Morphological plasticity, photosynthesis and chlorophyll fluorescence of *Athyrium pachyphlebium* at different shade levels

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Abstract

Athyrium pachyphlebium C. is a popular ornamental fern with considerable shade tolerance. The aim of this study was to investigate how the mature sporophytes acclimate to different light levels and to obtain an optimal light environment for their growth both in natural forest canopy and in urban landscapes. Plant growth and morphology, photosynthetic light-response curves and chlorophyll (Chl) fluorescence were measured at four different light levels (45% full sunlight, 30%, 20% and 8%). As the light intensities declined from 45% to 20%, seedling height, crown growth, foliage number and plant lifespan increased significantly. Seedlings grown at 20% light level were vigorous with great ornamental value. Plants grown in deep shade (8% light) showed severe symptoms of lodging and in 45% full sun, the plants showed high-light-stress symptoms. Seedlings in high light levels exhibited a higher light-saturated photosynthetic rate (P_{max}), light compensation point (LCP), light saturation point (LSP) and a reduced ability for nonphotochemical quenching (NPQ) of excess light than those in low light levels. However, seedlings in low light exhibited greater efficiency in absorbing and utilizing light energy, characterized by higher chlorophyll *b* (Chl *b*) and electron transport rate (ETR). These results indicated that a light level of about 20% full sun appeared to be optimal for *A. pachyphlebium* when both physiological and morphological performance in the landscape were considered.

Additional key words: *Athyrium pachyphlebium*; chlorophyll fluorescence; morphological plasticity; photosynthesis; shade tolerance.

Introduction

Light is an significant resource for photoautotrophic higher plants in survival, growth and site distribution. Plants have to develop special acclimation and plasticity mechanisms to cope with different light conditions (Ball and Critchley 1982, Durand and Goldstein 2001) and the shaded understory of forests, in particular, presents a challenge in acquiring sufficient photosynthetic energy to support growth and survival (Paquette *et al.* 2007).

Photosynthetic acclimation to different light irradiances is usually associated with morphological changes. Many studies have focused on the morphological reactions of plants in response to varying illuminations, such as height, crown geometry, total biomass, foliage number and arrangement (Hiroki and Ichino 1998, Bond *et al.* 1999, Cardillo and Bernal 2006). Shade-intolerant species tend to enhance photosynthesis by growing vertically to the forest canopy, whereas shade-tolerant species tend to intensify lateral growth to capture more light, as was reported in *Quercus suber* and some conifer species (Kitajima 1994, Chen *et al.* 1996, Olsen *et al.* 2002).

The main physiological features of shade-adapted plant acclimation to changing light conditions have been

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Abbreviations: AQE – apparent quantum efficiency; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; F_m – maximum fluorescence of dark-adapted state; F_m' – maximum fluorescence of light-adapted state ; F_o – minimal fluorescence of dark-adapted state; F_o' – minimal fluorescence of light-adapted state; F_s – steady-state fluorescence yield; F_v/F_m – maximal photochemical efficiency of PSII; g_s – stomatal conductance; LCP – light-compensation point; LMA – leaf dry mass per unit area; LSP – light-saturation point; LHC – light-harvesting complex; NPQ – nonphotochemical quenching; P_{max} – light-saturated photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PSII – photosystem II; q_p – photochemical quenching coefficient; V/F – the ratio of vegetative fronds to fertile fronds; Φ_{PSII} – actual photochemical efficiency of PSII.

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well described (Griffin *et al.* 2004, Walters 2005). Compared to high light, plants grown in low light generally have a lower light-compensation point (LCP) and light-saturation point (LSP), as well as lower synthesis of some components involved in electron transport (generation of ATP and CO_2 fixation). Conversely, increases in levels of these components in relatively high irradiances may allow for efficient photosynthesis, reducing the susceptibility to other environmental stress (Skillman *et al.* 2005). However, a failure to acclimate to high-light conditions could result in slower growth, foliage chlorosis and eventually fatal damage (Olsen *et al.* 2002, Zhang *et al.* 2003).

