

Effects of irradiance on the photosynthetic traits, antioxidative enzymes, and growth of *Cryptotaenia japonica*

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Abstract

Growth, photosynthetic characteristics, chlorophyll (Chl) fluorescence parameters, and peroxidation of membrane lipids of *Cryptotaenia japonica* were studied under differing irradiances (15, 35, 60, and 100 % of full irradiance). At full irradiance, *C. japonica* exhibited a typical decline in net photosynthetic rate (P_N) at midday, which was not observed in the other irradiance treatments. This indicates a possible photoinhibition for *C. japonica* at the high irradiance. Diurnal patterns of stomatal conductance (g_s) were remarkably similar to those of P_N in each irradiance treatment, and the intercellular CO_2 concentration (c_i) had the opposite trend. *C. japonica* growing under 60 % of the full irradiance exhibited the highest plant height, stem diameter, leaf area, and biomass. The initial fluorescence (F_0) value was lowest at 60 % of the full irradiance. Maximal fluorescence (F_m), potential activity of photosystem II (PS II) (F_v/F_0), and maximal photochemical efficiency of PS II (F_v/F_m) values were highest at 60 % of full irradiance and lowest at 15 % of the full irradiance. The malondialdehyde (MDA) content in 15 % and 100 % of the full irradiance were higher than under the other irradiances. During the treatment, catalase, peroxidase, and superoxide dismutase activities firstly increased and then declined under 15 % and 100 % of the full irradiance and were steadily low under 60 % of the full irradiance, indicating a low production of reactive oxygen species. Therefore, *C. japonica* thrived best under 60 % of the full irradiance.

Additional key words: catalase, chlorophyll fluorescence, malondialdehyde, peroxidase, photosystem II, superoxide dismutase.

Introduction

Many physiological processes in plants are affected by irradiance which is one of the most important environmental factors affecting plant survival, growth, reproduction, and distribution. Sun radiation is the energy source for all photosynthetic organisms which are finely tuned to harvest it efficiently. On the other hand, excess radiation captures result in photoinhibition (Anderson 1986) and production of reactive oxygen species (ROS). ROS can induce membrane lipid peroxidation which is one of the major hurts to cells under environmental

stresses (Chen *et al.* 1989). As an end product of membrane lipid peroxidation, malondialdehyde (MDA) content can be used to assess the response of plants to stress (Chen *et al.* 1991, Casano 1997). Superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) are major components of the enzymatic defence antioxidant system. The ability for a rapid up-regulation of the antioxidant system was found to be closely associated with a decreased oxidative damage (Beis and Patakas 2012). Wang *et al.* (1986) found that when rice seedlings

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Abbreviations: CAT - catalase; Chl - chlorophyll; c_i - intercellular CO_2 concentration; E - transpiration rate; F_0 - minimal fluorescence; F_m - maximum fluorescence; F_v/F_0 - ratio of variable to minimal fluorescence; F_v/F_m - ratio of variable to maximum fluorescence; g_s - stomatal conductance for CO_2 ; LA - leaf area; LAR - leaf area ratio; LMA - specific leaf mass; LMR - leaf mass ratio; MDA - malondialdehyde; P_N - net photosynthetic rate; POD - peroxidase; PPFD - photosynthetic photon flux density; RMR - root mass ratio; ROS - reactive oxygen species; LWC - leaf water content; SMR - stem mass ratio; SOD - superoxide dismutase; T_{leaf} - leaf temperature.

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are treated with a low temperature under irradiance, the increase of membrane lipid peroxidation is more evident than in those treated with the low temperature in the dark. Streb (1997) suggested that an excessive radiation can cause the decrease of CAT activity in leaves. All the above studies establish that under some stress conditions, a high irradiance can aggravate stress.

Cryptotaenia japonica Hassk is a perennial herb belonging to a family *Umbelliferae*. It ranges from Anhui, Hebei, and Jiangsu provinces of China to Japan and Korea (Shan and She 1985). The whole plants, roots, or fruits are used for aromatic oil extraction and in medicine (Mi *et al.* 1990). The content of nutrition constituents in *C. japonica* is equal to that in common vegetables excepting a higher asparagine and glutamine content (Zhang and Zhou 2008). Now, the studies of

C. japonica mainly focus on chemical composition and pharmacological action (Li *et al.* 2006), anatomy and tissue culture (Mou and Liu 2009, Wang *et al.* 2009), flower bud differentiation (Ren *et al.* 2005), and seed production (Wang *et al.* 2003, Wang *et al.* 2004, Zhou *et al.* 2009).

