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Strong leaf morphological, anatomical, and physiological responses of a subtropical woody bamboo (*Sinarundinaria nitida*) to contrasting light environments

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Abstract Dwarf bamboos are an important understory component of the lowland and montane forests in the subtropical regions of Asia and South America, yet little is known about their physiology and phenotypic plasticity in response to changing light environments. To understand how bamboo species adapt to different light intensities, we examined leaf morphological, anatomical, and physiological differentiation of *Sinarundinaria nitida* (Mitford) Nakai, a subtropical woody dwarf bamboo, growing in open and shaded natural habitats in the Ailao Mountains, SW China. Compared with leaves in open areas, leaves in shaded areas had higher values in leaf size, specific leaf area, leaf nitrogen, and chlorophyll concentrations per unit area but lower values in leaf thickness, vein density, stomatal density, leaf carbon concentration, and total soluble sugar concentration. However, stomatal size and leaf phosphorus concentration per unit mass remained relatively constant regardless of light regime. Leaves in the open habitat exhibited a higher light-saturated net photosynthetic rate, dark respiration rate, non-photochemical quenching, and electron transport rate than those in the shaded habitat. The results of this study revealed that the bamboo species exhibited a high plasticity of its leaf structural and functional traits in response to different irradiances. The combination of high plasticity in leaf morphological, anatomical, and physiological traits allows this bamboo species to grow in heterogeneous habitats.

Keywords Clonal plant · Leaf functional traits · Monocotyledon · Natural irradiance · Phenotypic plasticity · *Sinarundinaria nitida*

Abbreviations

$A_{\max}$	Light-saturated net photosynthetic rate
Chl	Chlorophyll
ETR	Electron transport rate
F_v/F_m	Maximal quantum efficiency of PSII
LCP	Light compensation point
LSP	Light-saturation point
NPQ	Non-photochemical quenching
PPFD	Photosynthetic photon flux density
PSII	Photosynthetic II

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R_d	Dark respiration rate
SLA	Specific leaf area
WUE	Water use efficiency
$\delta^{13}C$	Carbon isotopic composition

Introduction

Dwarf bamboo species are an important component of the lowland and montane forests in the subtropical regions of Asia and South America (Soderstrom and Calderon 1979; Veblen 1982). They form a dense thicket layer in the forest understories, and grow even more vigorously in forest gaps and edges, particularly after anthropogenic disturbance. Consequently, they strongly inhibit the regeneration of trees and hence species co-existence (Abe et al. 2002; González et al. 2002; Griscom and Ashton 2003; Holz and Veblen 2006; Larpkern et al. 2011). The bamboo thicket also strongly influences soil water availability, nutrient turnover, and litter decomposition rates (Singh and Singh 1999; Tripathi 2006; Montti et al. 2011). In the subtropical forests of Southwest (SW) China, dwarf bamboo species are very abundant in the forest understories and edges. For example, *Sinarundinaria nitida* (Mitford) Nakai is a dominant understory bamboo species in the subtropical evergreen broadleaf forest of Ailao Mountain, SW China. It is also widely distributed in forest gaps and edges. Despite the ecological importance of understory dwarf bamboos, little is known about their physiology and phenotypic plasticity to light, which is crucial in understanding their existence and performance in heterogeneous habitats. Understanding the physiological mechanisms for their ecological success in heterogeneous habitats will also explain their roles in inhibiting the natural regeneration of tree species in the subtropical forests.

Although the leaf plasticity to light is well studied for many plant lineages (e.g., Poorter and Oberbauer 1993; Küppers et al. 1996; Hanba et al. 2002; Chen et al. 2011; Zhang et al. 2012), the physiological and anatomical responses of monocotyledons to change in light regimes are not well understood. As one of the most significant factors affecting plant survival, growth, and distribution, light intensity is extremely different between forest edges and the understories. Knowing how plants respond morphologically and physiologically to contrasting light conditions can be useful to explain their occurrence and abundance patterns under specific environmental conditions. Some plants, such as *Acer* species, have the ability to survive and adapt to different light environments by special acclimation and phenotypic plasticity (Hanba et al. 2002). Dwarf bamboo species may also exhibit high plasticity and strong adaptability to contrasting light environments to facilitate their dominance in habitats with distinct light conditions, but this is yet to be studied.

Most plant species are able to acclimate to different light conditions, and although pioneer and early successional species have higher plasticity than some later successional or climax species (e.g., Poorter and Oberbauer 1993; Küppers et al. 1996; Chen et al. 2011; Zhang et al. 2012), several later successional species also have high acclimation capacity to different light environments (Hanba et al. 2002; Wyka et al. 2008). Acclimation to changing light conditions is achieved through adjustments at different levels, but leaf level adjustments play an especially important role as leaves are the main organs for gas exchange (Givnish 1988). Leaves usually exhibit a remarkable capacity to adjust their morphology and physiology in response to different light conditions due to their phenotypic plasticity (Bond et al. 1999; Valladares et al. 2007; Yoshimura 2010). Here, we focus on how bamboos regulate their leaf morphological and physiological characteristics under two different natural light intensities.

Clonal plant establishment is facilitated by vegetative growth and physiological integration. Some clonal plants, such as the strawberry (*Fragaria chiloensis*), can translocate assimilates, water, mineral nutrients, and other substances among individual ramets located in heterogeneous conditions (Friedman and Alpert 1991; Alpert 1996; Hutchings 1997). Physiological integration is also of great importance for the survival, growth, expansion, and resource utilization of some bamboo species (Saitoh et al. 2002). Although physiological integration generally confers advantages to ramets growing under less favorable conditions, phenotypic plasticity in clonal plants may improve their ecological adaptability (Dong 1995; Alpert 1999). Whether bamboo species solely depend on clonal growth and/or physiological integration for ecological success or they also employ phenotypic plasticity is unknown.

