DOI: 10.1007/s11099-016-0186-x PHOTOSYNTHETICA 54 (3): 390-395, 2016

Effect of shade on plant traits, gas exchange and chlorophyll content in four ramie cultivars

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Abstract

The objective of this study was to investigate a response to low-light environments in hybrids and commercial cultivars of *Boehmeria nivea* L. Two hybrids (Chuanzhu 11 and Chuanzhu 8) and two commercial cultivars (Chuanzhu 12 and Chuanzhu 6) of ramie were subjected to a shade treatment for 6, 12, and 18 days. The shade treatment led to a significant decrease in some plant traits and fiber yield in four ramie cultivars, whereas their leaf area and plant height increased. In addition, net photosynthesis and stomatal conductance significantly declined in response to shade, while transpiration rate and intercellular CO_2 did not significantly change. Moreover, chlorophyll (Chl) and carotenoid (Car) concentration, Chl/Car, and Chl (*a*+*b*) per leaf dry mass significantly increased in the response to shade, while the Chl *a*/*b* ratio decreased. Furthermore, Chuanzhu 6 and Chuanzhu 11 were more tolerant to shade than Chuanzhu 12 and Chuanzhu 8, thus, they could be potentially used for management practices and breeding programs.

Additional key words: abiotic stress; *Boehmeria nivea*; photosynthesis; pigments.

Introduction

Boehmeria nivea L., commonly known as China grass, is one of the oldest and most important fiber crops in China. Conventionally, ramie is reproduced by asexual means using rhizome cuttings, stem cuttings, buds, and shoots. It provides a habitat for pests and harbors diseases caused by pathogens, endangering growth of seedlings which is subsequently curtailing the expansion of ramie cultivation area. Recently ramie hybrids were developed from a cross between two genetically dissimilar parents, including a good male sterile line and one line belonging to the restoration line (Shi *et al*. 2000). Ramie hybrids have a higher yield potential than that of commercial varieties (Huang *et al*. 2013a). Nonetheless, the growth and fiber yield of commercial varieties and ramie hybrids are influenced by abiotic factors, such as drought, salt, and soil nutrient status (Huang *et al*. 2013a,b; 2014a,b).

Shade tolerance is one of strategies for plants in competition for light. It is a function of a species' ability to capture and utilize efficiently limited light resource in order to optimize the whole-plant carbon balance in shade (Khan *et al*. 2000). Shade tolerance is associated with a wide range of traits, including photosynthesis, pigment biosynthesis, and morphological and physiological traits (Khan *et al*. 2000, Jiang *et al*. 2004, Kim *et al*. 2011). Although many studies have been carried out to evaluate the effects of shade treatments on crops (Egli 1997, Zhao and Oosterhuis 1998, Moula 2009), there is no information available on the effects of shade treatments on ramie morphological and physiological traits. Thus, the aim of this research was to analyze the effects of shade treatments on physiological and morphological traits of ramie hybrids and commercial cultivars.

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Received 20 October 2014, *accepted* 30 October 2015, *published as online-first* 23 November 2015.
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Abbreviations: Car – carotenoids; Chl – chlorophyll; C_i – intercellular CO_2 concentration; DAT – days of treatment; DM – dry mass; E – transpiration rate; FM – fresh mass; g_s – stomatal conductance; LA – leaf area; P_N – net photosynthetic rate.
Acknowledgements: This work was supported by the national 'Twelfth 5-Year's scientific and technological support project (2012BAD20B05-04), the National Natural Science Foundation Program (31 371 704), scientific and technological project of Hunan (2010TP4004-1, 2010FJ2013 and 2012FJ4063).

Materials and methods

Study site: The field experiment was carried out at the College of Agronomy and Biotechnology, Southwest University, Chongqing, China (29°49'32"N, 106°26'02"E), during the growing season in 2012. The soil was a typical purple sandy loam soil.

The climate was characterized by a mean yearly air temperature of 18.6°C and a total annual rainfall of 1,131 mm. During the study period (March – August 2012), the mean air temperature was 22.8°C, total annual rainfall was 686.7 mm.