Chl fluorescence has been increasingly used to examine both the mechanism of photosynthesis and whether the plants are influenced by environmental stress (Van Kooten *et al.* 1990, Lovelock *et al.* 1998, Khan *et al.* 2000). Light energy absorbed by Chl molecules can undergo three fates: (*1*) be used to drive photosynthesis, (*2*) excess energy can be dissipated as heat (nonphotochemical quenching) or, (*3*) re-emitted as light-Chl fluorescence (Maxwell and Johnson 2000, Stefanov and Terashima 2008, Vredenberg 2008). Thus, photoprotection mechanisms could be different between leaves in full sun and those in shade. Chl *b* is mainly contained in the light-harvesting Chl protein complex II (LHCII) (Bailey *et al.* 2001, Walters 2005), and shaded leaves are relatively rich in Chl *b* (Zhang *et al.* 2007). Thus, shaded leaves can trap more light energy through LHCII to promote photosynthetic efficiency. While leaves in full sun have relatively low Chl *b* content, and in turn a low light-trapping ability in the antennae of LHC. Through this mechanism, more light energy can be dissipated as heat and fluorescence in sun leaves, avoiding severe damage to reaction centers (Iglesias-Prieto and Trench 1997, Bailey *et al.* 2004).

Ferns have been around for more than 300 million years. They have a great diversity of forms and they thrive in many habitats (Fernández and Revilla 2003). *A. pachyphlebium* is a perennial fern generally located in the moist understory of forests with photosynthetic photon flux density (PPFD) around 120–600 μmol m^{-2} s^{-1} (5–30% of full sunlight) in the temperate region of east Asia. In its natural habitats, the ornamental vegetative pinnate sustain vigorous growth until late autumn. As with many other ferns, the striking foliage, lack of pests and diseases, ease of propagation and high shade-tolerant ability have made it a popular ground-cover plant in low-light situations. However, when planted in high-light locations, they show symptoms of stress, such as leaf chlorosis and necrosis. In contrast, deep shade conditions may result in excessive vegetative growth and although typically not lethal, the aesthetic value is diminished. To date, there have been few studies on light acclimation and domestication of ferns (Gratani *et al.* 1998, Durand and Goldstein 2001). Furthermore, although *A. pachyphlebium* is widely distributed below the canopy of forests, there has been no research about its light acclimation capacity.

Therefore, the objectives of this study were to: (*1*) evaluate the effects of various light intensities on plant morphology, photosynthetic and Chl fluorescence traits of *A. pachyphlebium*, and (*2*) determine the optimal light intensities for its growth and application in urban landscapes.

Materials and methods

Plant materials and culture conditions: The experiment was run outdoors at Beijing Forestry University in China. The mean annual temperature and precipitation in this region were 11.8°C and 644 mm from 1990 to 2008, respectively. Spores of *A. pachyphlebium* were collected from Bai-hua mountain located in the northwest suburbs of Beijing in October 2007 and were sown immediately into plastic tubes in the greenhouse. After the roots had elongated adequately, the seedlings with mean heights of 10 cm and 5 leaves were transplanted into a substrate mixture of soil:sand:peat (4:2:2, v/v/v) on the experimental plots in May 2008.

Four light levels were generated by covering each plot with either 2, 3, 4, or 5 layers of shade cloth, respectively. A single layer of shade cloth excluded nearly 45% incident irradiance. Light intensities were measured on June 28, 2008, a sunny cloudless day, at 11:00 h using a PAR Quantum Sensor (*SKP216, Skye Instruments Ltd.,* UK). This showed that the actual photosynthetic photon fluxes for 2, 3, 4, and 5 layers of shade cloth and open side ranged from 813 to 886, 576 to 633, 335 to 402, 134 to 175 and 1846 to 1914 μmol m^{-2} s^{-1}, respectively. Consequently, the four treatments provided 45%, 30%, 20%, and 8% of full sunlight. Shade cloths were applied in spring (March 1, 2008) before bud break and removed in fall (December 10, 2008) after growth of the plants ceased. The seedlings were randomly grown under shade cloth shelters, 30 plantlets were planted in each treatment and the seedlings were irrigated to the field capacity of the substrate.

