that of the nonbarren stalk line ShB, both under a shade and CL environment, indicating that the light adaptability of ShB was better than ShA.

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