Photosynthetic responses of four *Hosta* cultivars to shade treatments

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Abstract

The effects of shade on the gas exchange of four *Hosta* cultivars were determined under differing irradiances (5, 30, 50, and 100 % of full irradiance) within pots. Irradiance saturation ranged between 400–800 µmol m^{-2} s^{-1} among the four cultivars, of which *H. sieboldiana* cv. Elegans and *H. plantagenea* cv. Aphrodite exerted the lowest saturation and compensation irradiances. The maximal photosynthetic rate (P_{max}) was significantly higher in shade than in full irradiance in Elegans and Aphrodite, and was at maximum in seedlings grown in 30 % of full irradiance. The best shade treatment for cvs. Antioch and Golden Edger was 50 % of full irradiance. The diurnal gas exchange patterns in four cultivars were greatly influenced by the irradiance. Single-peak patterns of net photosynthetic rate (P_N) and stomatal conductance (g_s) were observed under 5 and 30 % full irradiance for all the cultivars while Elegans and Aphrodite suffered from midday depression in 50 % of full irradiance. Under open sky, all four cultivars showed two-peak patters in their diurnal gas exchange, but the midday depression was less in Antioch and Golden Edger than in Elegans and Aphrodite. According to their photosynthetic responses to shade, the shade tolerance of the four cultivars was in the order: Elegans>Aphrodite> Antioch>Golden Edger.

Additional key words: diurnal course; irradiance; net photosynthetic rate; shade tolerance; stomatal conductance.

Introduction

To the genus *Hosta* belong perennial broad-leaved ornamental species found in many gardens (Diana 1990). Four cultivars of *Hosta* with blue, green, orange, and multicolour leaves are widely planted in China. According to their growth in the field, these four cultivars grow usually better in the shade than under the open sky. So, they are considered to be typical shade species (Harshbarger 1981). However, only a few studies have examined their CO_2 exchange under low irradiance and their shade tolerance.

Leaf responses to different irradiance vary widely among plant species. In general, shade leaves usually have low area-based photosynthetic and dark respiration rates and low saturation irradiance (Boardman 1977, Kitajima 1994). Sun leaves make more efficient use of high irradiance for carbon gain while avoiding a possible reduction in photosynthetic performance as a result of photoinhibition (Da Matta and Maestri 1997). Shade-tolerant plant species often have lower rates of photosynthesis (Koike 1988, Raaimakers *et al.* 1995) than do the light-demanding species under both shade and full sun. Eco-physiological characteristics of shade-tolerant species have often been studied (Medina *et al*. 2002, Walcroft *et al*. 2002, Da Matta 2003). A general hypothesis is that shade-tolerant species express some morphological and physiological traits that benefit energy capture (*i.e.* growth) under low irradiance (Björkmann 1981, Givnish 1988). Especially, the extent of shading can affect photon interception and photosynthetic activity of individual leaves (Sheehy and Cooper 1973). In addition, maximal irradiance-saturated net photosynthetic rate (P_{max}) has also been used as a physiological variable to predict the effect of shade on photosynthesis (Peri *et al*. 2002). Previous studies of photosynthetic response to fluctuating irradiance have been mainly conducted under storey species in tropical forests characterised by a sunfleck regime (Tinoco-Ojanguren and Pearcy 1993, Walcroft *et al*. 2002) or within crop canopies (Sassenrath-Cole and Pearcy 1994, Pearcy *et al*. 1996). Few studies were done under very low irradiance (<5 % of full sunlight). However, the physiological adaptability of leaves to a wide scope of irradiances related to net

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Abbreviations: g_s – stomatal conductance; P_{max} – maximal photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; T_{air} – air temperature.
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photosynthetic rate (P_N) of *Hosta* has received little attention yet.

The aim of our study was to evaluate the influence of shade on photosynthetic performance of four cultivars of *Hosta*. The underlying hypothesis is that *Hosta* species have the photosynthetic capacity of shade plants, but they differ in degree of shade tolerance.