Morphological measurements: From early spring to autumn 2008, five seedling subsamples from each plot were measured for plant height, mean crown width (crown diameters measured along north-south and east-west axes), number of fronds and the ratio of vegetative fronds to fertile fronds (V/F) at 2-week intervals. These measurements were used to form growth dynamic curves over time. Dormancy time was recorded for each seedling, when most vegetative leaves (> 90%) turned into fertile leaves and the plant ceased growth. Fresh vegetative pinnate samples were collected in the field. Pinnate area was measured with a leaf area meter (*LI-3000A, LI-COR Inc.,* Lincoln, USA), then dried at 80°C to a constant mass which was used to determine leaf dry mass per unit area (LMA). There were three replicates for each site.

Chl content: Fresh mass (FM) of pinnate samples were collected from recently matured healthy leaves in each treatment in the morning of July 10, 2008. Chl was extracted with a mortar and pestle in 80% chilled acetone plus $MgCO_3$ and purified sea sand. Chl content was analyzed with a spectrophotometer (*UV-2550, Shimadzu,* Kyoto, Japan) and calculated using equations developed by Inskeep (Inskeep and Bloom 1985). Three replicates were taken for each site.

Light-response curves: Photosynthetic responses to PPFD were determined on fully expanded sterile leaves with a *LI-6400* portable photosynthesis system (*LI-6400, LI-COR Inc.,* Lincoln, NE, USA), using *6400-02B* LED light source chamber (2 × 3 cm). The experiments were carried out on three sunny days between 8:30 h and 12:00 h in the middle of July 2008. After the leaves were supplied with CO_2 at 360 μmol mol^{-1} and given 20 min to stabilize, the net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured at 800, 700, 600, 500, 400, 300, 200, 100, 60, 40, 30, 20, 10, and 0 μmol m^{-2} s^{-1} PPFD. Throughout this process, leaf temperature and relative air humidity in the measuring chamber were maintained at 24 ± 1°C and 65 ± 5% , respectively,and the leaf-to-air vapour pressure deficit was kept between 1 and 1.3 kPa. Light-saturated photosynthesis (P_{max}), apparent quantum efficiency (AQE), LSP and LCP were determined using the P_N-PPFD curve.

Chl fluorescence measurements were made using an *FMS-2* pulse-modulated fluorometer (*FMS-2, Hansatech,* Kings Lynn, UK) in the morning between 6:00 h and 9:00 h on July 16, 2008. Five replicates were taken for each site. After 30 min of dark adaptation (using a leaf clip on leaf), the minimal fluorescence (F_0) was measured using a weak modulated light at a controlled temperature of 25°C, and the maximal fluorescence (F_m) was determined by a 0.8-s saturation pulse flash at 3000 μmol m^{-2} s^{-1} PPFD. Then the leaves were illuminated with an actinic light at an intensity of 600 μmol m^{-2} s^{-1} PPFD for about 20 min. Following this, the steady-state value of fluorescence (F_s) was recorded and a second saturating pulse at 3,000 μmol m^{-2} s^{-1} PPFD was imposed to determine the maximal light-adapted fluorescence (F_m’). The actinic light was removed and the minimal fluorescence level in the light-adapted state (F_0’) was determined after 3 s of far-red illumination. The fluorescence parameters were obtained from the following formulas according to Bilger and Bjorkman (1990) and Maxwell and Johnson (2000): the maximal quantum efficiency of photosystem II (PSII), $F_v/F_m = (F_m - F_0)/F_m$; the effective quantum yield of PSII, $\Phi_{PSII} = (F_m' - F_s)/F_m'$; photochemical quenching coefficient, $q_P = (F_m' - F_S)/(F_m' - F_0')$; the nonphotochemical Chl fluorescence quenching, $NPQ = (F_m - F_m')/F_m'$; the electron transport rate, ETR = Φ_{PSII} × PFDa × 0.5, where PFDa is calculated from the incident PFD assuming a leaf absorptance of 0.84 and 0.5 as a factor that accounts for the portioning of energy between PSII and PSI.

Statistical analysis was performed using *SPSS 13.0* (*SPSS Inc.*, Chicago, USA). All of the measurements were performed more than three times, the means and calculated standard errors (SE) were reported and analyzed using one-way *ANOVA* and LSD multiple comparisons tests.

Results

Growth and morphology: There were significant differences in growth and morphology of *A. pachyphlebium* in all four treatments. The differences increased as the treatment continued, as shown in the growth dynamic curves over time (Fig. 1). After about one month of growth, differences in several growth parameters occurred among treatments, particularly in plant height and leaf number (Fig. 1*A,C*). After two months, no further growth occurred with seedlings in 45% full sun, while seedlings in other light levels continued to grow until the dormancy time was reached.