In nature, *C. japonica* is usually distributed in sheltered moist slopes along streams in the mountains, edges of forests, and paddy fields. This species is a typical shade-tolerant plant, but some sunlight is benefit for the growth of this species. However, there is no report concerning photosynthetic characteristics and responses of this species to different irradiances. In this study, we were aimed at evaluating the influence of different irradiances on growth, photosynthetic gas exchange, Chl fluorescence, and antioxidant capacity of *C. japonica*.

Materials and methods

Plants and treatments: The seeds of *Cryptotaenia japonica* Hassk were collected from Nanling County (118° 32' E, 30° 91' N), Anhui, China. Research was conducted at the plantation of the Anhui Normal University (118° 22' E, 31° 20' N). After germination, seedlings were cultivated in pots (a height of 18 cm and a diameter of 25 cm, two seedlings per pot) containing garden soil (an organic matter of 11.90 g kg⁻¹, total N of 0.23 g kg⁻¹, total P of 1.47 g kg⁻¹, total K of 7.68 g kg⁻¹, and available K of 179 mg kg⁻¹). All the pots were placed in a greenhouse in the campus of the Anhui Normal University. Ten days later, they were transferred to four different irradiances: 100 % (CK), 60 % (T1), 35 % (T2), and 15 % (T3) of full ambient irradiance, respectively, which were controlled by different layers of shading nylon-nets being placed horizontally on a wood frame at a 120 cm height from the ground. Each treatment had ten pots. During the experiments, the seedlings were irrigated at regular intervals depending on weather and soil moisture status.

Gas exchange measurements: At the vigorous vegetation growth stage, the photosynthetic parameters were measured on a clear day (2nd August 2010) from 7:30 to 17:30 at two-hour intervals. The net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO₂ concentration (c_i), transpiration rate (E), photosynthetic photon flux density (PPFD), and leaf temperature (T_{leaf}) were measured using an open photosynthetic system (CI-340, CID, Camas, WA, USA) with a flow rate of 0.3 dm³ min⁻¹. For measurements, four plants of each treatment were selected (the central portion of one attached leaf was used).

Chlorophyll fluorescence: Chl *a* fluorescence was measured with a CI-510CF Chl fluorescence module (CID, Camas, WA, USA) also on 2nd August 2010. Leaf

clips were used to ensure dark adaptation in the field. After at least 20 min, minimum fluorescence (F_0) was measured under irradiance of 0.25 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Maximal fluorescence (F_m) was induced by a 1-s saturating flash (3 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Variable fluorescence (F_v) equals F_m minus F_0 . The maximum quantum yield of PS II electron transport was calculated as F_v/F_m (Zhou *et al.* 2010).

Morphology measurements: After the determination of photosynthetic characteristics and chlorophyll fluorescence, all the plants were harvested and then separated into roots, stems, and leaves for the following measurements. Plant height and stem diameter were measured with a ruler and a vernier caliper, and leaf area (LA) was determined using the grid method (1 × 1 mm). After the fresh masses of all samples were measured with electronic balances, they were dried in an oven at 80 °C for at least 72 h. Root mass per unit of total mass (root mass ratio, RMR), stem mass per unit of total mass (stem mass ratio, SMR), and leaf mass per unit of total mass (leaf mass ratio, LMR), leaf mass per unit leaf area (specific leaf mass, LMA), leaf area per unit of total mass (leaf area ratio, LAR), leaf water content (LWC), and root to shoot ratio were determined according to Zhou *et al.* (2010).

