Photosynthetic performance of *Lycoris radiata* var. *radiata* to shade treatments

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Abstract

The effects of shade on the growth, leaf photosynthetic characteristics, and chlorophyll (Chl) fluorescence parameters of *Lycoris radiata* var. *radiata* were determined under differing irradiances (15, 65, and 100% of full irradiance) within pots. The HI plants exhibited a typical decline in net photosynthetic rate (P_N) during midday, which was not observed in MI- and LI plants. This indicated a possible photoinhibition in HI plants as the ratio of variable to maximum fluorescence (F_v/F_m) value was higher and the minimal fluorescence (F_0) was lower in the , and LI plants. Diurnal patterns of stomatal conductance (g_s) and transpiration rate (E) were remarkably similar to those of P_N at each shade treatments, and the intercellular CO_2 concentration (C_i) had the opposite change trend. Under both shading conditions, the light saturation point, light compensation point and photon-saturated photosynthetic rate (P_{max}) became lower than those under full sunlight, and it was the opposite for the apparent quantum yield (AQY). The higher the level of shade, the lower the integrated daytime carbon gain, stomatal and epidermis cell densities, specific leaf mass (SLM), bulb mass ratio (BMR), leaf thickness, and Chl *a*/*b* ratio. In contrast, contents of Chls per dry mass (DM), leaf area ratio (LAR), leaf mass ratio (LMR), leaf length, leaf area and total leaf area per plant increased under the same shade levels to promote photon absorption and to compensate for the lower radiant energy. Therefore, when the integrated daytime carbon gain, leaf area and total leaf area per plant, which are the main factors determining the productivity of *L. radiata* var. *radiata* plant, were taken into account together, this species may be cultivated at about 60~70% of ambient irradiance to promote its growth.

Additional key words: chlorophyll fluorescence; diurnal course; irradiance; leaf anatomy; leaf morphology; net photosynthetic rate; shade.

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 (Smith 1982, Evans and Poorter 2001, Muraoka *et al*. 2002, Keller and Lüttge 2005). Irradiance is the energy source for all photosynthetic organisms, which are finely tuned to harvest it efficiently. On the other hand, excess irradiance captures result in photoinhibition of photosynthesis. As a result, plants have devised some sophisticated mechanisms to adapt them in irradiance environment that prevails. The adaptation of photosynthetic apparatus to the prevailing irradiance is known as irradiance acclimation of photosynthesis (Anderson *et al*. 1995). Photosynthetic irradiance acclimation involves a variety of responses, including changes in leaf anatomical, morphological,

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Abbreviations: AQY – apparent quantum yield; BMR – bulb mass ratio; Chl – chlorophyll; C_i – intercellular CO_2 concentration; DM – dry mass; E – transpiration rate; F_0 – minimal fluorescence; F_v/F_m – ratio of variable to maximum fluorescence; g_s – stomatal conductance for CO_2; HI – high irradiance; LAR – leaf area ratio; LCP – light compensation point; LI – low irradiance; LMR – leaf mass ratio; LSP – light saturation point; MI – medium irradiance; P_{max} – photon-saturated photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; RMR – root mass ratio; SLM – specific leaf mass; T_{leaf} – leaf temperature.
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biochemical, and photosynthetic characteristics (Pandey *et al*. 2003). Plants grown in low photosynthetic photon flux density (PPFD) have lower P_N and SLM and these two parameters affect the productivity of a plant (Anderson 1986). In contrast to this, plants grown under high PPFD increase their SLM due to extra layers of palisade or longer palisade cells (Vats *et al*. 2002). Besides, they absorb a large amount of photons and sustain high P_N and biomass accumulation. A long time of high PPFD exposure, however, may damage the photosynthetic apparatus (Zhang *et al*. 2003). Thus, study on the photosynthetic and growth responses of plant, will contribute to increase the understanding of physiological mechanism of plant distributions and assist in the development of approaches to rationally use and conserve this species.