Experimental details: The experiment was designed in a randomized complete block having three replications. Four ramie cultivars (Chuanzhu 11, Chuanzhu 8, Chuanzhu 12, and Chuanzhu 6) were obtained from the Dazhou Institute of Agricultural Sciences, Sichuan, China. Chuanzhu 11 and Chuanzhu 8 cultivars were two hybrid lines of ramie cultivars from F1 seeds of the cross between two genetically dissimilar parents, while Chuanzhu 6 and Chuanzhu 12 were two commercial cultivars reproduced by rhizomes. Chuanzhu 11 was developed by a male sterile line C9451 and a restorer line R79-20, while Chuanzhu 8 originated from a male sterile C26 and restorer line B8. In November 2011, the rhizomes of Chuanzhu 12 and Chuanzhu 6 were sown in nursery beds. After a dormancy of 4 months, the rhizomes developed spouts (March 2012). F1 seeds of the hybrid ramie cultivar Chuanzhu 11 and Chuanzhu 8 were also planted in the nursery beds early in March 2012. At the beginning of June, the seedlings were transplanted into fields, one plant per hole. The plant density was 42,000 plants ha^{-1}. The plants spacing was 60 cm between rows and 40 cm within rows. The experimental plots were 3 m × 6 m and consisted of five rows.

Shade treatment: Shade treatment started 40 d after ramie seedlings transplantion. Square shade shelters were built (2.3 m high, and 3 x 6 m) with bamboo pole and rope, made of ramie fiber, which supplied a 18 m^2 top shade area in ramie plots. This area was covered by black sun-shading net (55% of full sunlight) for 18 days (DAT). The net was made of polyvinyl chloride, with holes to allow air, wind, and rainfall to pass through the net. The treatments were control (100% of full sunlight), and shade treatments according to a shading duration: short-term shade (A, 6 DAT), middle-term shade (B, 12 DAT), long-term shade (C, 18 DAT).

Measurement of plant traits and yield: Plant traits were recorded from 30 randomly selected mature plants from each plot in order to measure a total leaf area (LA) per plant, plant height, stem diameter, and the number of stems per plant. LA was measured with a leaf area meter (*LI-3100, LI-COR,* Lincoln, NE, USA). Fresh stem bast was used to measure bast thickness and total bast fresh mass (FM). Fiber layer of fresh stem bast were separated and dried under sunlight and weighed in order to determine crude fiber dry mass (DM) per plant. The rest of the plants (except for fiber) include leaves, leaf stalk, woody stem, and residue of the fresh bast were oven dried for 72 h at 70°C to determine total leaf DM per plant (Eq. 1), stem DM per plant (Eq. 2), and total above ground DM per plant (Eq. 3). The fresh stem bast of the two central rows in the plots was collected and a fiber layer of fresh stem bast was separated and dried under sunlight and weighed to determine the fiber yield.

Total leaves DM per plant = leaf DM + leaf stalk DM (1)

Stem DM per plant = woody stem DM + DM of residue of the fresh bast + fiber DM (2)

Total above ground DM per plant = total leaves DM per plant + stem DM per plant (3)

Gas-exchange measurements: An open-system infrared gas-exchange analyzer (*LI-6400, LI-COR,* Lincoln, NE, USA) was used to estimate leaf gas exchange after 16 DAT. The 6–7th fully expanded leaf from a stem tip was measured according to Liu (2010) from 8:30 to 12:00 h. Sixteen leaves per plot from the middle rows were selected for each treatment with the following adjustments: molar flow of air per unit of leaf area was 499.66 mmol mol^{-1} m^{-2} s^{-1}, water vapour pressure into leaf chamber was 3.7 mPa, PAR at leaf surface was up to 999 µmol(photon) m^{-2} s^{-1}, temperature of leaf ranged from 36.6 to 38.3°C, ambient temperature was 37.5 to 39.7°C, ambient CO_2 concentration was 352.56 µmol mol^{-1}, and relative humidity was 68%. Net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured.