MDA content and antioxidative enzymes were measured on 1st June, 15th June, 1st July, 15th July, and 1st August according to Zhang and Qu (2003). Leaf blades (0.2 g) were homogenized on ice with 1.5 cm³ of a 50 mM phosphate buffer (pH 7.8). The homogenate was centrifuged at 12 000 g and 4 °C for 15 min and the supernatant was used for further analyses. For measurements of MDA content, 0.5 cm³ of the supernatant was mixed with 2.5 cm³ of 0.5 % (m/v) thiobarbituric acid (TBA, dissolved in 10 % (m/v) trichlorophenoxyacetic acid), boiled for 20 min, and then

cooled down quickly. Absorbances were determined at 450, 532, and 600 nm using a spectrophotometer (UV-3802, Unico, USA). SOD activity determination was based on the inhibition of photoreduction of nitroblue tetrazolium (NBT). Absorbance was determined at 560 nm. One unit of the enzyme activity corresponds to a 50 % inhibition of NBT photoreduction. A reaction mixture for POD determination contained 200 μm^3 of a 200 mM phosphate buffer (pH 6.0), 76 μm^3 of guaiacol, and 0.11 μm^3 of 30 % (v/v) H_2O_2 . Absorbance at 470 nm was recorded every minute for 3 min. CAT activity was determined in a reaction mixture containing 200 μm^3 of a

150 mM phosphate buffer (pH 7.0) and 0.31 μm^3 of 30 % H_2O_2 . The rate of decrease in absorbance was measured at 240 nm according to Chen *et al.* (1997). One unit of CAT and POD activities is defined as the amount of the enzyme that decomposes 1 μmol of H_2O_2 in 1 min.

Data analysis: A standard deviation (SD) was calculated and differences in measured variables between treatments were analyzed by one-way ANOVA according to the least significant difference (LSD) at $\alpha = 0.05$. All the analyses were performed using the statistical package for social sciences program (SPSS v. 13.0, SPSS Inc., Chicago, USA).

Results

The plant height in the T1 treatment was significantly higher than that in the other treatments, and it was lowest in the CK treatment. The stem diameter was highest in the T1 treatment but lowest in the T3 treatment. There was no difference in the stem diameter between the CK and T2 treatments. A maximum of LA was observed in the T1 treatment. The LA in the T2 treatment was higher

than that in the CK treatment and LA in the T3 treatment achieved a minimum. The LAR increased gradually with shading and LAR in the T3 treatment was significantly higher than that in any other treatments. In contrast, LMA declined gradually with shading and achieved the lowest value in the T3 treatment (Table 1).

Table 1. The effect of irradiance on growth indices and biomass allocation. Means \pm SD, $n = 10$. Different letters in each row indicate significant differences ($P < 0.05$) among four growth irradiances. LWC = (fresh mass - dry mass)/fresh mass.

Parameters	CK	T1	T2	T3
Plant height [cm]	16.43 \pm 0.73 ^d	27.17 \pm 1.13 ^a	24.92 \pm 1.54 ^b	21.34 \pm 1.72 ^c
Stem diameter [mm]	13.56 \pm 2.14 ^b	16.32 \pm 3.08 ^a	12.02 \pm 1.88 ^b	8.46 \pm 1.82 ^c
LA [cm ²]	31.74 \pm 3.01 ^c	44.13 \pm 4.20 ^a	38.57 \pm 4.12 ^b	26.07 \pm 2.81 ^d
LAR [m ² kg ⁻¹]	2.76 \pm 0.30 ^c	3.20 \pm 0.32 ^c	3.82 \pm 0.48 ^b	6.06 \pm 0.77 ^a
LMA [g m ⁻²]	151.13 \pm 15.5 ^a	127.64 \pm 14.00 ^b	136.14 \pm 15.26 ^b	91.27 \pm 9.99 ^c
Total dry mass [g]	1.15 \pm 0.04 ^b	1.38 \pm 0.02 ^a	1.01 \pm 0.03 ^c	0.43 \pm 0.01 ^d
Root dry mass [g]	0.30 \pm 0.01 ^b	0.12 \pm 0.01 ^a	0.09 \pm 0.01 ^b	0.03 \pm 0.00 ^d
Stem dry mass [g]	0.43 \pm 0.02 ^c	0.54 \pm 0.02 ^a	0.48 \pm 0.01 ^b	0.16 \pm 0.01 ^d
Leaf dry mass [g]	0.48 \pm 0.01 ^c	0.56 \pm 0.02 ^a	0.52 \pm 0.00 ^b	0.24 \pm 0.01 ^d
Root to shoot ratio	0.33 \pm 0.01 ^a	0.11 \pm 0.01 ^b	0.10 \pm 0.00 ^b	0.08 \pm 0.00 ^c
LWC	0.79 \pm 0.01 ^c	0.84 \pm 0.01 ^a	0.78 \pm 0.00 ^c	0.80 \pm 0.00 ^b

The total dry mass of *C. japonica* in the T1 treatment was appreciably greater than in the other treatments. The leaf water content (LWC) in the T1 treatment was a little higher than in the other treatments. The root dry mass and root to shoot ratio decreased with decreasing irradiance. The stem and leaf dry masses were highest in the T1 treatment but lowest in the T3 treatment. In the T2 treatment, they were higher than those in the CK treatment (Table 1).