Lycoris radiata var. *radiata*, a member of the Family Amaryllidaceae, is a typical hysteranthous geophyte with leaf appearing in autumn and an endemic species in East Asia, principally native to China, Japan, and Korea. In the wild, *L. radiata* var. *radiata* usually distributes in sheltered moist slops along streams in the mountains, edges of forests, paddy fields, and margins of plantations (Xu *et al*. 1994). It is a very popular bulb flower worldwide with considerable ornamental and medical value (Zhou *et al*. 2007). To date, studies of *L. radiata* var. *radiata* have focused mainly on karyotypes (Bose 1963, Kurita 1987, Xu *et al*. 1994, Zhou *et al*. 2007), morphology (Deng and Zhou 2005, Zhou *et al*. 2006), artificial propagation (Li *et al*. 2005), medicine (Wu *et al*. 2005, Du *et al*. 2007), allozyme (Chung 1999), and molecular aspect (Shi *et al*. 2006, Zuo *et al*. 2008). The growth and photosynthetic responses of three other *Lycoris* species with leaf appearing in spring to levels of irradiance were studied (Meng *et al*. 2008). Little is known about the leaf photosynthetic characteristics and responses of *L. radiata* var. *radiata* to different lights. By comparing the P_N of this species at 9:00–10:00 under full sunlight and grasshouse, Guo (2007) concluded that sun-grown plants had higher P_N than shade-grown ones at 9:00–10:00, and thought that this species would grow better under full sunlight than under shade. He did not consider that the leaf area and total leaf area per plant of this species under full sunlight would decrease significantly as we observed, accompanied with the decline in primary productivity, so the conclusion was very controversial. Because of the considerable ornamental and medical value and the increasing industrial demand for *L. radiata* var. *radiata*, its wild resource was destroyed and decreasing markedly day by day (Yuan 2009). The aim of our study was to evaluate the influence of shade on photosynthetic performance and growth of *L. radiata* var. *radiata* in order to scale up its growth and productivity.

Materials and methods

Plants and experiment design: The bulbs of *L. radiata* var. *radiata* were collected from Langya Mountain (118º15'E, 32º17'N), Anhui province, China. The karyotype formula of this species is 2*n*=33=33t (Zhou *et al*. 2007). In May 2007, ten bulbs with similar size or mass were put into each pot of 22-cm diameter and 18-cm height containing garden soil. 1 % of mono-ammonium phosphate ($NH_4H_2PO_4$) was added to each pot. A complete randomized design with one factor (PPFD regime) and four replicates was used. All the pots were placed under a greenhouse in the campus of Anhui Normal University (118º22'E, 31º20'N) until the leaf began to sprout out and then transferred to three different environments on September 4, 2007: high irradiance (HI), medium irradiance (MI) and low irradiance (LI), which were about 100, 65, and 15 % of full ambient irradiance, respectively, and controlled by different layers of shading nylon nets being placed horizontally on a wood frame with 110 cm height from the ground in the open field. During the experiments, the bulbs were watered and cultivated using standard methods depending on the weather and soil moisture status. The photosynthetic characteristics of *L. radiata* var. *radiata* were measured on clear days (November 19–20, 2007).

During this period the experimental site had a mean max/min temperature 23.3/15.7°C, relative humidity 77.9 %, wind speed of 2.2 km h^{-1}, bright sunshine of 4.4 h, and 25 rainy days with 227.6 mm rainfall (Meteorological Station of the Wuhu, China).

Photosynthesis measurements: At the vigorous vegetation growth stage, photosynthesis was measured on a clear day (November 19, 2007) throughout daytime from 7:00 to 17:00 at two-hour intervals. Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and transpiration rate (E) were measured using a hand-held photosynthesis system (*CI-340*, *CID*, Camas, WA, USA). For measurements the central portion of leaves was selected. The final value was the mean of four replicates. The integrated daytime carbon gain per unit leaf area of *L. radiata* var. *radiata* was estimated by integrating the areas beneath the diurnal photosynthetic CO_2 assimilation curves.