Materials and methods

Plants: Four-year-old seedlings of *Hosta* were selected in 2003 from Beijing Botanical Garden (39°9′N; 116°4′E), Institute of Botany, the Chinese Academy of Sciences. The four cultivars were *Hosta* cv. Golden Edger, *H.* cv. Antioch, *H. sieboldiana* cv. Elegans, and *H. plantagenea* cv. Aphrodite. Golden Edger has yellow leaves while Antioch has white brim leaves. These two cultivars were selected from a hybrid. Elegans is a natural mutant of *H. sieboldiana*, which has blue and green stripes in leaves. The cv. Aphrodite is a natural mutant of *H. plantagenea.*

Experiment design: In April the seedlings were germinated. They were put into pots of 21 cm diameter and 21 cm height containing soil mixture (garden soil : leaf mold = 1 : 1). 1 % of monoammonium phosphate ($NH_4H_2PO_4$) was added to each pot. All the seedlings were placed under tree shading for about two weeks and then transferred under shading nets or open sky. During the experiments, the seedlings were watered and cultivated using standard methods. Three shading treatments (50, 30, and 5 % of full sunlight) were arranged using the shading nets. They covered a 3×3 m area being placed horizontally on a vertically adjustable metal frame. The irradiance was monitored with quantum sensors installed below the shade source, but above the canopy height. At the same time, a non-shading treatment (control) was also conducted under open sky. Each treatment had eight replicates.

Photosynthesis measurements: After two months of treatment, photosynthesis was measured on clear days throughout daytime at two-hour intervals. Net photosynthetic rate (P_N) and stomatal conductance (g_s) were measured using a portable gas exchange system (*LCA*-4, *ADC*, Hoddesdon, England). Before measuring, the CO_2 and H_2O analysers were calibrated using CO_2 standards (460 µmol mol^{-1}) and *WG-602* Water Vapour Generator (*ADC*, Hoddesdon, England), respectively. Measuring conditions were ambient CO_2 concentration (C_a) of 350 mol mol^{-1} and vapour pressure deficit (VPD) of 2.0±0.4 kPa. The central portion of most leaves was approximately horizontal, and the leaf cuvette was clamped on this portion of the leaf and kept in the horizontal position so that the effect of leaf angle on incident PPFD was minimised during the measurements. For measurements fully expanded leaves in upper shoots were selected. The final value was the mean of three replicates.

Irradiance response of P_N: The response of P_N to step changes in PPFD was examined by an external, heat filtered radiation source under full irradiance. Ten irradiances (0, 50, 100, 200, 400, 600, 800, 1 000, 1 200, and 1 500 µmol m^{-2} s^{-1} PPFD) were set. Leaves were allowed to acclimate to each PPFD for at least 4 min, then steady-state gas exchange properties were observed and logged, and subsequently the PPFD in the cuvette was changed. P_N-PPFD curves were plotted using the mean values of P_N measured at each PPFD. Three replicates were made.

Data analysis: Differences in measured variables between treatments and species were analysed by ANOVA, and the means were compared with Tukey's multiple comparison tests. All tests for significance were done at $p<0.05$, unless otherwise indicated.

Results

PPFD-P_N response curves: The four cultivars were saturated at different irradiances: Elegans and Aphrodite got their maximal P_N at about 400 µmol m^{-2} s^{-1} while Antioch and Golden Edger at about 800 µmol m^{-2} s^{-1} (Fig. 1*A*). From 0 to 400 µmol m^{-2} s^{-1}, all the cultivars responded rapidly. After a while, curves of Elegans and Aphrodite reached a plateau while values for Antioch and Golden Edger kept on increasing. P_N of the four cultivars at the same PPFD was in the order: Elegans<Aphrodite<Antioch<Golden Edger. Elegans had the lowest compensation irradiance (5 µmol m^{-2} s^{-1}) while Golden Edger had the highest one (15 µmol m^{-2} s^{-1}) (Fig. 1*B*).

P_{max} under different shading treatment: P_{max} was significantly higher in shade than in full irradiance, and was maximal in seedlings grown in 30 % of full irradiance in Elegans and Aphrodite (Fig. 2). It increased by 24 and 20 % under 30 % full irradiance than under the open sky in Elegans and Aphrodite, respectively. P_{max} of Antioch and Golden Edger tended to increase under 30 and 50 % of full irradiance, and the maximal values occurred under 50 % treatment. However, they were reduced by 17 and 29 % for Antioch and Golden Edger, respectively, under 5 % of full sunlight (Fig. 2).

Diurnal course of photosynthesis: Both PPFD and T_{air} during the measuring days changed similarly (Fig. 3).

They increased from the morning and got the maximal values at 14:00 (PPFD and T_{air} were 1 800 mol m^{-2} s^{-1} and 33.7 °C, respectively) and then decreased. (Fig. 3). The shading treatments always decreased the PPFD and T_{air} (Fig. 3).