The RMR in the CK treatment was significantly higher than in the T3 treatment, and no difference between the T1 and T2 treatments emerged. The SMR in the T2 treatment was a little higher than that in the other treatments, and LMR gradually increased as irradiance declined.

Both PPFD and T_{leaf} during the measuring day changed similarly (Fig. 2). They increased to maximum values at 13:30 and declined after this time. The PPFD and T_{leaf} in the CK treatment were obviously greater than those in the other treatments, and shading always decreased PPFD and T_{leaf} .

In the CK treatment, this species showed a typical two-peak pattern of diurnal P_N changes (Fig. 3A). The first peak of 16.84 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ appeared at 11:30, the second of 13.88 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ at 15:30. Single-peak patterns (without a midday depression) of diurnal P_N were observed under the T1, T2, and T3 treatments. All the peaks occurred at 13:30 when PPFD was highest. In general, P_N in the CK treatment was higher than that in the other treatments except at 13:30.

Diurnal patterns of g_s were similar to those of P_N at each shading treatment (Fig. 3B). Initially, after sunrise, c_i was maximum, then decreased towards midday, and again increased in the late afternoon (Fig. 3C). The c_i in the CK treatment was markedly lower than that in the other treatments at 13:30. In contrast to this, E was very low in the morning, increased towards midday, and drastically declined in the late afternoon (Fig. 3D). The E in the CK treatment was mostly higher than that in the other treatments.

However, E in the T1 treatment increased rapidly and was higher than in the CK and other treatments at 13:30.

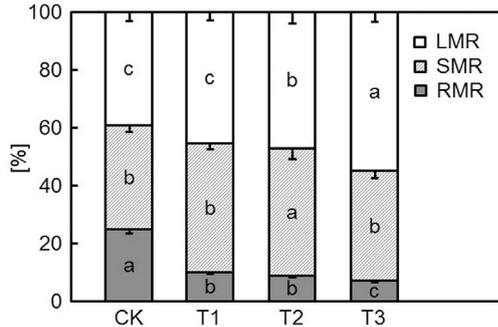


Fig. 1. The proportion of biomass allocated to leaves, stems and roots in *C. japonica* grown under four treatments; LMR - leaf mass ratio, SMR - stem mass ratio, RMR - root mass ratio. Means \pm SD, $n = 10$; different letters inside the histogram indicate significant differences ($P < 0.05$) among four growth irradiances.

The change of E was closely related to g_s : E increased with an increase in g_s , and declined with g_s decreased.

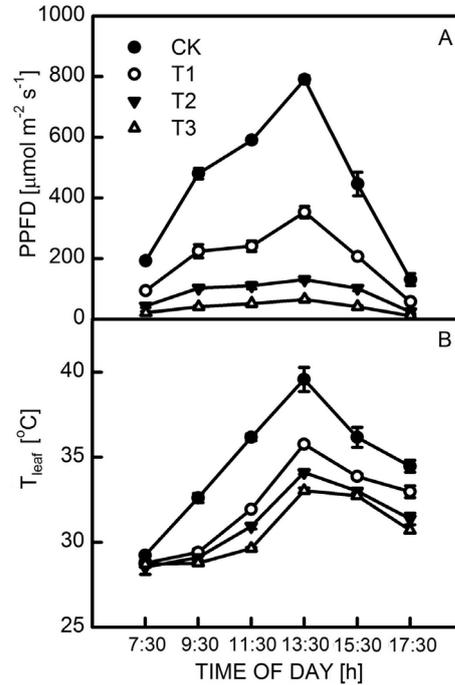


Fig. 2. Diurnal changes in photosynthetic photon flux density (PPFD) (A) and leaf temperature (T_{leaf}) (B) under four irradiances. Means \pm SD of four replicates.