In the present study, we tested the hypothesis that the dwarf bamboo leaves have a strong ability to modify their structural and functional traits for light acclimation. We have embarked on research attempting to understand: (1) the physiological performance and the phenotypic plasticity of a dwarf bamboo species, *S. nitida*, to differing light conditions; (2) the coordination between leaf water supply and transpiration demand in acclimating to different light conditions for *S. nitida*; and (3) coordinated adjustments of bamboo leaf structural and functional traits. The results could help explain its ecological success in both open and shaded habitats (forest understories, gaps, and edges) and its roles in inhibiting tree regeneration, and provide some preliminary understanding to the physiology of monocotyledons.

Materials and methods

Study site and plant material

This study was conducted in an old-growth forest near the Ailaoshan Station for Subtropical Forest Ecosystem Studies (24°32′N, 101°01′E, 2450 m above sea level), located in central Yunnan Province, SW China. Mean annual temperature is 11.3 °C and annual precipitation is 1,947 mm. With a strong seasonality, more than 85 % of precipitation occurs in the wet season (May–November). All measurements were performed in April, prior to the beginning of the wet season.

Sinarundinaria nitida (Mitford) Nakai (Bambusoideae, Gramineae), a dominant understory species in subtropical evergreen broad-leaved forest on the Ailao Mountains, was chosen for this study due to its ecological and economic importance. It is a subalpine evergreen and monocarpic bamboo species with ~4 m in height and a scattered sympodial rhizome system. It grows in both open (forest edge) and shaded (understory) areas. Leaf samples were collected from different ramets in six open sites (forest edge) and six shaded sites (forest understory), which were about 10–900 m away from each other. Since *S. nitida* is a clonal plant species and culms far away from each other could be connected with the same rhizome (i.e., the same individual), it is difficult to distinguish individuals for this species. Therefore, ramets were used as the replicates for anatomical and physiological measurements in the present study.

Light measurement

The light intensity and its diurnal variations where the sampled bamboo ramets grow were characterized by using a quantum sensor (LI-190SA) between 0730 and 1730 h on a sunny day. Photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) was recorded every 2 h with a LI-1400 data logger (LI-COR, Lincoln, NE, USA).

Leaf morphological and anatomical measurements

Terminal branches with leaves from six ramets at six different sites were collected under the two different light conditions, respectively. Ten fully expanded mature leaves were removed and their individual leaf area (cm^2) was measured using a Li-3000A portable area meter (LI-COR, NE, USA). These leaves were then oven-dried at 70 °C to a constant weight to obtain dry mass. Specific leaf area (SLA, cm^2 g^{-1}) was calculated as the ratio of leaf area to dry mass. In addition, another ten leaves from each site were measured for the length and width of the leaf blade. Leaf length (LL, cm) was measured from base of petiole to leaf tip, while leaf width (LW, cm) was measured as the maximum width of the blade.

Six mature, fully expanded leaves from six different ramets at six different sites in shaded and open habitats were cut and fixed in FAA (formaldehyde, glacial acetic acid, and alcohol, 5:5:90) for later microscopy studies. For leaf anatomical properties of transverse cross sections, a sharp double-sided razor blade was used to cut the middle of a mature leaf vertically. The sections were stained for 3 min in 0.05 % toluidine blue solution. Only well-stained and entire transverse sections of lamina were selected and photographed under a light microscope (Leica DM2500, Germany).

To characterize vein and stomatal properties, the middle of a bamboo leaf was selected and cut into segments (3 cm^2, approximately). A sharp, one-sided razor blade was used to peel off the cuticles and upper epidermis from the whole leaf segment. The remaining leaf sample was then put on a microscope slide and cleaned in commercial household bleach for 20 min. The residual mesophyll was removed with a single-hair paintbrush. The resulting section was rinsed in water to allow residual bleach to dissipate, then dyed with 1 % toluidine blue for 2 min, rinsed again with water, and digital photomicrographs of the section were taken at 200× and 400× magnification under a light microscope (Leica DM 2500, Germany).

Digital photos were scaled and analyzed with Image J (http://rsb.info.nih.gov/ij/). We measured the thickness (μm) of the cross-sectional lamina, the distance between adjacent, parallel veins (μm), and stomatal size (the length of the stomatal complex; μm) and counted the number of stomata on the field of view in each section, at 200×, 100×, 400×, and 100× magnification, respectively. From these measurements, we calculated the following parameters: leaf density [=1/(leaf thickness × SLA); g cm^{-3}], vein density (the total length of leaf vascular tissue per unit leaf area; mm mm^{-2}), and stomatal density (the number of stomata per unit leaf area; no. mm^{-2}).

Leaf physiological measurements

Six mature ramets at six different sites were selected for physiological measurements for both shaded and open habitats. Leaf samples were collected and oven-dried for 48 h at 70 °C. The dry leaves were sent to the Biogeochemical Laboratory of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for nutrient concentration determinations. Total carbon concentration (C, g kg^{-1}) and total nitrogen concentration (N, g kg^{-1}) were determined by an automated C/N analyzer (Vario MAX CN; Elemental Co., Germany), while total phosphorus concentration (P, g kg^{-1}) was determined using an inductively coupled plasma atomic-emission spectrometer (Icap6300; Thermo Fisher Scientific, USA) after the samples were digested with concentrated HNO_3–$HClO_4$. Leaf C to N ratio (C/N) and N to P ratio (N/P) was calculated for *S. nitida* from each light condition.

