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Full Length Research Paper

The photosynthetic physiological properties of *Illicium lanceolatum* plants growing under different light intensity conditions

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In this study, the photosynthetic properties and CO_2 conductance of four-year old plants of *Illicium lanceolatum* were measured under three different light conditions (full light, half shadow and shadow) treatments. The results show that during the peak growth season, compared to those under full light, plants growing under half shadow light condition had the highest net photosynthetic rate (P_n), water usage efficiency and higher solar energy utilization efficiency (SUE), these plants had the lowest transpiration ratio (T_r) which was the strategy for achieving high photosynthesis and water utilization efficiency. Partial shading has improved SUE of plants. For plants growing under all of three light conditions, the light saturation point (LSP) increased initially then declined in response to increasing light intensity. Light compensation point (LCP) declined when plants were growing under shaded condition with less amount of light. The daily maximum value of net photosynthetic rate (P_{max}) and the apparent quantum yield (AQY) decreased in the order of half shadow>shadow>full light. There are significant differences ($p \leq 0.05$) among the three light conditions. Plants growing under half shadow had the highest light utilization efficiency. Results from this study indicate that half shadow light condition is the most suitable light condition for *I. lanceolatum*. The partial shade environment promoted rapid growth and accumulation of biomass of the species. This study provided the scientific bases for domestication and cultivation of shikimic acid rich plants.

Key words: *Illicium lanceolatum,* light environment, photosynthetic properties.

INTRODUCTION

Plant growth depends on appropriate supply of light, which plays an important role in plant growth, development, and evolution. In addition, light is one of the most important environmental factors that affect morphological formation and physiological functions of plants (Bazzaz, 1996). Response of plant leaves to different light conditions has been a hot research topic (Walters and Reich, 2000). Many researches in China have been performed on plant growth under various artificial light conditions (full light, different degree of shade), or different light environments (natural light, forest gap, floor stratum), morphological development and plasticity, and photosynthetic physiological ecology (Cai et al., 2004; Zhang and Cao, 2004; Guo et al., 2006; Wang and Guo, 2007; Hu et al., 2008).

Illicium lanceolatum is a traditional medicinal plant species growing only in China. The plants produce large amount of shikimic acid, the natural product has the medicinal functions including anti-inflammatory, pain-killing, and inhibition of anti-blood platelet aggregation, anticoagulant and anti-cerebral thrombosis (stroke) formation, antivirus and anticancer. There is a spotty distribution of *I. lanceolatum* despite of wide ecological amplitude of the species. As a consequence of the destructive harvest of wild resources, the wild species is dwindling. Therefore, it is an urgent task to develop strategies for large scale domestication, protection and cultivation of the species (Cao et al., 2008; Cao. 2009). Plant response to various light conditions is a hot research area in the world (Tang, 2008). However, no

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relevant study has been reported on *I. lanceolatum* (Cao, 2009). The photosynthesis and water physiological ecology study of four different *I. lanceolatum* eco-types have been carried out to clarify the growth seasonal variations and the differences among eco-types seedlings under different cultivation environment, and reveal the physiological ecology adaptive response mechanism among 4 eco-types (Cao, 2009). This paper was based on the preliminary findings. In this study, photosynthetic properties under different light conditions were compared to determine the effect of light factor on potential photosynthetic capacity of this species. The objective was to identify the adaptability of this species to different eco-environment, in attempt to provide theoretical bases for high yield production on large scale under artificial cultivation condition.

MATERIALS AND METHODS

Description of the experimental site

The experiment was conducted in Forest Nursery, Tianmu Mountain, Linan city, Zhejiang Province. The geographical coordinates of this location are 118°51'- 119°52' E, 29°56'-30°23'N, the elevation is 47 m. It is in the Mid-North Asia tropical monsoon climate zone. The annual average temperature is 15.4°C, and the air temperature in January is above 3.2°C, average air temperature in July is 29.9°C, and the annual precipitation is 1,250 to 1,600 mm. The experimental site was chosen on the relatively flat land in a hilly area. It has acidic yellow loam clay soil, organic matter content at 23.95 g kg^{-1}, total nitrogen content at 0.44 g kg^{-1}, total phosphorus at 10.09 g kg^{-1}, total potassium at 6.31 g kg^{-1}, alkali-hydrolyzable nitrogen at 217.62 mg kg^{-1}, available phosphorus content at 363.97 mg kg^{-1}, and available potassium at 40.51 mg kg^{-1}. The soil pH value was 4.62.