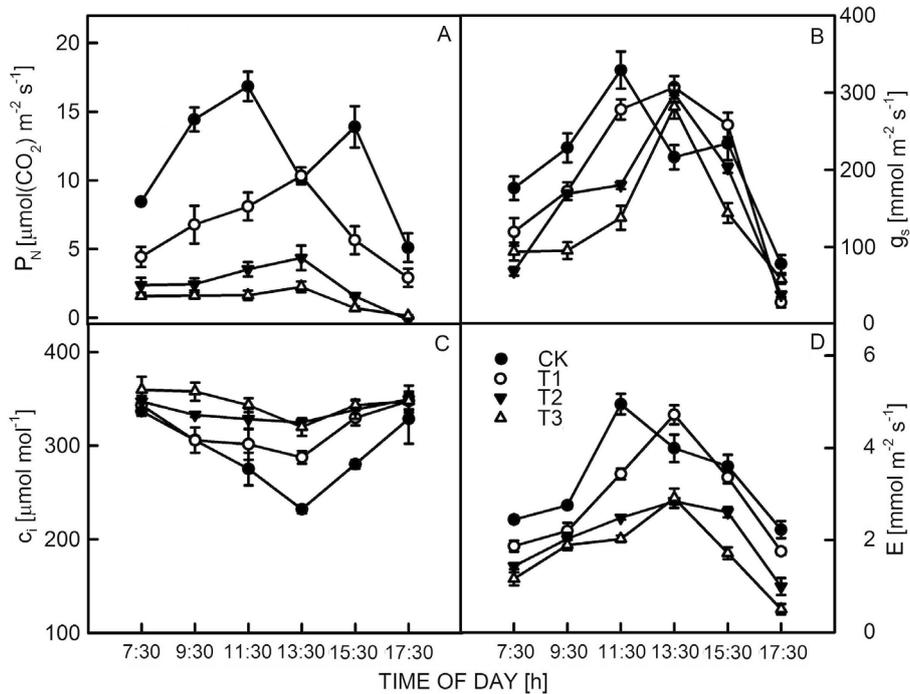


Fig. 3. Diurnal changes in net photosynthetic rate, P_N (A), stomatal conductance, g_s (B), intercellular CO_2 concentration, c_i (C), and transpiration rate, E (D) in leaves of *C. japonica* grown under four different irradiances. Means \pm SD of four replicates.

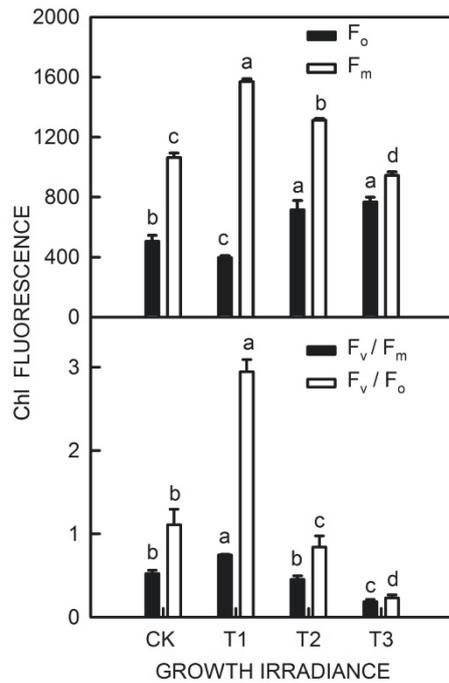


Fig. 4. Changes of chlorophyll fluorescence parameters, F_0 and F_m (A), F_v/F_m and F_v/F_0 (B) in leaves of *C. japonica* grown under four different irradiances. These data were measured at 10:00. Means \pm SD of four replicates; different letters indicate significant differences ($P < 0.05$) among four growth irradiances.