Irradiance response of P_N: The response of P_N to step changes in PPFD was examined by a red + blue LED light source (*CI-301LA*, *CID*, Camas, WA, USA). The light-response curve measurements were carried out on the morning of November 20, 2007 from 8:30 to 11:30. The CO_2 concentration and air temperature in the leaf chamber were maintained at about 360 μmol mol^{-1} and 25°C, respectively. Eleven irradiances (0, 50, 100, 200, 300, 400, 500, 700, 1,000; 1,200; and 1,500 μmol m^{-2} s^{-1} PPFD) were set and PPFD started at 1,500 μmol m^{-2} s^{-1}

and decreased stepwise to 0 μmol m^{-2} s^{-1}. Leaves were allowed to acclimate to each PPFD for at least 3 min, then steady-state gas exchange properties were observed and logged, and subsequently the PPFD in the cuvette was changed. Light-response curves were plotted using the mean values of P_N measured at each PPFD. Four replicates were made. AQY was calculated from the initial slopes by linear regression using PPFD values below 200 μmol m^{-2} s^{-1}. Light compensation point (LCP), light saturation point (LSP), and P_{max} were estimated by the method of Bassman and Zwier (1991).

Chl fluorescence: After at least 20 min of dark adaptation, the minimal level of Chl *a* fluorescence (F_0) was measured with a *CI-510CF* Chlorophyll Fluorescence Module (*CID*, Camas, WA, USA) under modulated light intensity of 0.25 μmol m^{-2} s^{-1} and the maximal level of Chl *a* fluorescence (F_m) was induced by a 1-s saturating flash with the intensity of the saturating pulse being 3,000 μmol m^{-2} s^{-1} provided by the *CI-510CF* Chlorophyll Fluorescence Module. Variable Chl *a* fluorescence (F_v) equals F_m minus F_0. From the various fluorescence levels, F_v/F_m was calculated (Schreiber *et al*. 1986).

Biomass, leaf area, and Chl content: After the determinations of photosynthetic characteristics and Chl fluorescence, all plants were harvested and then separated into roots, bulbs, and leaves for the following measurements. The leaf length and leaf width were measured and the leaf area was determined using a portable leaf area meter (*WDY-300A*, *HOIF*, Harbin, China). After the fresh mass of 30 plants for each treatment was measured, they were dried in an oven at 80°C for at least 48 h for determination of DM.

SLM, LAR, LMR, root mass per unit of total mass (root mass ratio, RMR), and bulb mass per unit of total mass (bulb mass ratio, BMR) were determined according to Hunt (1978) and based on DM. Leaf samples of 300 mg from the remaining 10 plants were ground and extracted with 80% acetone with four replicates in each treatment. The absorbance of extracts was measured at 645 and 663 nm by a spectrophotometer (*UV-3802*, *UNICO*, Shanghai, China) and the contents of Chls were calculated according to Zhang and Qu (2003).

Leaf morphological and anatomical measurements: Thirty leaf segments from the middle of 30 leaves of the remaining 10 plants for each treatment were fixed in FAA (50% ethanol:formaldehyde:acetic acid, 90:5:5) and dehydrated in a *t*-butyl alcohol series. Sections (10 μm thick) were stained with safranine-fast green, and the slides were mounted in neutral balsam *FMP* (China). Stomatal and epidermal cell densities were estimated from abaxial leaf surface impressions of 30 leaf segments. The photographs were taken under a biological microscope (*BA200*, *Motic*, Fujian, China) at 100 × magnification for both anatomical and morphological measurements. Micrographs were analyzed with *Motic Images Plus 2.0* software to determine thickness of palisade and mesophyll cells and stomatal and epidermal cell densities. Stomatal index was calculated by using formula $[S/(E + S)]\times100$, where S and E indicate number of stomata and epidermal cells per unit area of leaf, respectively.

Data analysis: Standard deviation (SD) was calculated and differences in measured variables between treatments were analyzed by *ANOVA*, and the means were compared with Student-Newman-Keuls' multiple comparison tests. All tests for significance were done at $p<0.05$, unless otherwise indicated.

Results

***P_N* -PPFD response under different growth irradiances**: From 0 to 300 μmol m^{-2} s^{-1}, all the curves responded rapidly, and then increased slowly to the maximum values (Fig. 1). In all treatments, the net assimilation increased remarkedly with decreasing light intensity until the PPFD was 700 μmol m^{-2} s^{-1}. HI-plants got P_{max} at about 700 μmol m^{-2} s^{-1}. P_{max}, LSP and LCP increased as growth irradiance increased, but the differences in P_{max} between HI- and MI-plants were not significant (Table 1). The AQY was significantly lower under HI than that under LI and MI, and the differences between LI and MI were statistically insignificant.