Under such conditions, all the four cultivars showed two-peak pattern of diurnal photosynthesis changes in open sky treatment (Fig. 4*G*). The first peak appeared at 10:00, while the other, much smaller than the first one, at 16:00. The depression extents among the four cultivars were different: at midday by 37 % in Elegans but only by 11 % in Golden Edger.

At 50 % of full irradiance, the photosynthesis pattern changed in Antioch and Golden Edger which did not suffer from the midday depression, while Elegans and Aphrodite still showed the two-peak pattern (Fig. 4*E*) with a 24 % depression at midday.

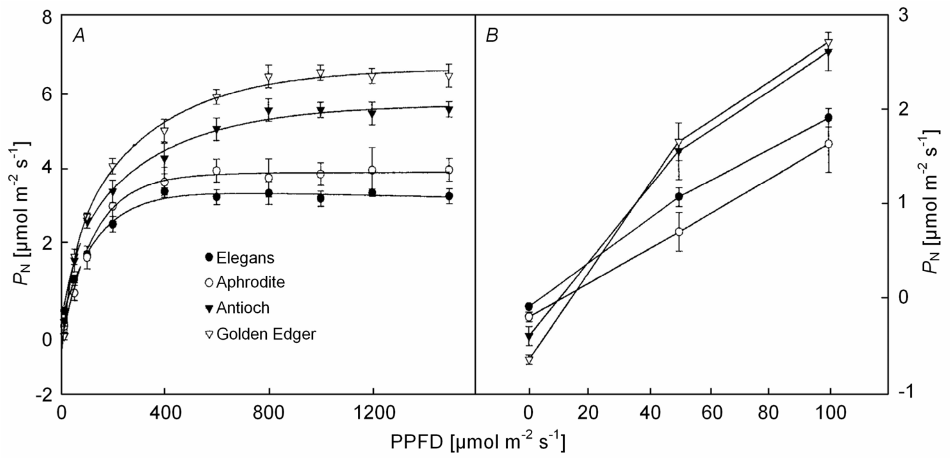

Fig. 1. Irradiance (PPFD) response curves of net photosynthetic rate (P_N) of four *Hosta* cultivars. *Data* in *A* as in *B*, but focused on the low PPFD**.** *Error bars* are ±S.E.

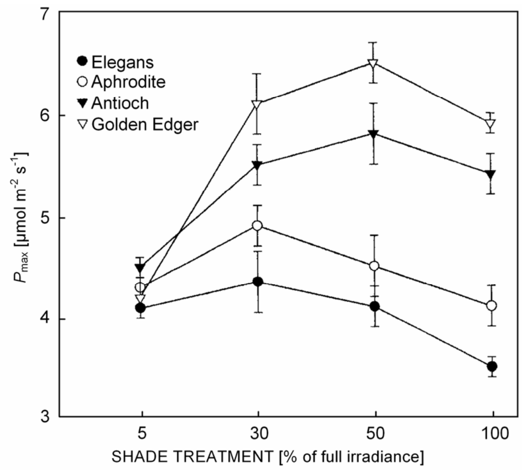

Fig. 2. Effects of shade treatment on the maximal photosynthetic rate (P_{max}) of four *Hosta* cultivars. *Error bars* are ±S.E.

The single-peak pattern in diurnal photosynthesis course was observed under both 5 and 30 % of full sunlight for all the cultivars (Fig. 4*A,C*). The peak occurred at 12:00 when PPFD was the highest during the day. However, the differences in P_N among the four cultivars were larger under 30 than 5 % irradiance, at which there were no obvious differences between them (Fig. 4*A*).

Diurnal patterns of g_s were remarkably similar to those of P_N for all the four cultivars at each shading treatments (Fig. 4*B,D,F,H*).

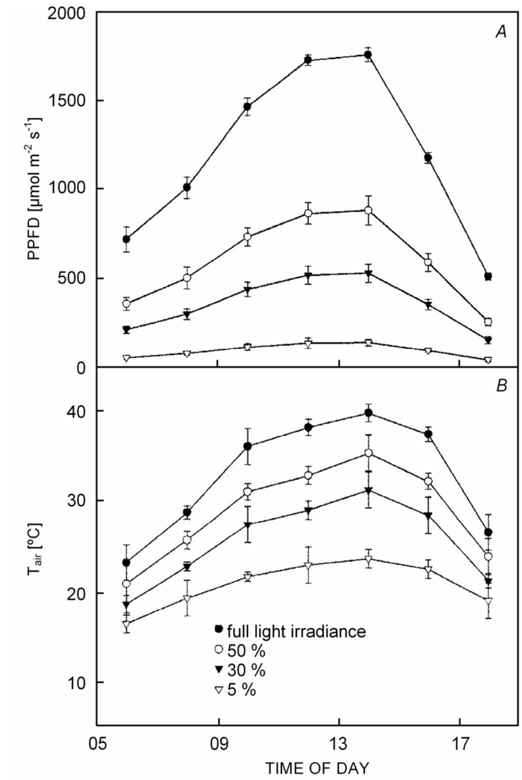

Fig. 3. Diurnal changes in photosynthetic photon flux density (PPFD) (*A*) and air temperature (T_{air}) (*B*) under different shade treatments. *Error bars* are ±S.E.