Photosynthetic pigment contents: The 6–7th fully expanded leaf from the stem tip was sampled on the 6, 12, and 18 DAT in order to assess photosynthetic pigment contents. The concentration of Chl *a*, Chl *b*, and Chl (*a*+*b*) was determined according to Arnon (1949). Carotenoids (Car) were measured according to Lichtenthaler and Wellburn (1983). Fresh leaves (0.1 g) were extracted at dark place and normal temperature for 48 h with 10 mL of miscible liquids by 95.5% acetone and absolute ethylalcohol in 1:1 ratio (v/v). Chl *a*, Chl *b*, Chl (*a*+*b*), and Car were measured using an UV-visible spectrophotometer (*UC-5500PC, Shanghai Yuanxi Co. Ltd.*, Shanghai, China). The absorbance was recorded at 470, 645, 652, and 663 nm for calculations of Chl *a*, Chl *b*, Chl (*a*+*b*), and Car contents.

Statistical analysis: Data were analyzed by one-way analysis of variance (*ANOVA*) test using *SPSS16.0* (*SPSS Inc.,* Chicago, IL, USA) for *Windows*. Means were compared using the *Newman–Keuls*' test at 5% level of significance. Data were presented as the mean ± SE for each treatment. Linear regression equations between P_N and g_s, Chl (a+b) (expressed as mg g^{-1}) were also shown.

Results

Plant traits and fiber yield: Plant traits and yield attributes of ramie cultivars were significantly affected by the shade treatment. Stem diameter, total leaf DM per plant, total stem DM per plant, and total above ground DM per plant decreased by 11.7, 11.5, 16.7, and 14.2%, respectively, compared with the control (Table 1). Moreover, the shade treatment decreased the fiber yield by 20.3%, crude fiber DM per plant by 16.2%, a number of stems per plant by 20%, bast thickness by 9.2%, and bast FM per plant by 20.5% (Table 2). The shade treatment increased LA per plant and plant height by 18.2% and 11.0%, respectively (Table 1). No significant difference was observed in bast stripping percentage neither between treatments nor between cultivars under shade conditions (Table 2).

Leaf gas exchange: The shade treatment caused the most significant decrease in P_N and g_s in Chuanzhu 12 (by 23.3 and 18.4%, respectively), while the least decline was found in Chuanzhu 11 (by 10.4 and 8.4%, respectively) (Table 3). Chuanzhu 11 and Chuanzhu 6 showed no reduction in E in response to shade, while E of the other two species decreased by more than 13.0% (Table 3). C_i showed a siginificant increase in Chuanzhu 11 and Chuanzhu 6, while no difference was observed in the other two species (Table 3). Moreover, Chuanzhu 11 had the highest P_N, while Chuanzhu 6 the lowest P_N in both sun and shade treatments (Table 3). Chuanzhu 11 and Chuanzhu 8 showed always higher P_N in both sun and shade treatments compared to Chuanzhu 12 and Chuanzhu 6 (Table 3).

Table 1. Influence of shade conditions on agronomic traits of four ramie cultivars. Values are means ± SE (n = 3). LA – leaf area; DM – dry mass. Values followed by *the different letter* within columns differ significantly according to *Newman–Keul*'s test (p<0.05).