Environmental conditions: PPFD reached its maximum value in all conditions at 13:00 and declined after this time (Fig. 2*A*). The leaf temperature (T_{leaf}) increased with increase in PAR under all the conditions just after sunrise, ranged maximum (25–28°C) at 13:00, and declined in afternoon. T_{leaf} under sunlight condition was slightly higher than in MI- and LI-plants (Fig. 2*B*). The shading treatments always decreased the PPFD and T_{leaf}.

Photosynthesis and carbon economy: In HI treatment, this species showed typical two-peak pattern of diurnal photosynthesis changes (Fig. 3*A*). The first peak appeared at 11:00, while the other, much smaller than the first one, at 15:00. Under MI and LI conditions, the diurnal variation of P_N became a single-peak curve, and the peak values both appeared at 13:00. In general, the P_N in LI-plants was lower than that in HI- and MI-plants all the time, and the P_N in HI-plants was higher than that in MI-plants except at 13:00. The integrated daytime carbon gain of *L. radiata* var. *radiata* leaf in HI, MI and LI conditions were 452 mmol m^{-2} day^{-1}, 399 mmol m^{-2} d^{-1} and 184 mmol m^{-2} d^{-1}, respectively. Shade of 35 and 85% reduced integrated daytime carbon gain by 11.7 and

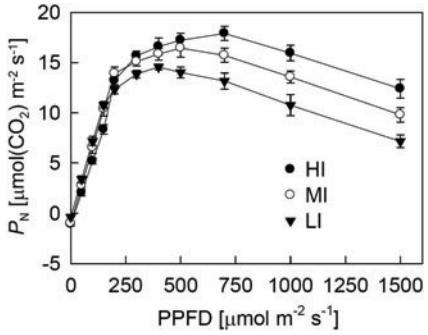

Fig. 1. Response of net photosynthetic rate (P_N) to PPFD in *L. radiata* var. *radiata* grown under high (full ambient), medium (about 65%) and low (about 15%) PPFD. Means ± SD (n = 4). *Error bars* are ± SD.

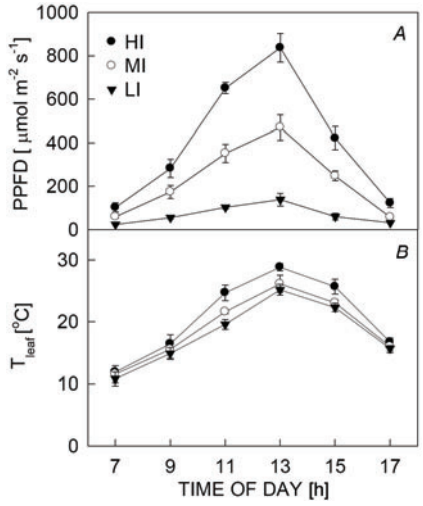

Fig. 2. Diurnal changes in photosynthetic photon flux density (PPFD) (*A*) and leaf temperature (T_{leaf}) (*B*) under different shade treatments. Means ± SD (n = 4). *Error bars* are ± SD.

59.3%, respectively. No significant difference existed in the integrated daytime carbon gain between HI- and MI plants, but in both it was significantly higher than that of LI plants.

***g*$_s$, *C*$_i$, and *E* of leaves**: Diurnal patterns of g_s were remarkably similar to those of P_N at each shading treatments (Fig. 3*B*). Intercellular CO_2 concentration was higher before the sunset than after the sunrise (Fig. 3*C*), then decreased towards midday, and again increased in the late afternoon. No significant difference in C_i was observed among all the irradiance conditions, except that the C_i in LI plants was markedly higher than that in HI- and MI plants at 11:00. In contrast to this, E was minimal in the morning (Fig. 3*D*), increased towards midday, and drastically declined in the late afternoon. E of LI plants was significantly lower than that of HI- and MI plants.