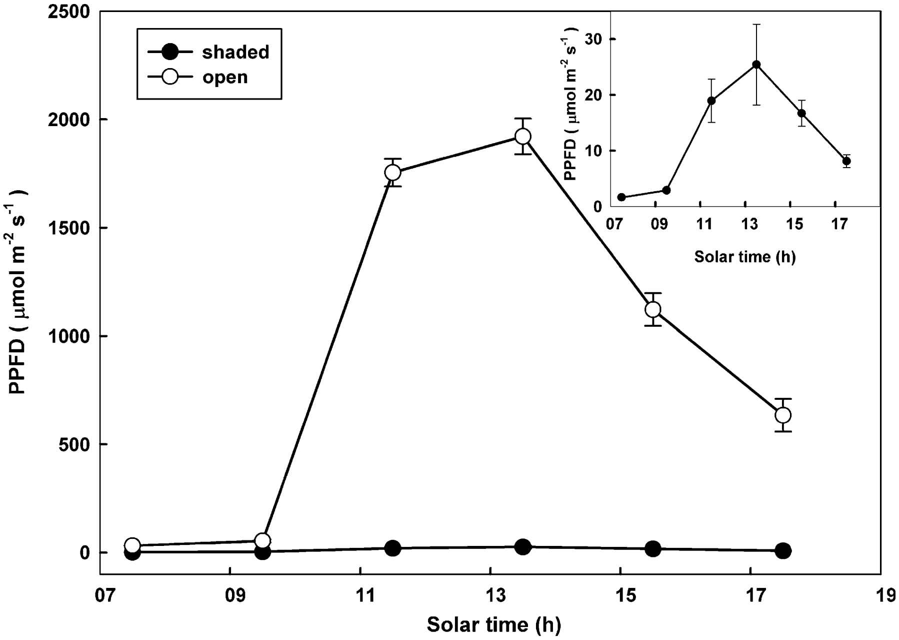
In recognition of a positive linear relationship between stable carbon isotope composition ($\delta^{13}C$) and water use efficiency (WUE), the $\delta^{13}C$ value of leaves is often used as an estimate of their WUE in natural vegetation (Farquhar et al. 1989; Holtum and Winter 2005). Healthy and mature leaves from each light habitat were collected, dried at 70 °C, and then pulverized to a fine powder through a sieve with holes of 0.25 mm in diameter. The carbon isotopic composition ($\delta^{13}C$; ‰) value of the leaves was analyzed with an isotope mass spectrometer (Isoprime 100; Isoprime, UK). The $\delta^{13}C$ values were expressed as the relative abundance of ^{13}C versus ^{12}C, compared with the Pee Dee Belemnite standard (Farquhar et al. 1982).

Chlorophyll content per unit leaf area was estimated with a chlorophyll meter (SPAD502; Konica-Minolta Sensing Inc., Osaka, Japan). The SPAD value was converted to chlorophyll content per unit leaf area (μg cm^{-2}) using an average of the regression equations between the two variables for six temperate species and as recommended by Anten and Hirose (1999).

Total soluble sugar concentration was determined using the anthrone-sulfuric acid colorimetric method. The dried and powdered leaf (0.1 g) was mixed with 5 ml of ethanol (80 %) in a 10 ml centrifuge tube. After the mixture was incubated in a water bath shaker for 30 min at 80 °C, it was centrifuged at 4,000 rpm for 5 min. The sediments were extracted three times with ethanol (80 %). The collected extracts were hydrolyzed for 15 min in 5 ml of 0.4 % anthrone-sulfuric acid solution in a boiling water bath. After cooling, the total sugar concentration was determined by the ultraviolet–visible spectrophotometer (Shimadzu UV-2550; Shimadzu, Kyoto, Japan) at 620 nm against a blank. Using glucose as a standard, the total soluble sugar concentration was calculated on a dry matter basis.

Leaf photosynthesis versus light response curves were detected using a portable photosynthesis system (LI-6400; LI-COR Biosciences Inc., Lincoln, NE, USA). A red-blue LED light source attached to the system was used to produce steady photosynthetic photo flux density (PPFD). All light response measurements were made between 8:30 a.m. and 11:30 a.m. when photosynthesis was most likely to be at its peak. Leaves were illuminated at a PPFD of 1,000 μmol m^{-2} s^{-1} until a steady state of net CO_2 fixation was reached. The PPFD was then increased to 1,500 μmol m^{-2} s^{-1} and then decreased in a stepwise manner (1500, 1200, 1000, 800, 500, 200, 100, 80, 50, 20, and 0 μmol m^{-2} s^{-1}. The net photosynthetic rate was recorded after exposing the leaf to each light gradient for 3–5 min as a steady state of photosynthesis approached. During the measurements, temperature, vapor pressure, and CO_2 concentrations in the leaf chamber were maintained at 25 °C, 1.5 kPa, and 380 μmol mol^{-1} CO_2, respectively. Light response curves were fitted

Fig. 1 Diurnal variation (mean ± SE) of photosynthetic photon flux density (PPFD) in shaded areas (*closed symbol*, shown more clearly in the *insert*) and open areas (*open symbol*)



by the non-rectangular hyperbolic model (Thornley 1976). The light-saturated net photosynthetic rate (A_{max}), dark respiratory rate (R_{d}), light compensation point (LCP), and light-saturation point (LSP) were calculated from leaf photosynthesis versus light response data.