Table 1 shows comparisons of morphological parameters in mid-August. Growth in 45% full sun was significantly slower compared to that in the other treatments, showing the least height growth, crown extension, foliage number, and more noticeable symptoms of high-light stress. Height and crown growth in 20% and 8% full sun were significantly more vigorous than those in the other two light levels in mid-August. In 20% light level, seedlings had the greatest crown width (46.5 cm) and foliage number (23.2). When illumination declined to the level of deep shade (8% light), height increase was greater than crown extension because of the relatively lower foliage number (13.2) and greater stem height. Owing to these features, seedlings in deep shade were thin and slender, leading to severe symptoms of lodging. The values of LMA in high-light irradiances were much higher than those in low light irradiances. The data clearly revealed that the dormancy time of seedlings in different illuminations was highly correlated to the value of V/F. As the value of V/F declined from 0.91 in 45% full light to 0.40 in 20% full light, the dormancy duration increased from early August to later October. Compared to other shade levels, seedling growth in 30% full sun was intermediate with slight chlorosis appearing in August, while plants in 20% full sun exhibited the most vigorous

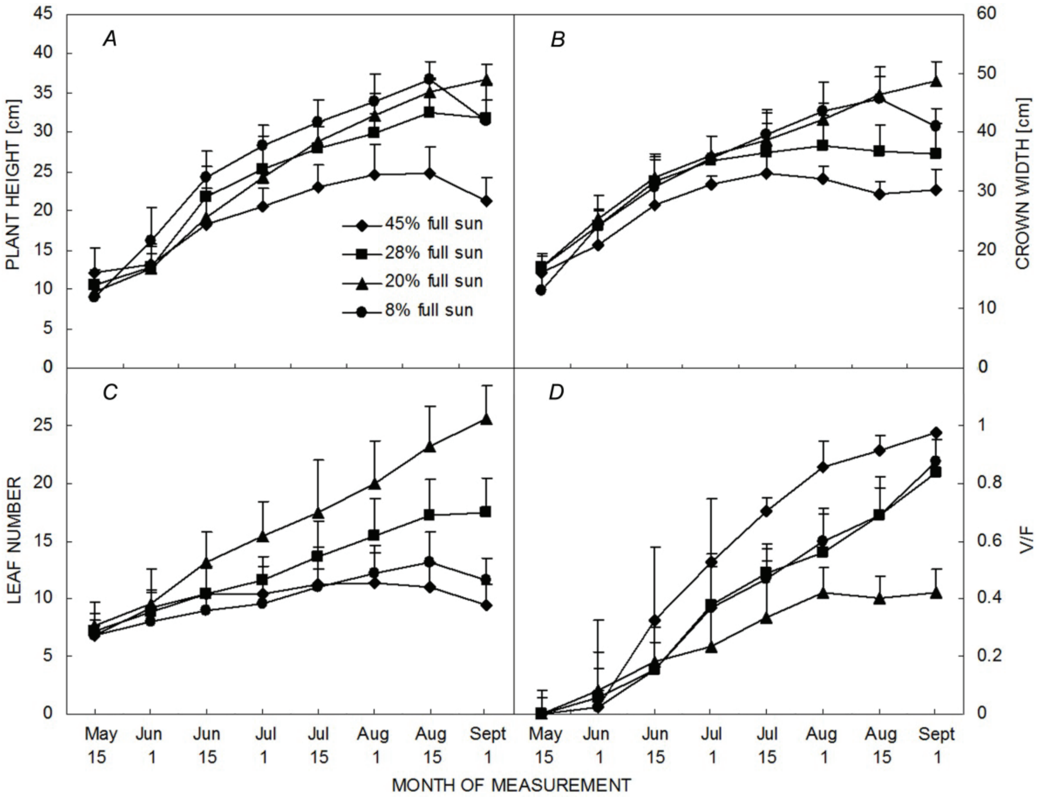

Fig. 1. Growth dynamics of *A. pachyphlebium* at four light levels over time. Each point represents the mean ± SE of five plants. V/F – the ratio of vegetative fronds to fertile fronds.

and enduring growth, maintaining an optimum balance in vegetative and fertile growth until late October.