The F_0 in the T1 treatment was lowest among all the treatments, and there was no significant difference in F_0 between the T2 and T3 treatments (Fig. 4A). However, the change of F_m exhibited the opposite trend, and a

Discussion

Phenotypic plasticity is the environmental modification of genotypic expression and an important means by which individual plants respond to a changing environment (MacDonald *et al.* 1988). In the present study, the irradiance strongly affected the morphological characters, biomass, and biomass allocation of *C. japonica* (Table 1). The plant height and stem diameter were higher in the T1 treatment than those in the other treatments whereas LAR increased and LMA decreased as the irradiance declined. These are very plastic growth traits and often strongly affected by irradiance (Jeangros and Nosberger 1992, Sakai 1995, Pothier and Prevost 2002). A decreasing irradiance causes an increase in LAR with the result that radiation captured by leaves increased (Semb 1996). Under a high irradiance, an increased LMA is associated with an adaptation to the high irradiance but it may be a result of adjustment to changes of temperature and humidity as well (Boardman 1977). Generally, a decrease in LMA with decreasing irradiance may

compensate for a reduced photosynthesis per unit leaf area and cause overall photosynthesis per plant to be equal (Kremer and Kropff 1999). In this study, therefore, a higher LAR and a lower LMA under the low irradiance could be parts of the strategy which *C. japonica* used to acclimate to the shade environment. In the CK treatment, *C. japonica* invested more biomass to roots (RMR) than under the other irradiances, which is beneficial for maintaining water balance at a whole plant level. In this study, decreasing irradiance caused a decrease in RMR and an increase in LMR. It may be the natural reflection for *C. japonica* during the low irradiance in order to maintain the growth. This reflection was similar to *Momordica charantia* (Tao and Zhong 2003), *Eupatorium adenophorum* and *Gynura* sp. (Wang and Feng 2004), and oriental lilies (Wang *et al.* 2007). *C. japonica* growing under the T1 treatment exhibited the higher plant height, stem diameter, LA, and biomass, so it showed that only this irradiance could be the most

maximum was in the T1 treatment and a minimum in the T3 treatment (Fig. 4A). The ratio F_v/F_m peaked in the T1 treatment and it was lowest in the T3 treatment indicating that the maximum quantum yield of PS II was inhibited by excessive shading (Fig. 4B). The ratio of F_v/F_0 in the T3 treatment was lower than that in the other treatments (Fig. 4B). The MDA content in the CK and T3 treatments was higher than in the T1 and T2 treatments.

With prolonging growing time, the CAT activities in all the treatments exhibited the same trend with maximums observed on 1st July. The CAT activities in the T1 treatment were lower than in the other treatments all the time (Fig. 5B). The variation of POD activity in the CK treatment was apparently different from that in the other treatments: firstly it increased slowly, however, 15 d later it showed a sharp increase and then declined. The POD activity in the other treatments increased at first and then decreased (Fig. 5C). At first, there were no sharp differences in SOD activities among the treatments; they increased slowly (Fig. 5D). But 15 d later, the activity in the CK treatment suddenly increased and the magnitude of the increase was more significant than that in the other treatments. On 1st July, it reached a maximum and then it began to fall. The SOD activity in the T3 treatment rose continuously and reached the maximum on 15th July, which was later than in the CK treatment. The SOD activities in the T1 and T2 treatments increased gradually during growth. In the beginning, the SOD activities in the T1 and T2 treatments were higher than in the other treatments, but with prolonging time, the activities in the T1 and T2 treatments were becoming lower than those in other treatments, and the SOD activity in the T1 treatment was the lowest (Fig. 5D).

beneficial to the plant growth (Table 1, Fig. 1).

C. japonica experienced a pronounced midday depression in P_N only under the CK treatment (Fig. 3A), and this phenomenon has been reported in many species (Roessler and Monson 1985, Pandey 2003, Zhang *et al.* 2004). According to Farquhar and Sharkey (1982), when the diurnal patterns of P_N and c_i are similar, and g_s

decreases, it is supposed that a decline in P_N is mainly caused by stomatal limitation. As shown in Fig. 3, P_N , c_i , and g_s decreased from 11:30 to 13:30, thus P_N under the full irradiance at midday was largely restricted by a low g_s , which functioned as protective response to limit an excess transpiration.