Diurnal changes in leaf chlorophyll fluorescence characteristics were measured using a portable chlorophyll fluorescence monitoring system (FMS2; Hansatech, Norfolk, UK) on a clear day. Six leaves from six different ramets were selected from each site to measure the maximal quantum efficiency of photosynthetic II (PSII) ($F_{\mathrm{v}}/F_{\mathrm{m}}$), the actual quantum yield of PSII electron transport (Φ_{PSII}), the non-photochemical quenching (NPQ), and the electron transport rate (ETR). At predawn, the minimal fluorescence (F_{o}) was determined. The maximum fluorescence (F_{m}) was determined by a 0.8 s pulse flash at 3,000 μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$PPFD. The steady-state chlorophyll fluorescence (F_{s}) and the maximal fluorescence in the light-adapted state (F'_{m}) were determined at incident sunlight, which was recorded with a quantum sensor attached to the leaf clip. The predawn maximal fluorescence (F_{m}) was used to determine NPQ throughout the day. The leaf chlorophyll fluorescence parameters were calculated as $F_{\mathrm{v}}/F_{\mathrm{m}} = (F_{\mathrm{m}} - F_{\mathrm{o}})/F_{\mathrm{m}}$; $\Phi_{\mathrm{PSII}} = (F'_{\mathrm{m}} - F_{\mathrm{s}})/F'_{\mathrm{m}}$; $\mathrm{NPQ} = (F_{\mathrm{m}} - F'_{\mathrm{m}})/F'_{\mathrm{m}}$; $\mathrm{ETR} = \Phi_{\mathrm{PSII}} \times \mathrm{PPFD} \times 0.84 \times 0.5$, where 0.84 is the leaf absorption coefficient and 0.5 is the fraction of light absorbed by PSII antennae (Bilger and Björkman 1990; Maxwell and Johnson 2000).

Statistical analysis

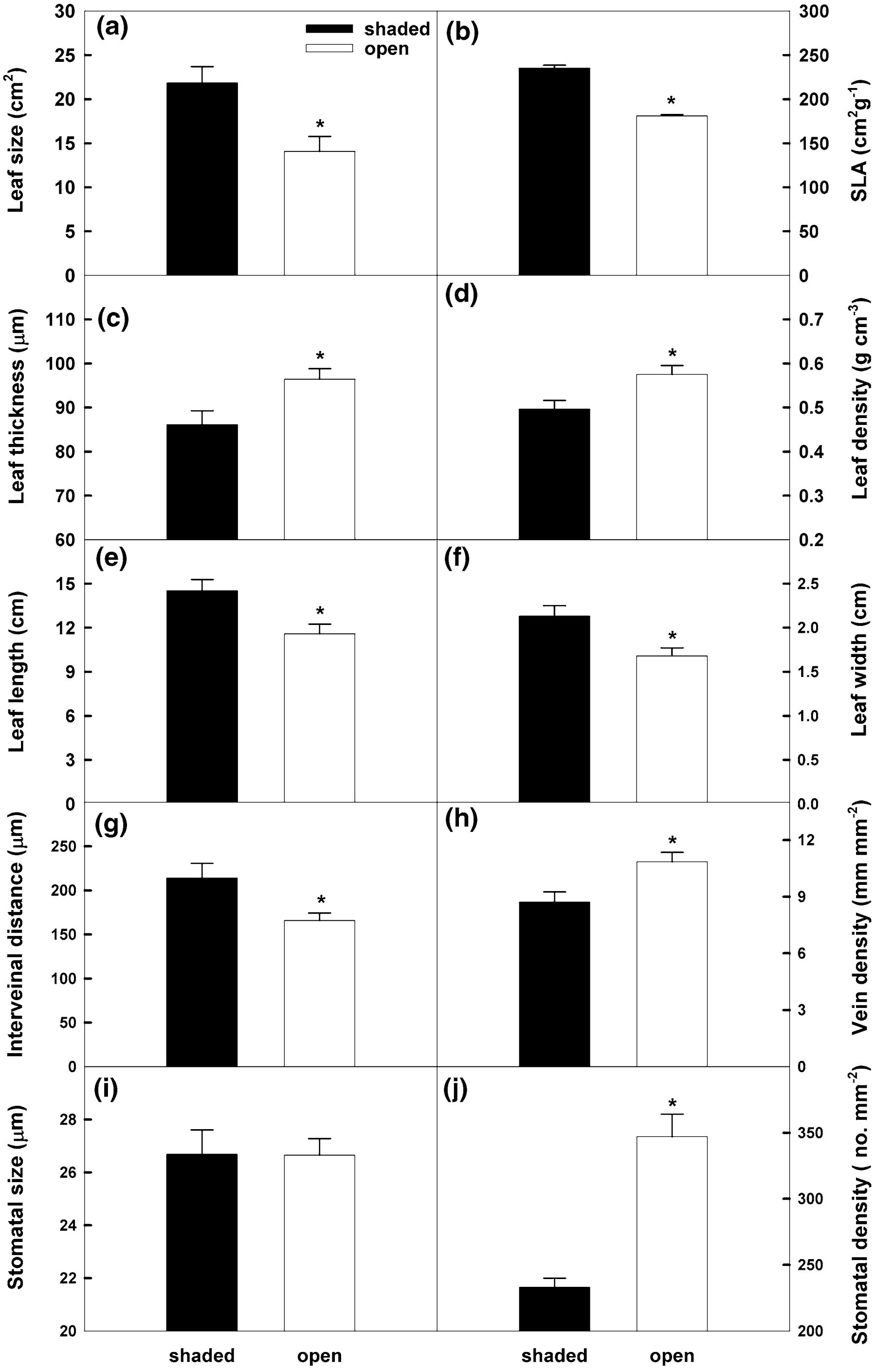
The differences in leaf morphological, structural, and functional traits between ramets in open and shaded areas were tested using one-way analysis of variance (ANOVA) in SPSS 16.0 (SPSS Inc., Chicago, IL, USA). Most variables were normally distributed and of equal variances, but the data for leaf thickness, leaf nitrogen concentration, and leaf chlorophyll content were log-transformed to meet the assumption of ANOVA (normal distribution and equal variances).