Light-response curves: The patterns of the light-response curves were similar for all four treatments (Fig. 2). Variation of P_N, g_s, and E showed similar trends, increasing rapidly up to 100 µmol m^{-2} s^{-1} PPFD, then rising slowly until reaching their maximum values (Fig. 2*A*,*C*,*D*). The variation trend of C_i was opposite to that of the others (Fig. 2*B*). Seedlings grown in higher light intensities had higher P_N, g_s and E than those grown in low light intensities. There were significant differences in AQE among the four light levels (Table 1) with seedlings in 20% full sun having the highest value (0.050). Both LCP and LSP decreased in line with the decline in light intensity with significant differences existing among different light treatments. The values of P_{max} for seedlings were significantly different among the four treatments, with the highest in 45% light (5.47 µmol m^{-2} s^{-1}) and lowest in 8% light (2.77 µmol m^{-2} s^{-1}).

Chl content: As shown in Table 1, total Chl content per unit area declined with increasing irradiance. Seedlings in 8% and 20% full sun had significantly higher Chl (*a*+*b*), Chl *a* and Chl *b* than those in the other two light levels. In contrast, there was a significant decrease in Chl *a*/*b* with declining irradiance.

Chl fluorescence: NPQ and ETR were sensitive to different light environments (Fig. 3*A*,*C*). ETR was significantly higher in deep shade than in sunny habitats. In contrast, NPQ were greatest in 45% full sun (0.69) and least in 20% full sun (0.21). Values of Φ_{PSII} and q_p increased as illumination decreased to 20% full sun, however, significant differences were only detected in Φ_{PSII} among treatments (Fig. 3*B*). Dark-adapted ratio of F_v/F_m for each light level was similar at around 0.85, and no significant differences were detected among treatments. The data of F_v/F_m and q_p was not shown in Fig. 3 as there were no significant treatment effects.

Discussion

A. pachyphlebium is a shade-tolerant fern naturally distributed below the forest canopy. Compared to growing in high light, seedlings in low light of 20% full sun grew vigorously with good height growth, crown extension, increased foliage number and life span duration. In deep shade of 8% full sun, however, seedlings tended to exhibit excessively height growth and leaf extention to trap more light, resulting in severe