Seeds were obtained from the Natural Protection Zone in Tianmu Mountain in Zhejiang Province. Seeds were sown in May, 2005, and 2-year-old seedlings were transplanted from seedling beds and intercropped under forest which had a density of 1,350 to 1,650 plants·hm^{-2}. The average ground diameter was 2.3 to 3.4 cm and plant height was 1.7 m. Soil condition was the same as described above, and plants were managed using routine fertilization and cultivation practices. According to differences in crown density between intercropping and monocropping, four-year old plants were divided into three groups: group 1 of full light where plants were growing under full natural light; group 2 of half shadow where plants were growing under *Acer albopurpurascens* tree for 3 year with 50% of crown density; and group 3 of shadow where the plants were intercropping with *Acer buergerianum* for 3 years with 80% crown density of canopy.

The experiment was done using four-year old plants. Plants growing under full light were considered as control. *The IL-1700* quantum radiation meter was used to measure the relative light transmittance ratio at 10:00 am for five consecutive sunny days in Sept., *2009. Based on* light transmittance ratio, the three light conditions were assigned as full light, half shadow, and shadow.

Measurement of photosynthesis and light response parameters

The measurements were done continuously for a whole day on a sunny day in Mid-Sept, 2009. Li-6400 Portable Photosynthesis and Fluorescence System (LI-COR, Lincoln, USA) was used to measure each of the photosynthetic physiological parameters, and a photosynthesis light response curve was constructed using the data collected. For each plant, measurements were done on mid-height three leaves on the current year branch; each leaf was measured three times. At the end of each measurement, the leaf was marked, detached from the plant, and stored in storage plastic bags before being transported to the laboratory for measuring chlorophyll content. The time from cutting the leaves to the beginning of chlorophyll extraction must be controlled within 30 minutes. Chlorophyll content was determined following the method of Johnston et al (1984). At the same time, other leaves were detached and collected to determine leaf dry weight and nitrogen content. Leaf area was calculated using scanned images. The harvested leaves fixed at 105°C in an oven for 10 min and then dried at 80°C to constant weight. Dry weight was measured to an accuracy of 0.0001g. The specific leaf weight (LMA) ($g.m^{-2}$) was calculated as the ratio between leaf dry weight and leaf area (Feng et al., 2002). Samples were digested in H_2SO_4-H_2O_2 to determine nitrogen content using the diffusion method (Zhang and Shangguan, 2007).

Response to light conditions was assessed using the Li-6400 red-and blue light sources under the following conditions: air flow rate at 0.5 L·min^{-1}, leaf temperature at 26 to 35°C, relative humidity of 60%, and CO_2 concentration at 365 μmol·mol^{-1}. At the beginning of the measurement, light intensity was 2000 umol·m^{-2}·s^{-1}, which was gradually reduced to 1,800, 1,500, 1,200, 1,000, 800, 500, 200, 120, 80, 50, 20, 0 μmol·m^{-2}·s^{-1}.

The curve of light response was constructed using data collected from 9-11:00 am on a sunny day. To construct the light response curve, the light quantum flow density (PPFD) (X-axial) was plotted against net photosynthetic rate (P_n) (the Y-axial), and P_n-PAR (Photosynthetically Active Radiation) curve was fitted using the Thornley Non-rectangular hyperbola model (Thornley, 1976; Liu et al., 2005). The derived equation was used to calculate the photosynthetic physiological parameters. The solar energy utilization efficiency (SUE) was the ratio between P_n and PAR, and transient water utilization efficiency (WUE) the ratio between P_n and T_r. SUE and WUE are the potential resource utilization efficiency of plants.

Data analysis

Data of photosynthetic physiological parameters were tested by one-Way ANOVA ($p \leq 0.05$) using the SPSS 10.0 statistical software. The least significant difference method (LSD) was used to determine significant difference between the means and multivariate groups of all parameters. LSD is a method commonly used in multiple comparison methods for mutual significance test in average among more deals.