Cultivar	Treatment	Total LA per plant [cm^2]	Plant height [cm]	Stem diameter [mm]	Total leaf DM per plant [g]	Total stem DM per plant [g]	Total aboveground DM per plant [g]
Chuanzhu 11	Control	6,392 ± 365^b	151.50 ± 1.32^b	11.77 ± 0.21^a	29.91 ± 0.24^b	36.32 ± 0.73^a	66.23 ± 1.17^a
	Shade	7,207 ± 190^a	165.67 ± 2.34^a	10.71 ± 0.28^b	26.97 ± 1.20^b	32.56 ± 0.85^b	59.52 ± 0.62^b
Chuanzhu 8	Control	4,729 ± 163^d	144.92 ± 0.52^c	12.09 ± 0.19^a	32.47 ± 0.57^a	32.44 ± 1.15^b	64.89 ± 1.11^a
	Shade	5,685 ± 183^c	161.33 ± 2.33^a	10.68 ± 0.07^b	27.91 ± 0.47^b	26.97 ± 0.77^c	54.86 ± 1.49^c
Chuanzhu 12	Control	4,925 ± 110^d	132.06 ± 0.71^d	10.21 ± 0.04^b	29.30 ± 1.27^b	29.79 ± 1.30^b	59.08 ± 0.92^b
	Shade	6,309 ± 107^b	151.67 ± 0.88^b	8.53 ± 0.34^d	24.58 ± 0.13^c	22.46 ± 0.46^d	47.04 ± 0.97^c
Chuanzhu 6	Control	4,495 ± 97^d	124.83 ± 0.73^e	9.10 ± 0.33^c	24.12 ± 0.77^c	26.25 ± 0.81^c	50.36 ± 1.14^d
	Shade	5,015 ± 93^d	135.50 ± 0.87^d	8.21 ± 0.07^d	22.65 ± 0.34^c	22.34 ± 0.57^d	44.96 ± 0.91^e

Table 2. Influence of shade conditions on the fiber yield and yield-related traits of ramie cultivars. FM – fresh mass; DM – dry mass. Values in the table are mean ± SE (n = 3). Values followed by *the different letter* within columns differ significantly according to *Newman–Keul*'s test (p<0.05).

Cultivar	Treatment	Fiber yield [kg ha^{-1}]	No. of stems per plant	Bast thickness [mm]	Bast FM per plant [g]	Bast stripping percentage [%]	Crude fiber DM per plant [g]
Chuanzhu 11	Control	214.72 ± 3.30^a	2.01 ± 0.07^b	0.873 ± 0.009^a	35.47 ± 0.81^a	12.95 ± 0.80^a	4.58 ± 0.15^a
	Shade	181.64 ± 1.50^c	1.69 ± 0.04^c	0.804 ± 0.005^{bc}	29.81 ± 1.22^b	12.80 ± 0.50^a	4.02 ± 0.09^b
Chuanzhu 8	Control	193.87 ± 2.57^b	1.89 ± 0.07^b	0.875 ± 0.024^a	33.57 ± 0.66^a	12.16 ± 0.15^a	4.08 ± 0.05^b
	Shade	154.71 ± 1.21^e	1.47 ± 0.10^d	0.784 ± 0.019^{cd}	26.93 ± 0.92^c	12.94 ± 0.29^a	3.44 ± 0.07^c
Chuanzhu 12	Control	173.13 ± 2.00^d	2.31 ± 0.05^a	0.841 ± 0.012^{ab}	31.24 ± 0.64^b	12.02 ± 0.61^a	3.75 ± 0.12^{bc}
	Shade	121.15 ± 1.38^f	1.70 ± 0.02^c	0.745 ± 0.016^{de}	22.59 ± 0.44^d	11.30 ± 0.46^a	2.81 ± 0.05^d
Chuanzhu 6	Control	151.30 ± 1.32^e	2.03 ± 0.04^b	0.761 ± 0.005^{cd}	28.53 ± 0.63^{bc}	11.48 ± 0.40^a	3.28 ± 0.08^c
	Shade	127.85 ± 1.46^f	1.72 ± 0.02^c	0.706 ± 0.010^e	23.27 ± 0.51^d	11.71 ± 0.34^a	2.89 ± 0.02^d

Table 3. Influence of shade conditions on gas-exchange traits and water-use efficiency of four ramie cultivars. P_N – net photosynthetic rate; E – transpiration rate; g_s – stomatal conductance; WUE – water-use efficiency; C_i – intercellular CO_2 concentration. Values in the table are mean ± SE (n = 3). Values followed by *the different letter* within columns differ significantly according to *Newman–Keul*'s test (p<0.05).