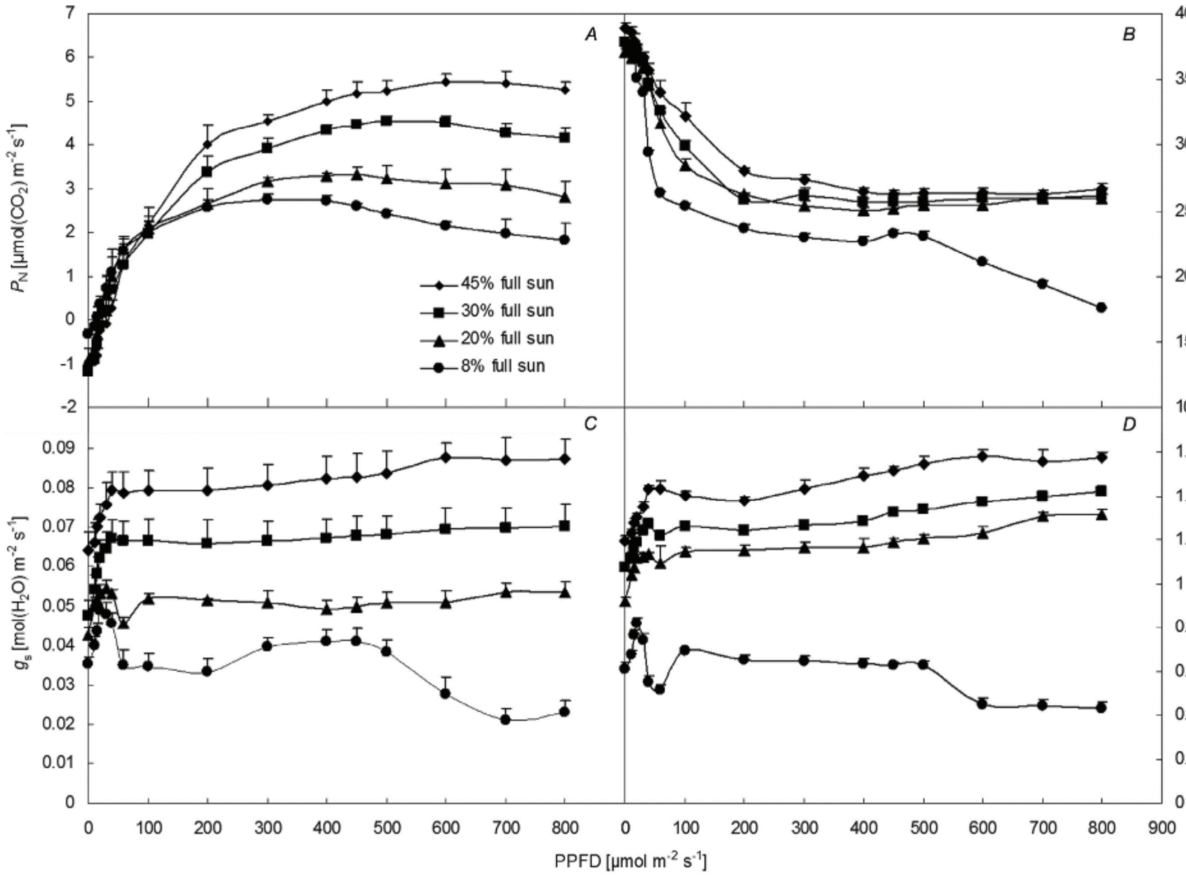

Fig. 2. Response of net photosynthetic rate (P_N), intercellular CO$_2$ concentration (C_i), stomatal conductance (g_s) and transpiration rate (E) to increasing photosynthetic photon flux density (PPFD). Each value represents the mean ± SE of three days.

Table 1. Comparisons of growth and photosynthetic parameters of *A. pachyphlebium* under four light irradiances in mid-August in 2008. The chlorophyll amounts are presented as related to fresh mass (FM). Mean values ± SE (n>3) were analyzed with a one-way *ANOVA*. *Different letters* adjacent to each value indicate significant differences between light levels (P<0.05; LSD tests). AQE – apparent quantum efficiency; Chl – chlorophyll; Chl (a+b) – total chlorophyll content; LCP – light-compensation point; LMA – leaf dry mass per unit area; LSP – light-saturation point; V/F – the ratio of vegetative fronds to fertile fronds; P_{max} – light-saturated photosynthetic rate.

	Light irradiance [%]			
	45	28	20	8
Plant height [cm]	24.8 ± 3.35^b	32.6 ± 4.4^a	35.2 ± 1.48^a	37.0 ± 2.22^a
Crown width [cm^2]	29.6 ± 2.04^c	36.80 ± 4.41^b	46.50 ± 2.98^a	45.60 ± 5.4^a
Leaf number	11.00 ± 2.12^c	17.20 ± 3.11^b	23.20 ± 3.42^a	13.20 ± 2.59^{bc}
V/F [%]	0.91 ± 0.09^a	0.70 ± 0.14^b	0.4 ± 0.08^c	0.69 ± 0.14^b
LMA [mg cm^{-2}]	0.98 ± 0.16^a	0.83 ± 0.08^b	0.72 ± 0.05^c	0.58 ± 0.07^d
LCP [μmol m^{-2} s^{-1}]	33.33 ± 5.77^a	28.33 ± 7.64^a	18.33 ± 2.89^b	16.33 ± 2.89^b
LSP [μmol m^{-2} s^{-1}]	633.3 ± 57.74^a	533.3 ± 57.74^b	450.0 ± 50^b	300.0 ± 0^c
P_{max} [μmol m^{-2} s^{-1}]	5.47 ± 0.2^a	4.57 ± 0.11^b	3.4 ± 0.12^c	2.77 ± 0.12^d
AQE [CO$_2$ photon^{-1}]	0.04 ± 0.001^b	0.04 ± 0.001^b	0.05 ± 0.001^a	0.03 ± 0.002^c
Chl a [mg g^{-1}(FM)]	1.14 ± 0.02^c	1.35 ± 0.03^b	1.50 ± 0.06^a	1.50 ± 0.03^a
Chl b [mg g^{-1}(FM)]	0.64 ± 0.01^c	0.78 ± 0.02^b	0.94 ± 0.06^a	0.96 ± 0.03^a
Chl (a+b) [mg g^{-1}(FM)]	1.78 ± 0.02^c	2.12 ± 0.05^b	2.44 ± 0.15^a	2.47 ± 0.04^a
Chl a/b	1.80 ± 0.04^a	1.74 ± 0.04^a	1.60 ± 0.01^b	1.56 ± 0.06^b
Leaf color	Chlorosis	Yellowish	Green	Dark green
Dormancy time [month]	Early Aug	Early Sept	Later Oct	Early Oct