Results

Light environments

Although sunflecks emerged occasionally in the natural forest understory, total daily photosynthetic photon flux density (PPFD, μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) in shaded

Fig. 2 Leaf morphological and structural traits (mean ± SE) of *Sinarundinaria nitida* in shaded (*filled bar*) and open areas (*open bar*). Significant differences ($P < 0.05$) are indicated with *asterisk*



areas was very low. It was around 20 μmol m^{-2} s^{-1} during the middle of the day. The maximum PPFD in open areas was approximately 1,800 μmol m^{-2} s^{-1}, which was close to two orders of magnitude higher than that measured in shaded areas (Fig. 1).

Response of leaf structural traits to two contrasting light environments

Leaves of *S. nitida* from the shaded habitat exhibited significantly greater (35.5 %) leaf size and higher

(26.0 %) SLA than the ones from the open habitat ($P < 0.05$; Fig. 2a, b). Leaf thickness and leaf density were significantly lower in shaded than those in open areas ($P < 0.05$; Fig. 2c, d). Although there were significant differences in leaf length and width between two different light environments ($P < 0.05$; Fig. 2e, f), the ratio of leaf length to width was not sensitive to different light conditions (data not shown).

Compared to the leaves in open areas, vein density in shaded areas was significantly lower ($P < 0.05$; Fig. 2h). There was no difference in stomatal size ($P > 0.05$; Fig. 2i) between different light conditions, but stomatal density in open areas was markedly higher (about 48.9 %) than that in shaded areas ($P < 0.05$; Fig. 2j). Across all the ramets in the two different light environments, leaf vein density was positively correlated with stomatal density ($P < 0.0001$; Fig. 3a), but no correlation was found between stomatal size and stomatal density across ramets and habitats (Fig. 3b). The distance between two adjacent, parallel veins was greater in leaves in shaded areas than that in open areas (Fig. 4).

Response of leaf nutrient concentration to two contrasting light environments

Compared with the leaves in open areas, leaf C concentration and mean δ^{13}C value were significantly lower in shaded areas ($P < 0.05$; Fig. 5a, b), but leaf N concentration was significantly higher in shaded areas compared to that in open areas ($P < 0.05$; Fig. 5c). The ratio of carbon to nitrogen (C/N) was smaller in shaded than in open areas ($P < 0.05$; Fig. 5d). No significant differences were found in leaf phosphorus concentration (P) per unit of leaf mass and leaf N/P ratio ($P > 0.05$; Fig. 5e, f). Leaf Chl content per unit leaf area was 27.4 % greater in shaded areas than that in open areas, whereas total soluble sugar concentration increased significantly with rising irradiance, from 2.4 ± 0.1 % (in shaded areas) to 5.1 ± 0.3 % (in open areas) ($P < 0.05$; Fig. 5g, h).

Effects of light availability on photosynthetic gas exchange

Leaf photosynthetic characteristics differed significantly under the contrasting light environments. The mean light-saturated photosynthetic rate (A_{max}) of leaves grown under open areas was 7.7 μmol m^{-2} s^{-1}, which was 52.3 % greater than that under shaded areas ($P < 0.01$; Fig. 6). Leaves grown under open areas also had a greater LCP (5.9 ± 0.7 μmol m^{-2} s^{-1}), LSP (524 ± 12 μmol m^{-2} s^{-1}), and leaf dark respiration rate (R_d, −0.01 ± 0.02 μmol m^{-2} s^{-1}) than those grown under shaded areas (1.8 ± 0.2 μmol m^{-2} s^{-1}, 196 ± 4 μmol m^{-2} s^{-1}, −0.21 ± 0.03 μmol m^{-2} s^{-1}, respectively). However, the apparent quantum efficiency (AQE), which was determined by the linear portion of light response curves, was independent of light environments ($P > 0.05$; Fig. 6).

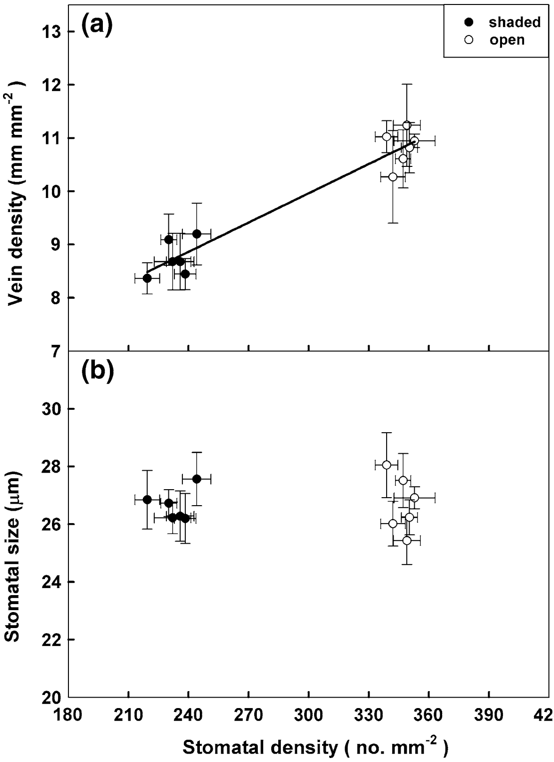


Fig. 3 Correlation of **a** leaf vein density and **b** stomatal size with stomatal density (mean ± SE) of *Sinarundinaria nitida* in shaded (*closed symbol*) and open areas (*open symbol*). A highly significant linear correlation ($r^2 = 0.93$; $P < 0.0001$) between leaf vein density and stomatal density was observed

Leaf chlorophyll fluorescence under two contrasting light environments

No significant difference in the predawn F_v/F_m was found between shaded (0.83 ± 0.01) and open (0.84 ± 0.01) ramets. However, the dynamics in Φ_{PSII}, ETR, and NPQ showed distinct differences between the different irradiance levels (Fig. 7). Φ_{PSII} was