Chl fluorescence: The F_v/F_m under MI- and LI conditions remained high (~0.75) throughout the day, and a decrease was observed during the noon under HI condition, followed by a recovery in the late afternoon (Fig. 4*B*). The F_0 under HI condition was higher than that under MI and LI conditions all the day, and there were no significant differences in F_0 between MI and LI conditions (Fig. 4*A*).

Chl content, leaf morphology and anatomy: HI- and MI plants had significantly thicker leaves, palisade parenchyma and spongy parenchyma than LI plants (Fig. 5 and Table 2). The higher was the level of shade, the lower were stomatal and epidermis cell densities and Chl *a*/*b* ratio. Shade of 35 and 85% reduced stomatal density by 15.2 and 34.3%, respectively, while the corresponding reduction in epidermis cell density by 19.4 and 40.1%. There was no marked difference in the

Table 1. Comparison of photosynthetic characteristics (P_{max} – photon-saturated photosynthetic rate; AQY – apparent quantum yield; LSP – light saturation point; LCP – light compensation point) of *L. radiata* var. *radiata* grown under high (HI, full ambient), medium (MI, 65% ambient), and low (LI, 15% ambient) irradiances. Means ± SD. (n = 4). *Different letters* in superscript following the values in each column indicate significant differences (p<0.05) among three growth irradiances.

Growth irradiance	P_{max} [μmol(CO$_2$) m^{-2} s^{-1}]	AQY [mol mol^{-1}]	LSP [μmol m^{-2} s^{-1}]	LCP [μmol m^{-2} s^{-1}]
HI	17.82±1.41^a	0.0626±0.0023^b	742±25^a	17.09±1.56^a
MI	16.26±0.98^a	0.0753±0.0015^a	521±18^b	13.20±1.12^b
LI	14.15±1.12^b	0.0757±0.0013^a	391±23^c	5.07±0.85^c

stomatal index among three treatments. LI plants had significantly larger contents of Chl *a*, Chl *b* and Chl (*a*+*b*) than HI- and MI plants, for each of which MI plants had nonsignificantly higher content than HI plants (Table 2).

Growth and biomass allocation: Plant DM in LI condition was significantly lower than that in HI- and MI conditions. There was no difference in leaf width among three treatments. Leaf length, leaf area and total leaf area per plant of HI plants were significantly lower compared with those of MI- and LI plants. Although leaf length, leaf area, and total leaf area per plant were higher in LI condition than in MI condition, differences were not statistically significant. With shading intensity increased, SLM declined gradually, and SLM in HI condition was

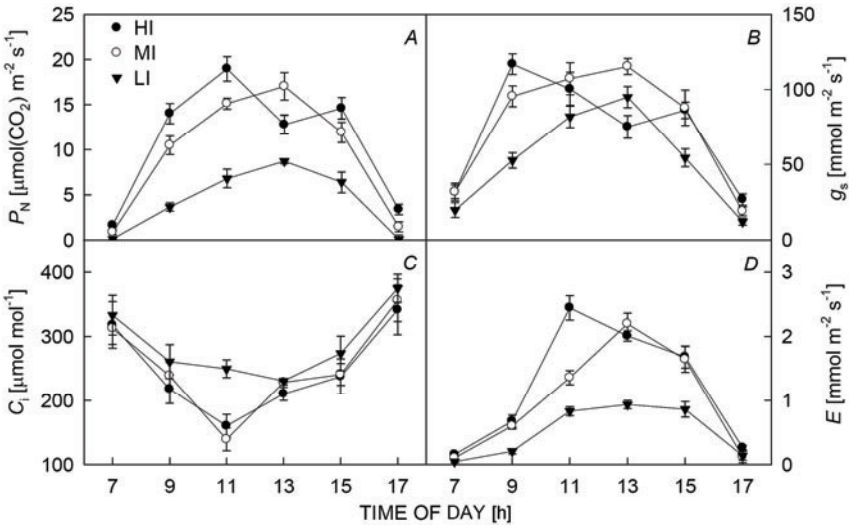

Fig. 3. Changes in net photosynthetic rate, P_N (*A*), stomatal conductance, g_s (*B*), intercellular CO_2 concentration, C_i (*C*), and transpiration rate, E (*D*) of *L. radiata* var. *radiata* plants grown under high (full ambient), medium (about 65%), and low (about 15%) PPFD. Means ± SD (n = 4). *Error bars* are ± SD.

significantly higher than that in LI and MI conditions. In contrast to this, LAR increased significantly as the growth irradiance decreased (Table 2).