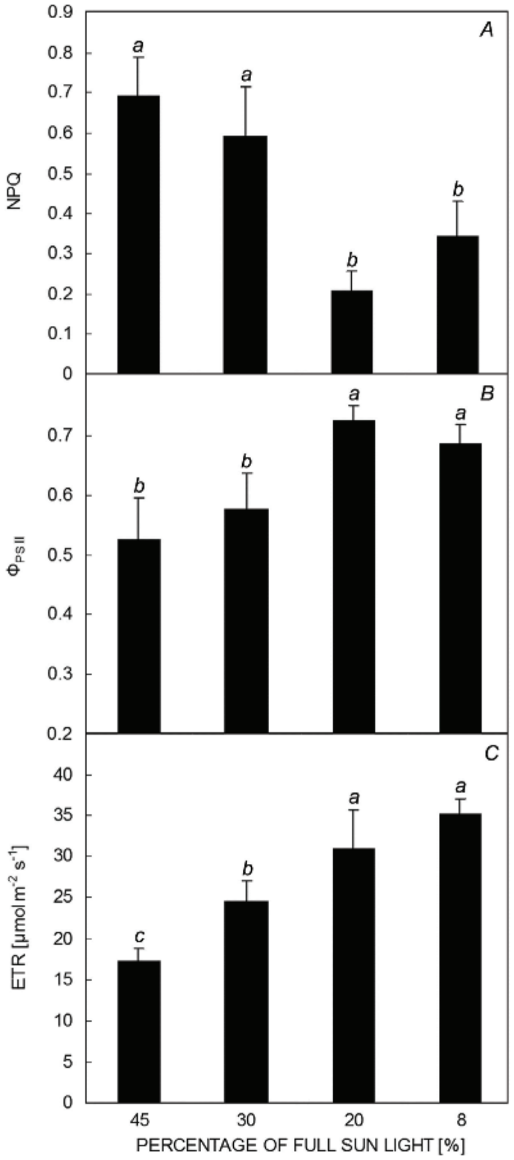

Fig. 3. Comparisons of nonphotochemical quenching (NPQ), actual photochemical efficiency of PSII (Φ_{PSII}) and electron transport rate (ETR) for *A. pachyphlebium* in four light levels. Each value represents the mean ± SE of five leaves. Leaf temperature was 33°C. *Different letters* above to each bar indicate significant differences between light levels ($P<0.05$; LSD tests).

lodging. Most shade-tolerant plants perform poorly in deep shade, while moderate shade does not have an adverse effect, as was reported for seedlings of *Fraxinus pennsylvanica* and *Quercus suber* (Bartlett and Remphrey 1998, Khan *et al.* 2000, Cardillo and Bernal 2006, Zhang *et al.* 2007).

Many studies have shown that, to make the best use of light in light-limited environments, shade-tolerant plants will increase their height, crown extension, leaf area, as well as adjust their branch and leaf arrangement (Bartlett and Remphrey 1998, Paquette *et al.* 2007). When growing in a high-light environment, however, shade-adapted plants become extremely distressed, they are not able to adjust quickly or efficiently to a high light, and thus are less likely to survive, such as the fern *Sphaeropteris cooperi* and the genus *Cibotium* native to Australia (Hiroki and Ichino 1998, Durand and Goldstein 2001, Paquette *et al.* 2007). Furthermore, they tend to finish their growth season earlier to facilitate a faster recovery from photoinhibition. In understory-adapted species, a relationship between higher yields of PSII electron transport and shorter leaf life span exists (Lovelock *et al.* 1998, Durand and Goldstein 2001).