Cultivar	Treatment	P_N [µmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	g_s [µmol m^{-2} s^{-1}]	WUE [µmol mmol^{-1}]	C_i [µmol mol^{-1}]
Chuanzhu 11	Control	18.77 ± 0.18^{a}	6.96 ± 030^{c}	0.628 ± 0.009^{a}	2.71 ± 0.10^{a}	283.99 ± 1.76^{d}
	Shade	16.81 ± 0.52^{bc}	6.65 ± 0.11^{c}	0.575 ± 0.011^{b}	2.45 ± 0.08^{ab}	290.42 ± 1.25^{c}
Chuanzhu 8	Control	17.20 ± 0.30^{b}	7.91 ± 0.09^{b}	0.615 ± 0.017^{a}	2.19 ± 0.11^{bc}	292.97 ± 1.02^{bc}
	Shade	14.89 ± 0.23^{d}	6.88 ± 0.20^{c}	0.531 ± 0.004^{cd}	2.16 ± 0.10^{bc}	297.71 ± 1.80^{ab}
Chuanzhu 12	Control	15.93 ± 0.40^{cd}	8.15 ± 0.09^{b}	0.603 ± 0.005^{a}	1.96 ± 0.07^{cd}	293.94 ± 1.40^{bc}
	Shade	12.62 ± 0.09^{e}	7.06 ± 0.16^{c}	0.484 ± 0.007^{e}	1.79 ± 0.06^{de}	300.64 ± 2.31^{a}
Chuanzhu 6	Control	14.90 ± 0.20^{d}	8.98 ± 0.14^{a}	0.551 ± 0.005^{bc}	1.66 ± 0.07^{de}	278.87 ± 2.04^{d}
	Shade	13.31 ± 0.29^{e}	8.74 ± 0.29^{ab}	0.517 ± 0.006^{d}	1.58 ± 0.08^{e}	290.01 ± 1.87^{c}