Fig. 6 shows the proportion of plant dry biomass allocated to leaves, bulbs, and roots in *L. radiata* var. *radiata* grown under three treatments. No difference in RMR was found. The proportion of biomass allocated to bulb (BMR) was significantly lower in LI condition than that in HI- and MI conditions. Leaf mass ratio (LMR) significantly increased as irradiance declined.

Discussion

The changes in morphological and anatomical characteristics and their influences on photosynthetic and growth performances of *L. radiata* var. *radiata* grown under different PPFD were studied in this paper. The findings presented here will advance our understanding of photosynthetic characteristics of *L. radiata* var. *radiata* and assist in the optimization of irradiances needed to improve its productivity.

L. radiata var. *radiata* experienced a pronounced depression in P_N under HI condition at midday unlike MI and LI (Fig. 3*A*), and the phenomenon was reported in many species (Pandey 2003, Zhang *et al*. 2004, Roessler and Monson 1985). According to the opinions of Farquhar and Sharkey (1982), only when the C_i and g_s decrease simultaneously, it is supposed that the decline in P_N was mainly caused by stomatal limitation. As shown in Fig. 3, the change of C_i was nearly opposite to that of g_s under HI condition at midday from 11:00 to 13:00, and C_i increased, while g_s decreased. The results obtained in this study showed that decrease in P_N under HI condition at midday was not caused by stomatal limitation and g_s should not be a limit to photosynthesis in three conditions. The high irradiance or the associated increase in temperature or the limitation of the water conductivity may be the cause of decreased CO_2 assimilation in HI-plants.

The F_v/F_m ratio indicates the intrinsic efficiency of PSII photochemistry. A reduction in F_v/F_m is often taken to indicate photoinhibition (Powles 1984). The damage of the apparatus of PSII often results in increase in F_0 (Wu *et al*. 1997). In HI plants, F_v/F_m decreased (Fig. 4*B*) at noon and failed to recover back to morning rates even after significant decrease in PPFD in the afternoon (Fig. 2*A*). Under shading conditions, the F_v/F_m ratios remained constant (~0.75), which is slightly lower than the average of the values found in leaves of a wide range of C_3 species (0.83; Björkman and Demmig 1987) and shading decreased the minimal fluorescence (F_0)

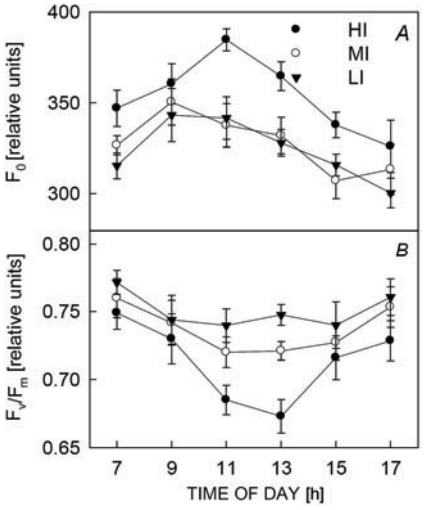

Fig. 4. Diurnal changes in F_0 (*A*) and current photochemical capacity, F_v/F_m (*B*) of *L. radiata* var. *radiata* plants grown under three irradiance conditions. Means ± SD (n = 10). *Error bars* are ± SD.