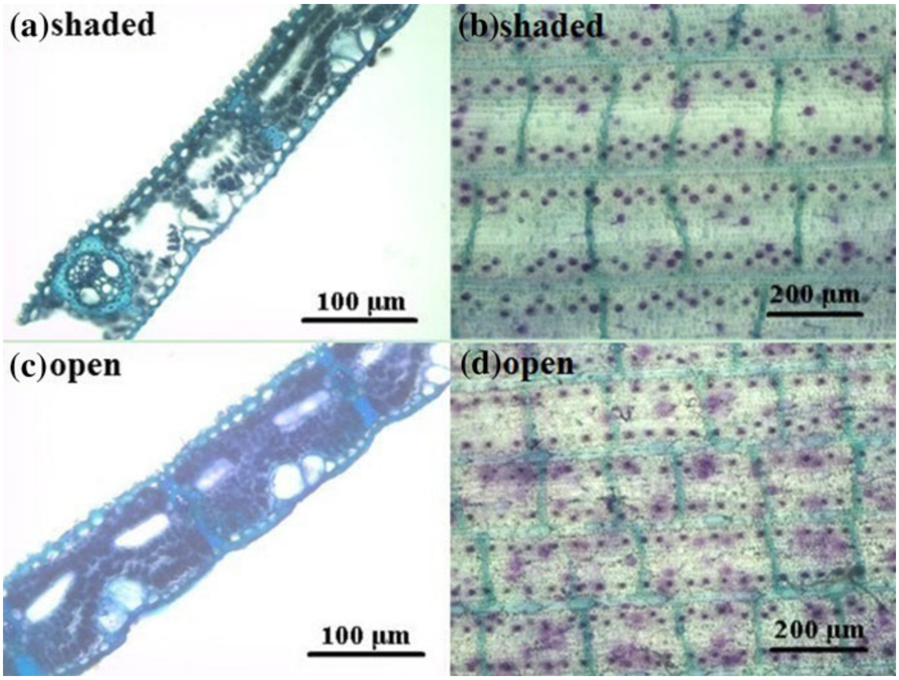


Fig. 4 Representative images for transverse cross sections (**a**, **c**) and abaxial tissues (**b**, **d**) of leaves of *Sinarundinaria nitida* in shaded (**a**, **b**) and open areas (**c**, **d**). Note stomata (the *black circular dots* in **b**, **d**) are regularly distributed along leaf parallel veins

always lower while NPQ was always higher in open than in shaded areas (Fig. 7a, c). ETR in open areas showed a bimodal diurnal pattern (Fig. 7b), indicating a significant depression of photosynthesis around noon. For leaves in shaded areas, no significant change could be detected in ETR and NPQ because light intensity was low during the day ($P > 0.05$; Fig. 7b, c). The leaves in open areas had a higher daily mean NPQ than those in shaded areas ($P < 0.01$; Fig. 7c).

Discussion

Our results indicate that this bamboo species, which dominates in habitats with contrasting light conditions, exhibits a strong plasticity in morphological, anatomical, and photosynthetic characteristics. This high structural and functional plasticity may partially explain its ecological success in both open and shaded habitats.

Response of bamboo leaves to contrasting natural light conditions

Plants are able to adjust their leaf morphology, structure, and physiology to accommodate variation in irradiance (Bond et al. 1999; Poorter 1999). The structural and physiological responses of this bamboo species to light are similar to that documented for other plant species. Bamboo SLA, a measure of the amount of leaf area for light capture per unit biomass invested, was sensitive to different irradiance conditions (Fig. 2b). SLA is the product of leaf thickness and density (Niinemets 1999), both of which may vary independently in response to a change in natural irradiance. Consistent with the finding of the previous studies (Reich et al. 1991; Wright et al. 2002; Poorter et al. 2009), bamboo leaves in shaded areas exhibited lower leaf thickness and density and larger leaf size and SLA (Fig. 2). With increasing SLA, light harvesting capacity per unit leaf mass resources may improve (Lusk et al. 2008). There was no difference in the ratio of leaf length to width between the two different light environments, indicating that leaves in open areas minimize overheating by altering their size rather than their shape.

Leaf water supply and transpiration demand are coordinated in acclimating to contrasting light environments in this bamboo species. High leaf vein density increases the pathways for water flow and decreases the distance water travels outside the xylem,