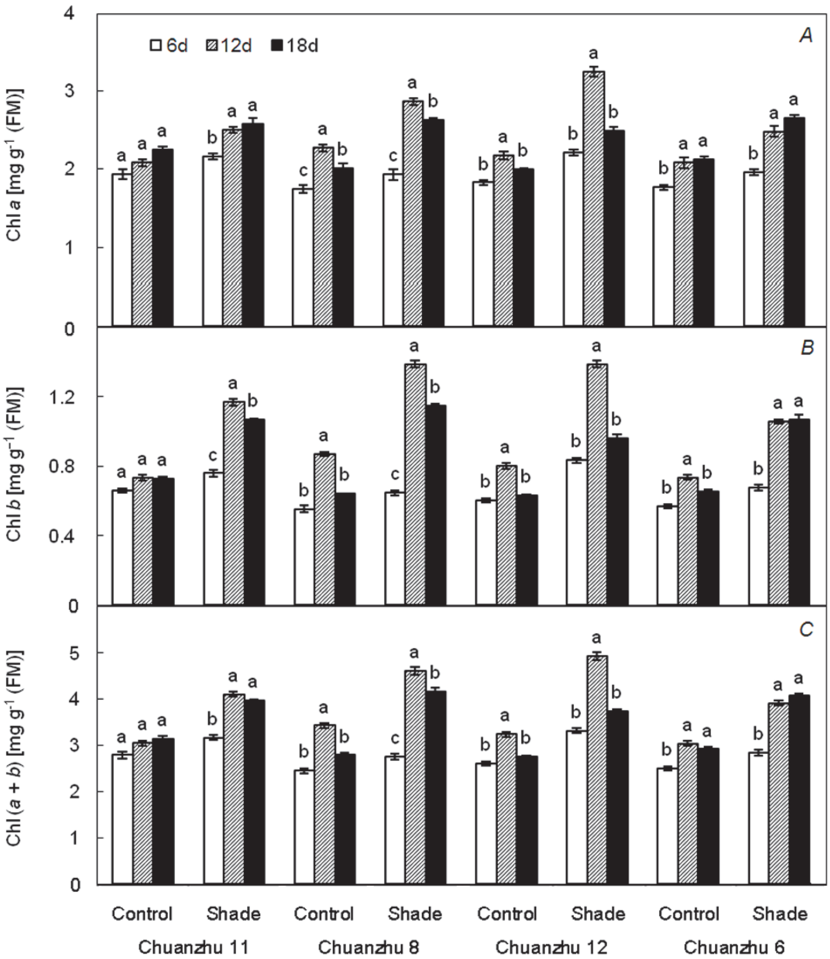

Fig. 1. Effects of shade on chlorophyll (Chl) *a* (*A*), Chl *b* (*B*), and Chl (*a*+*b*) (*C*) in four ramie cultivars. FM – fresh mass. Values in the figures are mean ± SE (n = 3). Values followed by *the different letter* within columns differ significantly according to *Newman–Keul*'s test (p<0.05).

Photosynthetic pigment contents: Chl *a*, Chl *b*, Chl (*a*+*b*), and Car significantly increased by the shade treatment in all ramie cultivars compared with the control (Figs. 1*A*,*B*,*C*; 2*A*). The A treatment caused the least increase, while the B treatment resulted in the highest ones (Figs. 1*A*,*B*,*C*; 2*A*). The Chl *a*/*b* ratio declined, whereas Chl (*a*+*b*)/Car ratio increased in all cultivars under shade conditions (Fig. 2*B*,*C*). The pigment contents increased from A to C treatment in both control and shaded plants in Chuanzhu 11 and Chuanzhu 6, while they peaked in the B treatment in Chuanzhu 8 and Chuanzhu 12, and decreased in the C treatment (Figs. 1*A*,*B*,*C*; 2*A*).