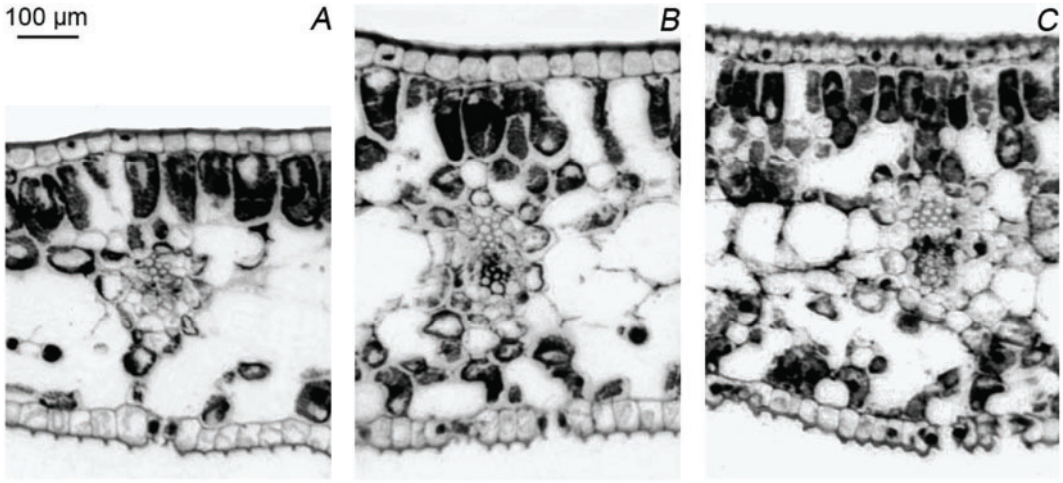

Fig. 5. Light micrographs showing the leaf structure and thickness of *L. radiata* var. *radiata* leaves grown under 15% light (*A*), 65% light (*B*) and full light (*C*).

Table 2. According to the order of parameters: The effect of irradiance on chlorophyll (Chl) contents (means ± SD, $n = 4$), stomatal density and leaf anatomical characteristics, and growth indices (means ± SD, $n = 30$) for three treatments. DM – dry mass; LAR – leaf area ratio; SLM – specific leaf mass. *Different letters* in superscript following the values in each row indicate significant differences ($p<0.05$) among three growth irradiances.

Parameter (leaf characteristics)	HI	MI	LI
Chl *a* [mg g^{-1}(DM)]	13.46 ± 1.35^a	15.20 ± 1.11^a	18.42 ± 1.53^b
Chl *b* [mg g^{-1}(DM)]	4.17 ± 0.83^a	5.10 ± 0.43^a	6.65 ± 0.91^b
Chl (*a*+*b*) [mg g^{-1}(DM)]	17.63 ± 1.91^a	20.30 ± 1.60^a	25.07 ± 2.70^b
Chl *a*/*b*	3.23 ± 0.11^a	2.98 ± 0.04^b	2.77 ± 0.06^c
Stomatal density [n mm^{-2}]	72.8 ± 12^a	61.7 ± 17^b	47.8 ± 14^c
Stomatal index	17.72 ± 1.39^a	18.35 ± 1.15^a	18.06 ± 1.20^a
Leaf thickness [µm]	765.1 ± 35.3^a	737.9 ± 42.5^a	587.4 ± 55.7^b
Palisade thickness [µm]	184.3 ± 20.4^a	150.5 ± 17.2^b	138.9 ± 22.9^b
Spongy thickness [µm]	491.3 ± 24.7^a	466.5 ± 28.7^a	359.4 ± 26.3^b
Epidermis cell density [n mm^{-2}]	242 ± 47^a	195 ± 45^b	155 ± 35^c
DM per plant [g]	2.82 ± 0.33^a	3.01 ± 0.41^a	2.03 ± 0.26^b
Leaf width [cm]	0.49 ± 0.07^a	0.52 ± 0.09^a	0.53 ± 0.09^a
Leaf length [cm]	13.4 ± 3.09^a	21.5 ± 4.45^b	26.2 ± 5.57^b
Leaf area [cm^2]	6.28 ± 1.06^a	11.01 ± 1.97^b	13.14 ± 2.43^b
SLM [g m^{-2}]	62.8 ± 3.14^a	55.5 ± 3.47^b	51.1 ± 5.16^b
LAR [m^2 kg^{-1}]	1.38 ± 0.24^a	2.17 ± 0.35^b	3.55 ± 0.39^c
Total leaf area per plant [cm^2]	37.5 ± 5.4^a	65.2 ± 6.7^b	72.2 ± 8.2^b

(Fig. 4*A*). The results showed that shading might protect the integration of the photosynthetic membrane systems and photochemical efficiency in leaves of *L. radiata* var. *radiata* against the strong light stress during midday, and in open environment, the combination of high PPFD level and temperature during midday might damage the apparatus of PSII in leaves of this species.