Morphology and life span of ferns are closely linked to leaf production and the time of fertile fronds formation. According to this study, seedlings in deep shade (8% full sun) and high light (45% full sun) entered into dormancy earlier, because a lower number of new fronds sprouted over the year compared to that in moderate light intensities (20% and 30% full sun). Many studies have shown that more leaves sprout out over a year, the life span of a plant tends to be longer (Bond *et al.* 1999, Durand and Goldstein 2001). This study also found that the sooner more vegetative fronds developed into fertile fronds, the earlier plants lost their ornamental value and ceased growth.

Plants may change their photosynthetic characteristics to acclimate to varying light conditions. In the current study, the values of LSP, LCP, and P_{max} were significantly higher in high light than those in low light. High P_{max} in high light is beneficial for plant growth, as the plants can make full use of light to balance intense dark respiration and vigorous metabolism (Griffin *et al.* 2004, Zhang *et al.* 2005). Plants acclimated to low light levels tend to have low photosynthetic capacity and LCP, which may help maintain a positive carbon balance (Durand and Goldstein 2001, Olsen *et al.* 2002). In addition, the relatively high AQE in low light indicates that shaded leaves have a higher light-use efficiency, which is important for seedling establishment and growth (Zhang *et al.* 2007). P_N increased with the increasing of PPFD, which in turn commanded more CO_2, contributing to the decline of C_i and a rising g_s. Before the PPFD increased to 100 µmol m^{-2} s^{-1}, the values of g_s, E and C_i varied dramatically which may be due to the quick light induction of the enzymes involved in the Calvin cycle and forming a metabolism center (Sassenrath *et al.* 1994, Buckley *et al.* 2003).

Increased light irradiances also resulted in a reduction in Chl content, especially Chl *b* content. Chl *b* is most abundant in the antennae of LHC, whereas Chl *a* is concentrated around PSII. Low Chl *b* in high-light leaves facilitates photoprotection of the reaction center of PSII by reducing light absorption (Walters 2005, Feng 2008). Shaded leaves (in 8% and 20% full sun), in turn, had a relatively high Chl content and high levels of LHC to receive as much light as possible (Anderson and Aro 1994, Feng 2008). All these features contribute to the efficient interception and absorption of light for use in carbon gain.

Dark-adapted F_v/F_m reflects the potential quantum efficiency of the PSII and is used as a sensitive indicator of plant photosynthetic performance, with optimal value of around 0.83 measured for most plant species (Maxwell and Johnson 2000). It is generally accepted that F_v/F_m will decline when shade-adapted plants are exposed to high-light stress (Anderson and Aro 1994, Khan *et al.* 2000). In this study, although F_v/F_m declined with decreasing illumination, all values were close to 0.83 in all four treatments. This may be misleading because the morphological characteristics were quite different between in 45% and 20% full sun. Light energy in plants can be consumed by photochemical processes and non-photochemical processes (Lin and Hsu 2004, Stefanov and Terashima 2008). In this study, seedlings in 45% full sun decreased light absorption by reducing leaf area and Chl content. Furthermore, values of NPQ were significantly higher in sunny habitats than in shade. High NPQ indicates that high levels of light energy that exceed photosynthetic capability will be transformed into thermal dissipation. Thus, severely chlorotic leaves in 45% light maybe the result of high light intensity. Φ_{PSII} is the proportion of absorbed energy being used in photochemistry, and q_p gives an indication of the proportion of PSII reaction centers that are open (Maxwell and Johnson 2000, Zhang *et al.* 2007). In this study, as light irradiance decreased to 20%, both Φ_{PSII} and ETR reached their maximum, indicating that seedlings in low light had higher photochemical capacity and a greater efficiency at transferring light energy from the light-harvesting complex to PSII.

Successful acclimation to different light environments requires a balance between plant physiological mechanisms and morphological modification. Seedlings in 20% light level appeared to be best at capturing and using light resources, thus achieving vigorous and enduring growth. Though seedlings in 45% and 30% light levels attained high P_{max}, chlorotic leaves and short life span weakened their aesthetic values. Severe symptoms of lodging and the low P_{max} for seedlings in 8% full sun proved that heavy shade is detrimental for seedlings' growth both physiologically and morphologically .

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