Discussion

Shading influenced photosynthesis: Shade species have usually higher P_N under shade than under full sun (Regnier *et al*. 1988, Stoller and Myers 1989, Fischer *et al*. 2000). However, this response is not always true per leaf area unit. Regnier *et al*. (1988) found similar P_{max} at low PPFD for both shaded and non-shaded plants when P_{max} was measured per leaf area unit, but rates were significantly different between treatments when P_{max} was measured per unit leaf volume. We found that shading extent greatly impacted photosynthesis performance. There were different thresholds of shading for the cultivars. The best shade treatment was 30 % of full irradiance for Elegans and Aphrodite and 50 % for Antioch and Golden Edger (Fig. 2). The previous shading experiments have seldom been conducted at very low PPFD (<5 % of full irradiance). We found that P_{max} was limited by the 5 % treatment in Antioch and Golden Edger (Fig. 2). These results indicated that 5 % of full irradiance was

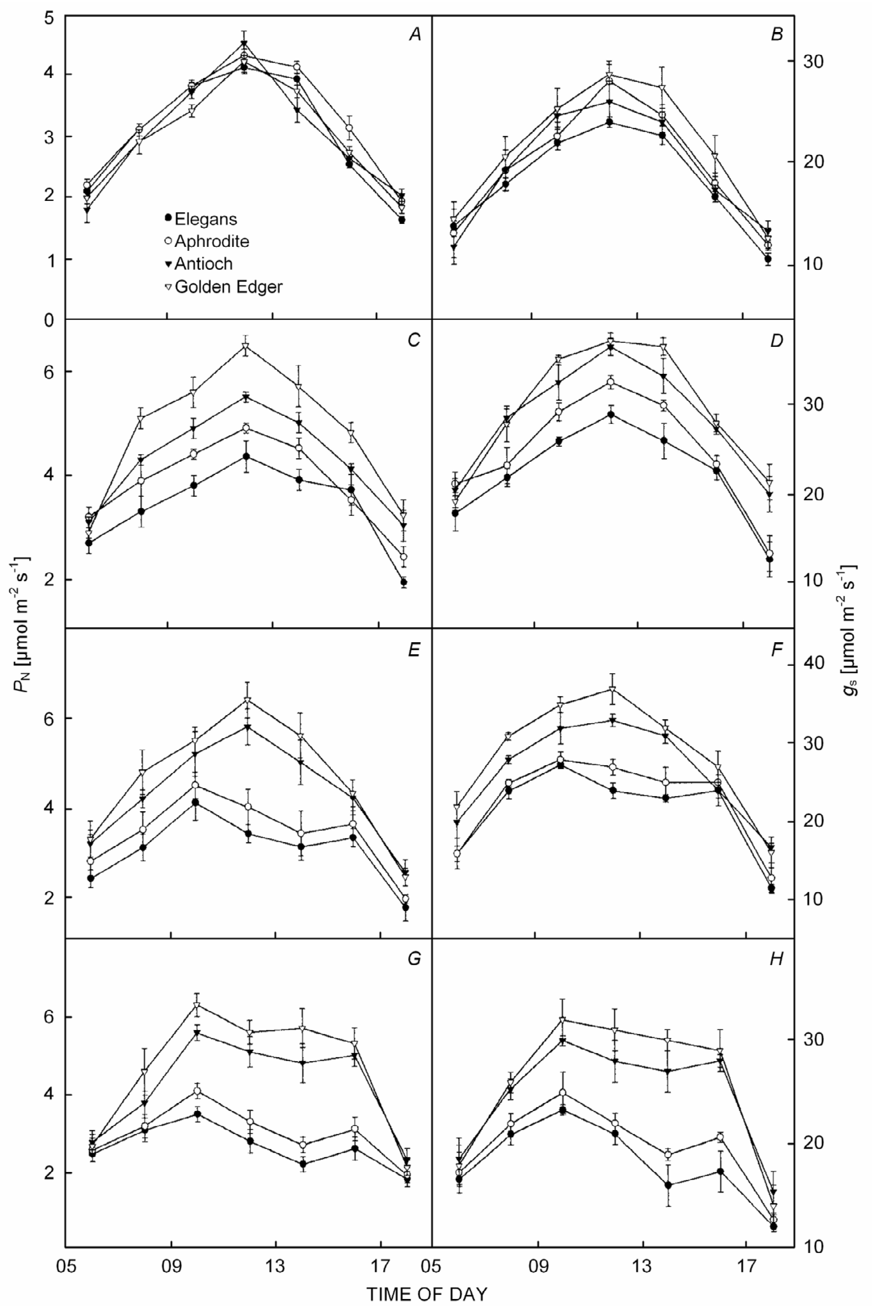

Fig. 4. Diurnal changes in net photosynthetic rate (P_N) and stomatal conductance (g_s) in the four cultivars under 5 (*A, B*), 30 (*C, D*), 50 (*E, F*), and 100 (*G, H*) % of full irradiance. *Error bars* are ±S.E.

too low while the open sky irradiance was too high for Antioch and Golden Edger photosynthesis. However, 5 % shade was better than full sunlight for Elegans and Aphrodite. The different shading threshold for cultivars reflect their different shade tolerance.

The reduction of P_{max} in full irradiance may be partially explained by lower g_s for exposed leaves. Kumar and Tieszen (1980), for example, pointed out that shade-grown plants photosynthesised at nearly twice the rate of those grown in the sun, with corresponding changes in leaf conductance, since stomata aperture was larger under shade (Fanjul *et al.* 1985, Medina *et al.* 2002). As to the regulatory role of g_s in photosynthesis, our results were similar to those of the above reports (Fig. 4). Under the shading net, water deficit was probably not established due to lower irradiance and air temperature (Fig. 3) and the maintenance of stomata aperture was possible. So, we suggest that under full sunlight, photosynthesis would be largely restricted by low g_s in shade-tolerant species, which functions as a protective response to excess transpiration. A similar result was also reported by Cohen *et al.* (1997) who demonstrated that midday reduction of citrus leaf conductance was reduced under shading.