RESULTS AND DISCUSSION

Effect of light conditions on daily changes of photosynthetic activity

During the peak growing season of *I. lanceolatum*, daily change in net photosynthetic rate (P_n) and transpiration ratio (T_r) differed significantly among the three light conditions (Figure 1). The daily maximum value of P_n was the highest for the half shadow followed by the shadow and then the full light condition. The average daily P_n was ranked in decreasing order as half shadow (2.80 μmol m^{-2} s^{-1}) >full light (1.43 μmol m^{-2} s^{-1}) >shadow (1.14 μmol m^{-2}

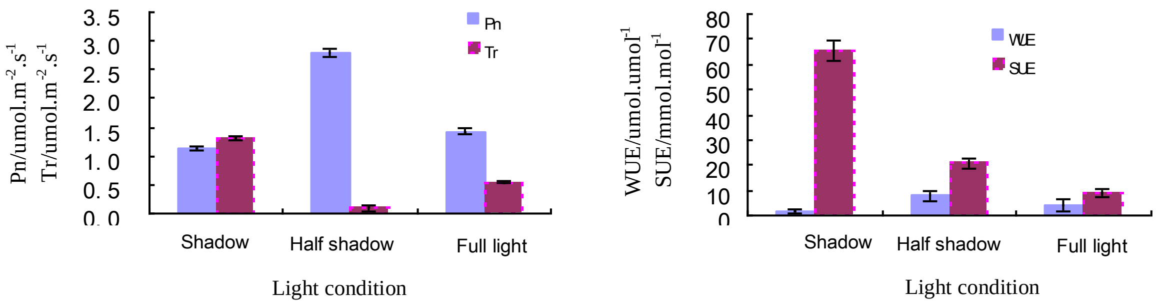

Figure 1. The diurnal average value of photosynthesis indices for *I. lanceolatum* seedlings under different light conditions.

s^{-1}). Based on the P_n value, moderate shade improved the net photosynthetic rate of young plants. Different from P_n, the average daily T_r was ranked as shadow (1.31 μmol m^{-2} s^{-1}) >full light (0.54 μmol m^{-2} s^{-1}) >half shadow (0.10 μmol m^{-2} s^{-1}).

Under influence of the two factors including net photosynthetic rate and photosynthetic effective irradiance, plants growing under different light conditions showed significant difference in solar energy utilization efficiency (SUE). As shown in Figure 1, the daily average SUE decreased in the order of shadow (65.36 mmol mol^{-1}) >half shadow (20.90 mmol mol^{-1}) >full light (8.77 mmol mol^{-1}). The SUE value at full light is significantly different from those from shadow and half shadow treatments. Based on these results, moderate shade increased solar energy utilization efficiency of *I. lanceolatum* plants.

Water utilization efficiency (WUE) is the amount of CO_2 fixation or dry matter produced per unit of water consumed. WUE is a measurement of water utilization efficiency of plants, it represents photosynthesis properties at a given transpiration rate (Su et al., 2003). This parameter is also used to determine *the* adaptability of plants *to* environmental changes. When compared among plants of *I. lanceolatum* growing under different light conditions, the daily average WUE was ranked as half shadow (7.80 μmol CO_2 μmol^{-1} H_2O)>full light (4.12 μmol CO_2 μmol^{-1} H_2O) >shadow (1.61 μmol CO_2 μmol^{-1} H_2O). Furthermore, half shadow was significantly different from shadow, whereas there is no significant difference between the half shadow and full light treatments. Taking into account that plants growing under half shadow have lower T_r level, the high WUE could be an indication that plant used this property to maintain certain level of photosynthesis and carbon assimilation.

Results from this analysis indicate that compared to full light, shade condition have both positive and various effects on photosynthetic physiological properties of young *I. lanceolatum* plants. Under half shadow light condition, plants had the highest P_n, WUE and relatively high SUE. The lowest Tr was used to achieve high photosynthesis and water utilization efficiency. Under shadow light condition, plants had relatively high P_n and T_r, and the highest SUE but lowest WUE. On the contrary, under full light, plants had lower P_n and T_r, the lowest SUE and lower WUE. In summary, half shadow is the most appropriate light condition for growing *I. lanceolatum*.

The response of *I. lanceolatum* plants to different light conditions

Light saturation point (LSP) and light compensation point (LCP) are the physiological parameters of light requirement of plants. LSP or LCP each represents the upper or lower limit of the light intensity required for photosynthesis, they are used to measure the utilization efficiency of *I. lanceolatum* for strong and weak light, respectively. LSP value was in the range of 454.7-881.3 μmol m^{-2} s^{-1} for the three light treatments, there is no significant difference between the full light and shadow, however the LSP of half shadow is significantly higher than full light and shadow light conditions ($p \leq 0.05$) (Figure 2).