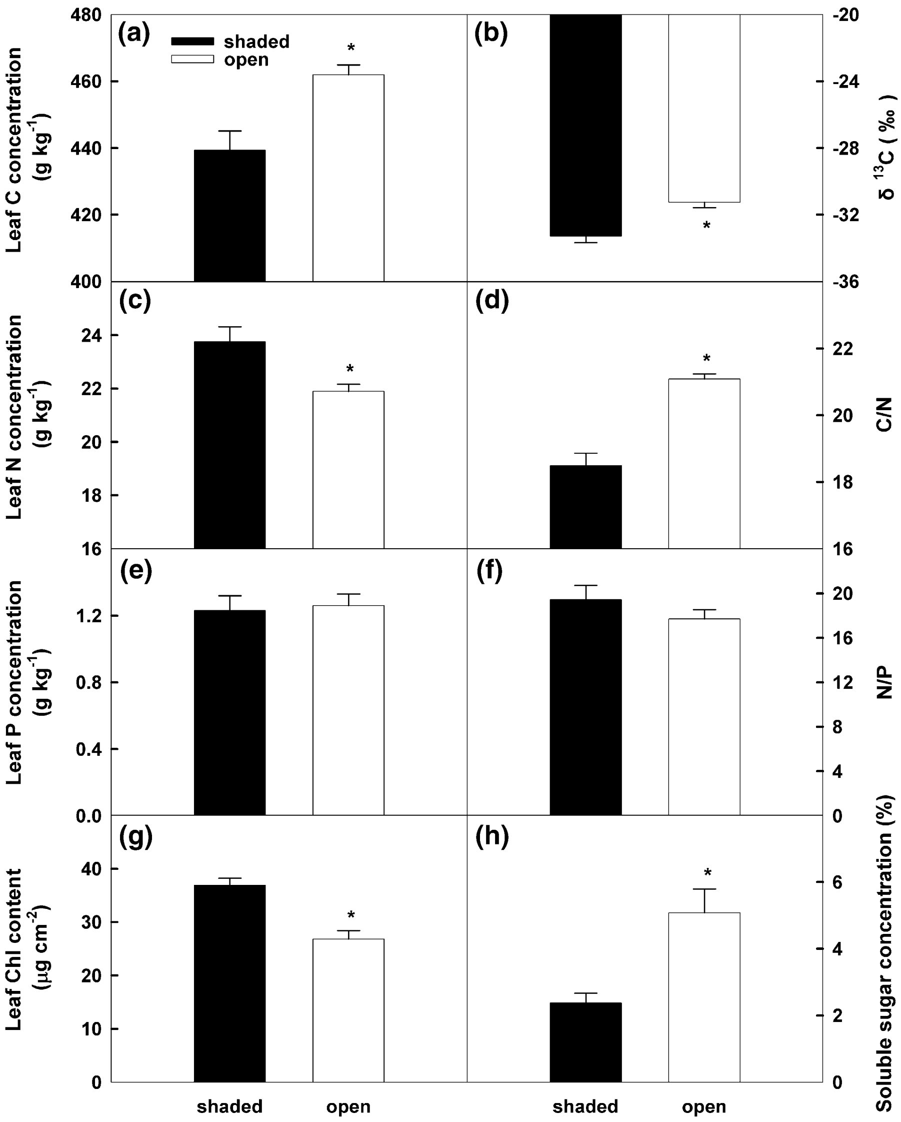


Fig. 5 Leaf nutritional concentrations (C; N; P) and their ratios (C/N; N/P), carbon isotope composition (δ^{13}C), total chlorophyll content, and total soluble sugar concentration (mean ± SE) of *Sinarundinaria nitida* in shaded (*filled bar*) and open areas (*open bar*). Significant differences ($P < 0.05$) are indicated with *asterisk*

and thus is strongly positively related to leaf hydraulic conductance (Sack and Frole 2006; Brodribb et al. 2007; Sack and Scoffoni 2013). Higher leaf vein density in leaves in the open habitats therefore allows high leaf water supply and consequently the development of high stomata density and the maintenance of high stomatal conductance (and thus high transpiration rates). This coordination between vein density and stomatal density in adapting to different light environments has also been found in many tree species in recent studies (Brodribb and Jordan 2011; Murphy et al. 2012). In contrast to the extensive literature (Sack et al. 2003; Franks and Beerling 2009) on a negative relationship between stomatal size and stomatal density, we did not observe significant differences in stomatal size between the different light habitats.

Leaves grown in open areas had less nitrogen per unit mass than leaves developed in shaded areas (Fig. 5c). A greater investment of leaf nitrogen per unit mass for light harvesting in low-light conditions is a common strategy for many other plant species (e.g., Evans 1989; Pearcy and Sims 1994; Niinemets et al. 1998). Most species display substantial plasticity in leaf structure and leaf chlorophyll concentration in response to different light conditions (e.g., Cao 2000; Zhang et al. 2007; Huang et al. 2011). In order to capture more light, leaves in shaded areas had a

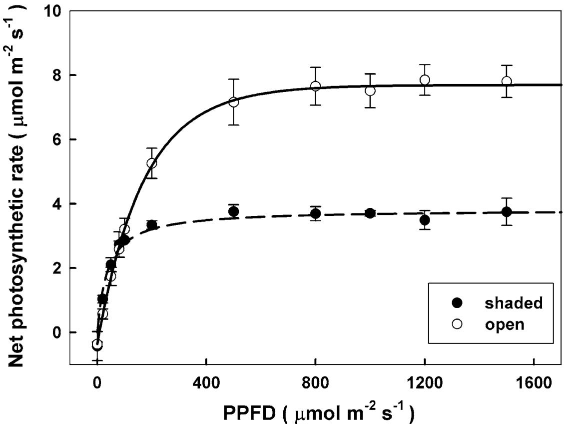


Fig. 6 Photosynthetic light response curve of *Sinarundinaria nitida* in shaded (*closed symbol* and *dashed line*) and open (*open symbol* and *solid line*) areas. The mean ± SE were calculated from six ramets. Curves were fitted by a non-rectangle hyperbola model

relatively high Chl content and large leaf size. On the contrary, the leaves in open areas could decrease their light absorption by reducing leaf size and Chl content (Fig. 5g). In general, leaves in shaded areas have a larger size, lower thickness, and higher Chl content in order to increase light absorption.

Adjustments to leaf anatomy and leaf physiology are apparently integral features in the process of acclimating to contrasting light environments. Leaf traits, such as SLA, stomatal density, and chlorophyll concentration, are important determinants of leaf photosynthetic capacity. Many studies have shown that, leaves will increase their size and Chl content, as well as adjust their photosynthetic traits to maximize the use of light in shaded areas (Zhang et al. 2007; Huang et al. 2011). The $A_{\max}$, LCP, LSP, and dark respiration rate (R_d) of this bamboo species were significantly higher in open areas than those in shaded areas. This response followed the same pattern reported for other studies (e.g., Huang et al. 2011; Zhang and Yin 2012). *S. nitida* had high photosynthesis capacity in open areas, as observed in other bamboo species (*Sasa senanensis* Rehd., *Chusquea ramosissima* Lindm., and *Chusquea tenella* Nees.) in previous studies (Lei and Koike 1998; Montti et al. 2013). The leaves grown in open areas also had a higher long-term WUE (indicated by less negative values of δ^{13}C) than those grown in shaded areas, probably owing to their higher maximum photosynthetic rate. The increase in WUE was also found in three species of understory herbaceous bamboo when grown in the sun treatment (Mulkey 1986). Bamboo leaves in shaded areas improved their light use efficiency by increasing SLA, leaf Chl content and total nitrogen content, and by lowering leaf thickness, LSP, LCP, and R_d. Lei and Koike (1998) also showed that a dominant dwarf bamboo (*S. senanensis*) grown in forest understory had lower photosynthetic rate and higher SLA, leaf total chlorophyll, and nitrogen concentrations than those grown in open sites. All these features contribute to the efficient interception and absorption of light for use in carbon gain. The photosynthetic capacity of this bamboo species in