L. radiata var. *radiata* is a typical shade plant (Xu *et al*. 1994). We confirmed this from the regression of the maximum P_N and the relatively low saturating irradiance in the range of about 400~750 µmol m^{-2} s^{-1} under three treatments. It was suggested that plants grown at low irradiance for a long time had lesser contents of electron transfer components and photosynthetic enzymes in comparison with plants grown at high irradiance, which caused the P_{max} decrease (Liao *et al*. 2005). LSP and LCP are the important traits for photon energy utilization capability, whose declines are thought to adapt to low irradiance.

Mesophyll (spongy and palisade) anatomy of *L. radiata* var. *radiata* leaf varied with growth irradiance (Table 1). The thicker leaves in sun plants are due to thicker epidermis and mesophyll cell tissue (Pandey *et al*. 2003, Lambers *et al*. 1998). SLM and LAR are also very plastic growth traits which are strongly affected by photon supply (Jeangros and Nösberger 1992). Decreasing irradiances cause the increase of LAR with the result that photon capture by the leaves is increased

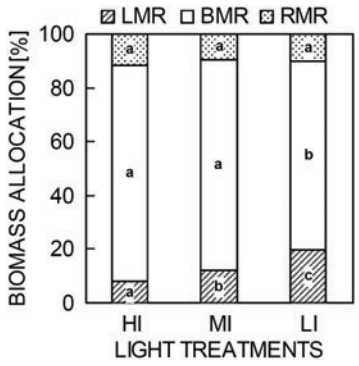

Fig. 6. The proportion of biomass allocated to leaves, bulbs, and roots in *L. radiata* var. *radiata* grown under three treatments; LMR = leaf mass ratio; BMR = bulb mass ratio; RMR = root mass ratio.

(Semb 1996). It is suggested that the high SLM corresponds with high proportions of support tissues and small cells (Castro-Díez *et al*. 2000). The SLM was higher in sun leaves indicating increased thickness and particularly proportion of support tissues as compared to the shade leaves (Table 2). The increased SLM is associated with the adaptation to high irradiance but it may be a result of adjustment to changes of temperature and humidity as well (Boardman 1977). The increase in leaf thickness at high irradiance is related to increased photosynthetic efficiency. It looks like that HI-plant leaves "work" most effectively in order to compensate low leaf area, LAR or total leaf area per plant.

The biomass accumulation and allocation patterns of *L. radiata* var. *radiata* grown under HI, MI, and LI were closely linked with their physiological activities. Kremer and Kropff (1999) suggested that LMR quantifies the fraction of total dry matter of a plant invested in leaves. In our study, irradiance did significantly affect LMR of *L. radiata* var. *radiata*. To increase photon absorption and to compensate for the lower radiant energy in shade environment, the plants had greater leaf area, contents of Chls and LMR. The significant increase in contents of Chl *a*, Chl *b* and Chl (*a*+*b*) in LI-plant leaves, with remarked change in Chl *a/b* ratio (Table 1) as compared to HI- and MI plants was most likely due to changes in both photon harvesting and electron transport components (Pandey *et al*. 2003, Vats *et al*. 2002). The stomatal index did not vary with growth irradiance and remained constant with the value being around 18 (Table 2), which was consistent with the other reports (Deng and Zhou 2005, Guo 2007). Whether the stomatal index is an invariable characteristic for *L. radiata* var. *radiata* across genotypes and environments or not needs further detailed research.

The integrated daytime carbon gain of *L. radiata* var. *radiata* leaf in HI condition was only 12.5% higher than that in MI condition, but the leaf area and total leaf area per plant were both significantly lower about 43% than those of MI plants. Under LI condition, although the leaf area and total leaf area per plant were higher than 19.2% and 10.7%, respectively, compared with those in MI condition, the integrated daytime carbon gain was lower significantly by 53.9% than that of MI plants. These results indicated that 15% of ambient irradiance was too low and the open sky irradiance was too high for *L. radiata* var. *radiata* growth. Therefore, this species may be grown in moderate-shade environment with about 60~70% of ambient irradiance to meet the increasing industrial demand.

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