The LCP was in the range of 5.5 to 88.83 μmol m^{-2} s^{-1}, there is a significant difference between pairs of the three light treatments. The LSP value was ranked as half shadow (881.28 μmol m^{-2} s^{-1}) >shadow (601.35 μmol m^{-2} s^{-1}) >full light (454.69 μmol m^{-2} s^{-1}). The LCP value was ranked as full light (88.83 μmol m^{-2} s^{-1})>half shadow (23.27 μmol m^{-2} s^{-1}) >shadow (5.53 μmol m^{-2} s^{-1}). The results indicate that under the three light treatments conditions, LSP escalated initially then declined as light intensity increased to higher level. The LCP value decreased as the light intensity weakened under shaded condition. These results indicate that plants growing under shade used the strategy of lowering LCP to adapt to weak light condition. By utilizing weak light these plants soon reached the point of light saturation. When growing under full light, the ability of plants to utilize strong light was obviously reduced to the lowest level. However, plants under half shadow showed much higher ability in using strong light.

The maximum net photosynthetic rate (P_{max}) was

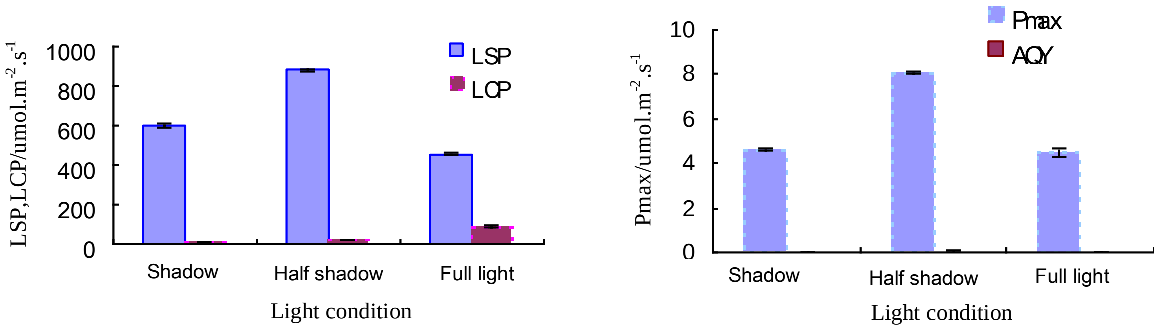

Figure 2. The photosynthesis-light response characteristics of *I. lanceolatum* seedlings under different light conditions.

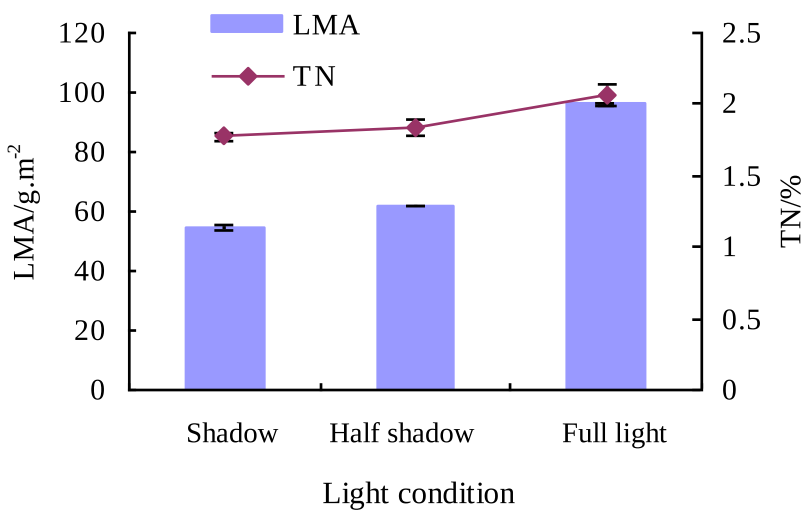

Figure 3. The leaf mass per area and nitrogen content of *I. lanceolatum* seedlings under different light condition during growth phases.

ranked as half shadow (8.05 μmol m^{-2} s^{-1}) >shadow (4.59 μmol m^{-2} s^{-1}) >full light (4.50 μmol m^{-2} s^{-1}). The P_{max} value of half shadow was significantly higher than the other two light conditions ($p \leq 0.05$), there is no significant difference between full light and shadow light conditions. The apparent quantum yield (AQY) is in the range of 0.011-0.043 μmol CO_2 μmol^{-1} H_2O, it decreased in the order of half shadow >shadow >full light. There is no significant difference between shadow and half shadow light conditions, but both are significantly different from full light ($p \leq 0.05$). These results indicate that plants growing under shaded conditions are better adapted to weak light. Plants growing under half shadow had the highest utilization efficiency for weak light. Under full light, the ability of using weak light rapidly declined to a level far below those under shade.