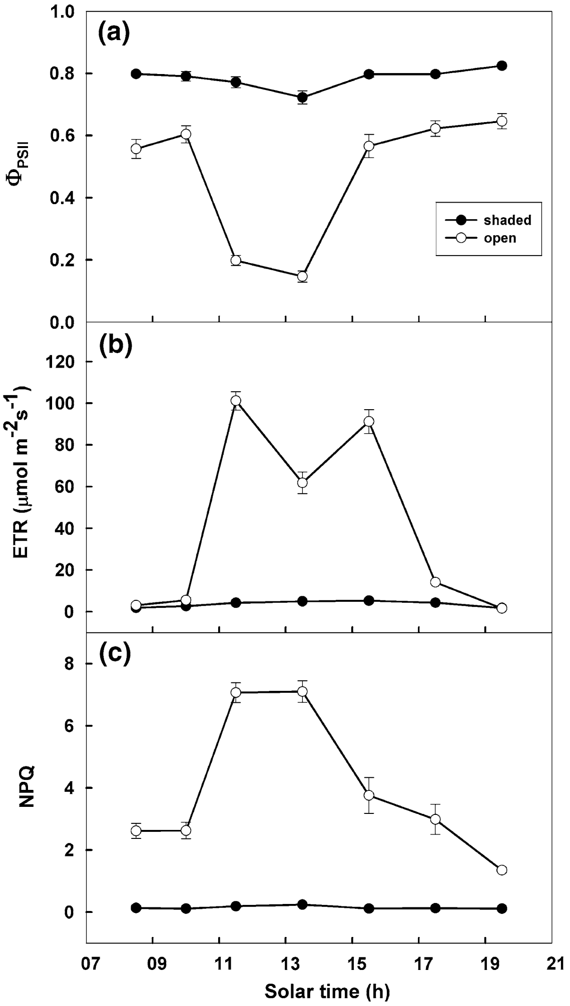


Fig. 7 Diurnal variation (mean ± SE) of actual quantum yield of PSII electron transport (Φ_{PSII}), electron transport rate (ETR), and non-photochemical quenching (NPQ) of leaves of *Sinarundinaria nitida* in shaded (*closed symbol*) and open areas (*open symbol*)

shaded areas is low, in situ; the maximum net photosynthetic rate in shaded areas was 1.29 mol m^{-2} s^{-1} (Yang et al. 2012). However, they may rely on sunflecks for keeping their carbon budget positive, which is similar to other tree seedlings under low-light growth conditions (Chen et al. 2011).

The parameters of chlorophyll fluorescence, such as F_v/F_m, Φ_{PSII}, and ETR, are related to photochemical processes. The bimodal diurnal pattern of ETR in bamboos grown in open areas is consistent with a midday depression of photosynthesis. Leaves of this bamboo species in open areas also exhibited a similar trend of diurnal variation in stomatal conductance and net photosynthetic rate (Yang et al. 2012). NPQ has been described as the most common form of protection against excess light. Besides lowering leaf areas and Chl content to reduce light absorption, leaves in open areas can transform the high levels of light energy that exceed their photosynthetic capability into thermal dissipation in the form of NPQ. The values of NPQ, which paralleled the changes of light intensity in open areas, indicate that NPQ contributes to avoidance of the deleterious effects of excess light energy on photosynthetic machinery. The high NPQ in open areas indicated that the light energy absorbed by the bamboo leaves exceeded the capability of the photosynthetic apparatus to transform it into chemical energy. The high predawn F_v/F_m values in open areas remained essentially constant, maybe due to the relaxation of NPQ, which indicate that no chronic photo-inhibition occurred in the leaves. Another understory dwarf bamboo (*S. senanensis*) was less sensitive to photo-inhibition than the seedlings of two co-occurring tree species under high light conditions (Tobita et al. 2010).

Ecological implications and Conclusions

Leaf plasticity plays an important role in the adaptation of plants to different light environments. Different species and leaf traits show different sensitivities to irradiance (Rozendaal et al. 2006). The microclimatic conditions between forest edges and understories are different, especially in light, temperature, nutrients, and moisture, however, light is usually the most important abiotic factor for plant survival, growth, and distribution. The strong leaf plasticity of this bamboo species to light intensity may at least partially explain its dominance in both forest understories and edges. Previous studies have shown that bamboos with clonal fragments may depend on physiological integration through their long rhizomes, which enable translocation of assimilates and nitrogen from the high light environments such as gap edges to the shaded understories (Saitoh et al. 2002). As an important feature of clonal plants, physiological integration results in an increased ability of clones to exist in heterogeneous environments (Dong 1995; Alpert 1999). In addition to physiological integration, our results show that the strong leaf plasticity also contributes to the ecological success of the bamboo under contrasting light environments. In conclusion, the high leaf plasticity, in combination with their physiological integration, may provide benefits for this bamboo species in dominating the habitats with heterogeneous light conditions.

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