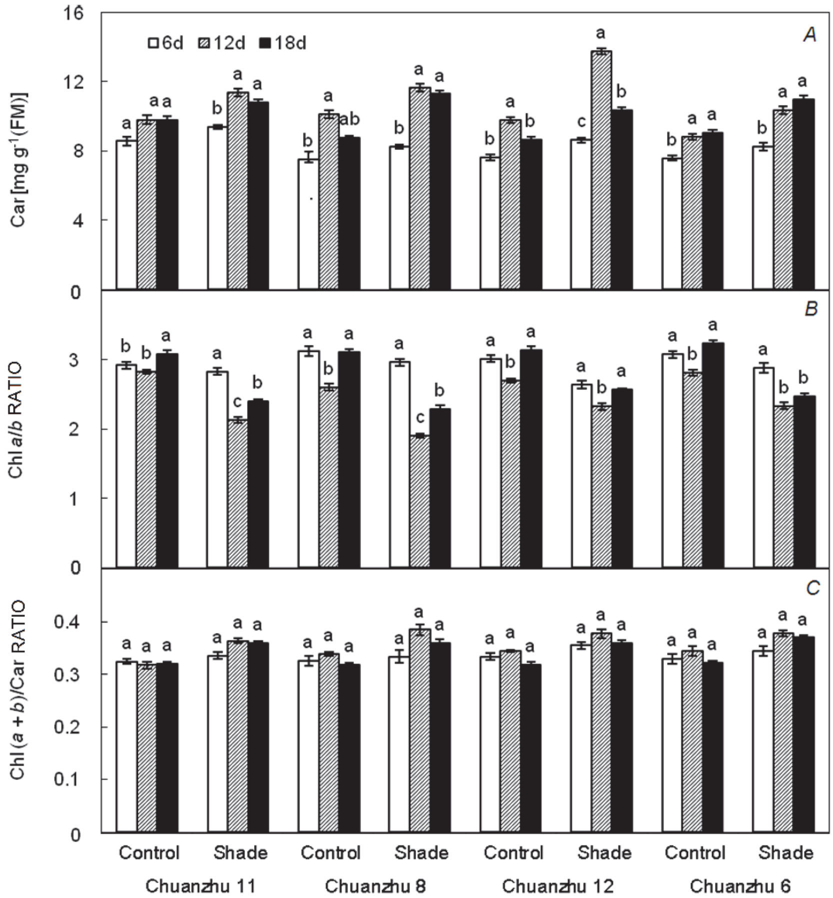

Fig. 2. Effects of shade on carotenoids (Car) (*A*), chlorophyll (Chl) *a*/*b* ratio (*B*), and total Chl (*a*+*b*)/carotenoids (Car) ratio (*C*). FM – fresh mass. Values in the figures are mean ± SE (n = 3). Values followed by *the different letter* differ significantly according to *Newman–Keul*'s test (p<0.05).

Chl (*a*+*b*) per leaf mass significantly increased under shade conditions. Chuanzhu 11, Chuanzhu 8, Chuanzhu 12, and Chuanzhu 6 showed signifcantly higher Chl (*a*+*b*) [0.147, 0.149, 0.152, and 0.180 mg g^{-1}(FM), respectively] as compared with the control [0.105, 0.086, 0.094, and 0.121 mg g^{-1}(FM), respectively].

Correlation analysis: The results showed that P_N was linearly and positively correlated with g_s (y = 37.027 x – 5.315; R^2 = 0.878), whereas, it was linearly and negatively correlated with Chl (*a*+*b*) (y = – 1.528 x + 20.793; R^2 = 0.200).

Discussion

Generally, our results showed that shade treatment led to significant alterations in plant and leaf traits of the four ramie cultivars. In particular, plant height and leaf area increased under shade conditions, suggesting that photosynthate allocation patterns favored shoot elongation and leaf area in order to increase light-harvesting capabilities in a light-limited environment (Smith and Huston 1989, Johnston and Onwueme 1998, Khan *et al*. 2000). In contrast, the stem diameter and total above ground DM decreased in all ramie cultivars. A similar trend was also observed in the fiber yield and yield components, which might be attributed to the inhibition of P_N under shade conditions (Table 3).

P_N decrease was related to g_s decrease as attested by the significant correlation between the two variables. In contrast, C_i unchanged or increased in shade conditions; it suggested that P_N decrease might be related to nonstomatal limitations (Brodribb 1996). Chl *a*, Chl *b*, Chl (*a*+*b*), and Car, as well as Chl (*a*+*b*) per leaf mass significantly increased under the shade treatments (Figs. 1*A*,*B*,*C*; 2*A*), indicating an adaptive response to reduced light in all ramie cultivars. However, a higher proportion of Chl *b* relative to Chl *a* enhanced the efficiency of blue light absorption in low-light environments (Givnish 1988, Yamazaki *et al*. 2005). This led to the lower Chl *a/b* ratio.

Shade-tolerant species have higher photosynthetic capacity and are able to maintain adequate growth rates under low light compare to intolerant species (Givnish 1988, Johnston and Onwueme 1998, Walters and Reich 1999, Jiang *et al*. 2004, Valladares and Niinemets 2008). When subjected to a shade treatment, shade-tolerant species also exhibit a lower decrease of P_N and growth than that of shade-intolerant species (Schrader *et al*. 2006). Our results showed that Chuanzhu 11 and Chuanzhu 6 seemed to be more tolerant to shade as they showed a lower reduction in plant traits and yield components, as well as a lower P_N decrease in comparison to Chuanzhu 8 and Chuanzhu 12.

Ramie is mainly cultivated in the mountain area of the Yangtze River Basin in China, where light varies greatly both in time and space. This phenomenon intermittently affects growth and yield of many crops including ramie. A tolerant cultivar to shade is crucial for ramie fiber production. Thus, shade tolerance is an important factor to consider in breeding programs and agronomic trials (Johnston and Onwueme 1998). Our results suggested that Chuanzhu 11 is suitable to be planted in the Yangtze River Basin due to its high fiber yield under both high and low light, while the commercial cultivar Chuanzhu 6 could be an optimal shade-tolerant material for breeding programs.

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