For plants growing under natural light, low AQY is indication of serious photo-inhibition. The increase in AQY for plants growing under shade indicates that these plants are using this strategy to maintain photosynthetic rate under lower photosynthetic photon quanta flux density. This property is beneficial for maintaining normal growth of plants under shaded environmental condition.

The effect of light conditions on leaf mass per area (LMA) and leaf nitrogen content

Functional leaves are the most important and major tissues conducting photosynthesis activity. The leaf mass per area (LMA) is an important parameter measuring plant relative growth rate. Nitrogen element is one of the most important nutrient minerals, and leaf nitrogen content and the utilization efficiency have a strong correlation with photosynthesis activity. Leaf nitrogen content is also an important parameter used to assess the ability of plant to adapt to growth environment (Zheng and Shangguan, 2007).

As shown in Figure 3, as stronger light was provided, plant LMA and leaf nitrogen content both increased

Table 1. The regression analysis between leaf nitrogen content (x) and P_{max}(y) of *I. lanceolatum* seedlings under different light condition.

Light treatment	Parameter of linear regression equation			
	c	k	R^2	F-value
shadow	13.053	-4.870	0.988	42.282**
half shadow	0.596	3.968	0.965	13.683**
full light	5.369	-0.414	0.850	2.607**

"y" denotes maximum net photosynthesis rate, "x" denotes leaf nitrogen content, "c" and "k" denote parameters.

gradually. The level of the two parameters was ranked in the order of full light>half shadow>shadow. The results indicate that plants growing in the shadow light environment reduced LMA to adapt to the weak light condition, in order to maintain the highest possible photosynthetic carbon assimilation activity. This result supports the other finding in this study that this species has relatively lower maximum photosynthetic rate (as low as 4.59 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and agrees to previous findings that shade tolerant plants have thinner leaf and smaller LMA (Givnish et al., 2004; Miller et al., 2004; Osone and Taleno, 2005).

Nitrogen utilization efficiency measures the capacity of plants to properly utilize and redistribute the nutrient element. It is an important parameter for evaluating the effect of nitrogen on photosynthetic productivity and growth of plants. In the correlation analysis of leaf nitrogen content and maximum net photosynthetic rate (P_{max}) (Table 1), the two factors have significant correlation under the three light conditions. The highest correlation index was 0.965-0.988 between shadow and half shadow light conditions. Therefore, leaf nitrogen content has a strong effect on photosynthetic capacity of *I. lanceolatum* plants.

Conclusion

Effect of light conditions on daily photosynthesis activity of I. lanceolatum

With global warming and ecological damage, the water shortages increasingly become a serious ecological problems and short-term and long-term water shortages become a most important environmental factor that affects plant production and distribution (Shao et al., 2008, 2009).The low WUE and SUE values under full light suggest that plants need partial shade during the peak growing season, therefore the average daily WUE value was relatively higher whenever there was a low average daily T_r. This confirms that plants have to reduce transpiration to ensure certain level of WUE during the peak growing season, which may be an adaption mechanism to full sun condition. Moreover, plants growing under moderately shaded condition have higher net photosynthetic rate, higher stomatal conductance and utilization efficiency of light energy and water (Liu and Kang, 2002; Zhang et al., 2000). This study found that moderate shade improved net photosynthetic rate and light energy utilization rate of *I. lanceolatum*. The half shadow is the most effective in promoting vegetative growth, accumulation of biomass and production of medicinal compounds.

Comparison of photosynthetic parameters under different light conditions

To summarize results from this study, *I. lanceolatum*, growing under moderate shade by intercropping with tall trees may effectively increase photosynthetic capacity and light saturation point while maintaining low light compensation point. These properties enable plants to capture and utilize strong light, as well as developing the capacity for utilization of weak light. The half shadow is the most ideal environment for growing *I. lanceolatum*. The theoretical initial maximum quantum yield of plants is in the range of 0.08 to 0.125. But under natural condition, the AQY is always far below the upper limit of the expected level. For healthy growing plants, the AQY is normally from 0.04 to 0.07 (Long et al., 1994). Partial shading increased AQY values (Zhang et al., 2005), which was found in this study. During the peak growth season, the AQY of plants under half shadow and shadow light conditions was significantly higher than those from full light. These results indicate that intercropping can improve AQY of *I. lanceolatum*.

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