Irradiance also greatly influenced the daily course of photosynthesis in the four *Hosta* cultivars. Under 5 % of full irradiance, the diurnal gas exchange patterns of all the seedlings were consistent with PPFD change during the day (Fig. 3). This pattern was similar to that of the well watered temperate C_3 plants (Tenhunen *et al.* 1987). In contrast, when the seedlings of all four cultivars were exposed to the full irradiance, high PPFD at midday induced the depression of P_N and g_s (Fig. 4*G,H*), which is the normal pattern in most semi-arid or Mediterranean species (Jiang and Zhu 2001, Niu *et al*. 2003). The differences in irradiance threshold when midday depression occurred and the depression extents in the four cultivars (Fig. 4) reflected the different shade tolerance. Hence Elegans and Aphrodite were more shade tolerant than Antioch and Golden Edger.

Shade-tolerance of cultivars: In comparison with the average saturating irradiance of most C_3 temperate plants in the summer (Pearcy and Calkin 1983), most of the *Hosta* cultivars had relatively low saturating irradiance in the range 400–800 µmol m^{-2} s^{-1} under full sunlight. Elegans had the lowest saturating irradiance while Golden Edger had the highest one (Fig. 1*A*), reflecting different light reactions among cultivars. In addition, some shade adaptation attributes, *e.g*. low compensation irradiance, were also used to judge the shade adaptation (Rena *et al*. 1994). Taking the saturating and compensating irradiances into consideration (Fig. 1*AB*), the shade tolerance of four cultivars was in the order Elegans> Aphrodite> Antioch>Golden Edger.

The change of P_{max} under different shade degree and the responses during induction could also be used as physiological indicators to define shade-tolerant species from the physiological perspective (Gibson *et al*. 2001). Thus, species with a higher P_{max} when exposed to shade would be classified as more shade-tolerant because they would increase the photosynthetic carbon gain.

In conclusion, photosynthetic performance of *Hosta* cultivars can be improved by shade treatment that reduces incident PPFD and T_{leaf} (Fig. 3). However, the shading threshold was different for the four cultivars. Both P_N values and change patterns were influenced by the shading treatments. According to their photosynthesis response to shade, the four cultivars can be considered as shade-tolerant species of the above mentioned tolerance order.

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