The analysis of Chl fluorescence parameters is helpful

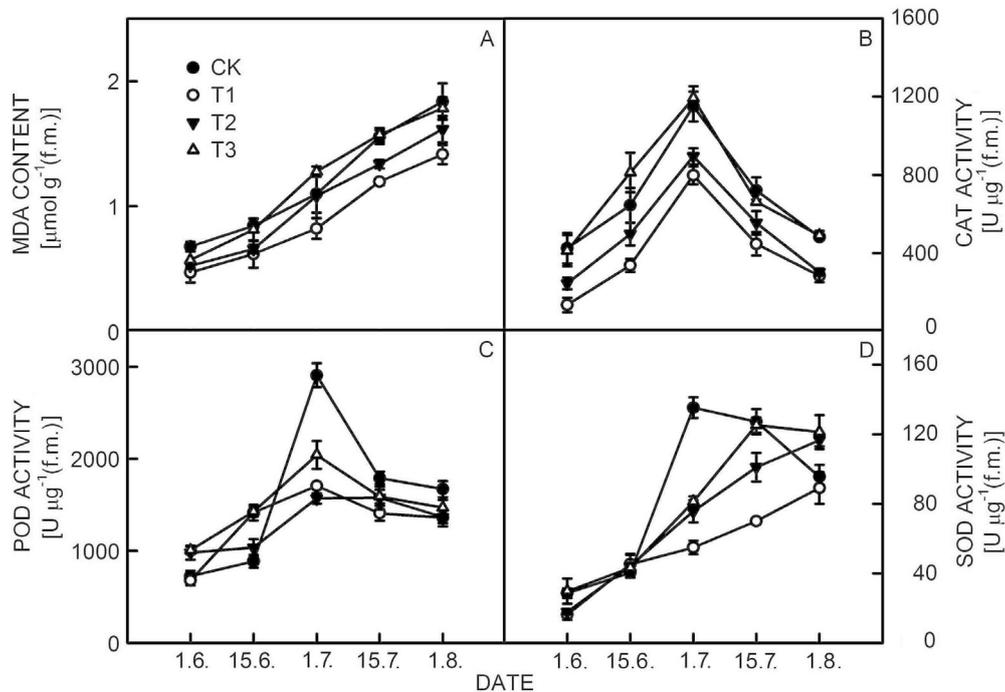


Fig. 5. Dynamic variation of MDA content (A) and activities of membrane protecting enzymes CAT (B), POD (C), and SOD (D) in leaves of *C. japonica* under different radiation treatments. Means \pm SD of four replicates.

to ascertain the possible damage of photosynthetic apparatus under stresses (Li *et al.* 2009, Xue *et al.* 2012). A reduction in F_m , F_v/F_0 , and F_v/F_m is often taken to indicate photoinhibition (Powles 1984). The damage of PS II often results in an increase in F_0 (Van Kooten and Snel 1990). In this study, the minimum F_0 was achieved in the T1 treatment, where the maximum F_m , F_v/F_0 , and F_v/F_m were obtained (Fig. 4). These results show that moderate shading protected best photosynthetic membrane systems and the higher or lower irradiances were less suitable for *C. japonica*.

A substantial body of research in recent years has demonstrated that environmental stress would cause the accumulation of free radicals in plants and thereby trigger a series of reactions. Among these reactions, the most common is membrane lipid peroxidation (Chen 1989). The MDA is the end product of membrane lipid peroxidation, and its production and accumulation is an important index of cell damage (Du *et al.* 2001). Our results (Fig. 5A) suggest that the MDA content of *C. japonica* leaves rose significantly during growth and the MDA content in the CK and T3 treatments were higher

than in the T2 and especially T1 treatments. We also found that the CAT, POD, and SOD activities in the T1 treatment were relatively low, which suggests a low ROS production (Fig. 5B-D). Further, the CAT, POD, and SOD activities firstly increased and then declined during growth in the CK and T3 treatments (Fig. 5B-D). It was speculated that one reason was because the change of the activity was related to the time of stress. At the beginning of the stress with the accumulation of the toxic active oxygen, the enzyme activity was induced to rise for eliminating the active oxygen and thereby alleviating the membrane lipid peroxidation. But this protection might weaken or disappear with the increasing of time of stress, due to the damage of enzyme structure and thus loss of activity. The other reason is that the change of one enzyme activity might be related to the other enzyme activities. To get rid of free radicals in the cell, the three enzymes, CAT, POD, and SOD, need to work together, and there was a dynamic balance.

Summarizing our experimental results regarding the effect of irradiance on growth, morphology, photosynthesis, Chl fluorescence, MDA content, and activities

of antioxidative enzymes, the following conclusion could be drawn: 15 % of the ambient irradiance was too low, and the open sky irradiance was too high for *C. japonica*

growth. Most suitable for growth was 60 % of the ambient irradiance.

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