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ARTICLE

Effects of Canopy Closure on Photosynthetic Characteristics of *Ilex latifolia* Thunb. in *Phyllostachys pubescens* Forests

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ARTICLE INFO

Article history
Received: 5 March 2019
Accepted: 7 April 2020
Published Online: 30 April 2020

Keywords:
Ilex latifolia Thunb
Canopy closure
Photosynthetic
Phyllostachys pubescens

ABSTRACT

Plantation under the forest is a good way of agroforestry, but the canopy closure has a great influence on understory herbs' growth. In the study, different canopy closures of *Phyllostachys pubescens* forests were set up to explore its influence on the growth of *Ilex latifolia* Thunb. The photosynthetic characteristics of *Ilex latifolia* leaves under different canopy closures were determined by Li-6400 portable photosynthetic system. The results showed that the net photosynthetic rate curve of *Ilex latifolia* leaves of T1 (canopy closure of 0.56) was bimodal with an obvious "midday depression" phenomenon, while the net photosynthetic rate curves of T2 (canopy closure of 0.72) and T3 (canopy closure of 0.86) were unimodal. The results of light response curve showed that the photosynthetically active radiation and transpiration rate reduced with the increasing of canopy closures. The photosynthetically active radiation, transpiration rate, stomatal conductance, and net photosynthetic rate of *Ilex latifolia* leaves of T2 were higher than those of T3. Although the net photosynthetic rate of T2 was lower than that of T1, it had no obvious photo-inhibition which affected plant growth. Overall, the canopy closure of 0.72 was more suitable for the growth of *Ilex latifolia*. The herb plantation in the bamboo forest should be considered with the canopy closure for a better growth.

1. Introduction

Ilex latifolia Thunb, called "Ku-ding-cha" in Chinese, is an important traditional tea and herbal medicine that favored by Asian people [1]. *Ilex latifolia* is popular because of its medicinal health functions such as cooling, detoxifying, reducing cholesterol, lowering blood pressure, decomposing blood fat, relieving fatigue and aging resistance of human body in East Asia [2]. *Ilex latifolia*, however, prefers living in a shady environment [3, 4]. Under the natural condition, *Ilex latifolia* often grows in a cool shade of the canopy. It mainly distributes in Zhejiang, Jiangsu and Guangxi provinces of China [5]. *Ilex latifolia* cannot grow in a pure stand due to its special living condition. Therefore, interplantation with other plants is a best candidate for the cultivation of *Ilex latifolia*.

Interplantation refers to the use of difference in time and space to grow two or more plants on the same land [6-8]. Under the artificial control, it makes full use of the mutually beneficial relationship between plants to form a reasonable composite structure to improve the photosynthesis efficiency of the group [9,10]. In addition, the high and low

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  DOI: https://doi.org/10.30564/re.v2i2.1366

layers of plants are not only beneficial to improve the ventilation and light transmission of plants in the interplantation system that are beneficial to the improvement of ventilation and light energy [11]. Chen *et al*. suggested the citrus intercropping in the forest can facilitate its growth and improve quality of the citrus, which resulted in ecological and economic benefits [12]. Moreover, interplantation was also an effective way to improve the soil physical structure and soil nutrient status [13,14].

Phyllostachys pubescens is an important bamboo species that mainly cultivated as pure stand. However, studies have shown that large areas of pure *Phyllostachys pubescens* forest would decline in productivity after a period of high yield [15]. To change the pure bamboo stand for improving ecological and environmental functions is an important silviculture for *Phyllostachys pubsecens* forest. Therefore, the interplantation of *Ilex latifolia* and *Phyllostachys pubescens* forest is a good combination method and has not been done before yet [16,17]. As reported, interplantation can improve soil degradation and regional ecological environment deterioration of *Phyllostachys pubescens* forest [18]. A suitable interplantation is necessary for the pure bamboo forest improvement. *Ilex latifolia* is difficult to be raised in single seeding, meanwhile, it always shows a low quality and inadequate yield under the natural condition [19]. Accordingly, we interplanted *Ilex latifolia* in *Phyllostachys pubescens* forests to reduce the cost of *Ilex latifolia* seedlings, and improve the quality and yield, and make significant economic benefits.

Canopy closure is one of the important ecological factors of forest communities that affects the light conditions (light intensity, light quality) in the forest [20-21]. Canopy closure determines photosynthesis of plants to a large extent [22]. Inappropriate size of canopy closure would affect the growth, distribution and expansion, even leads to death of plants [23,24]. Different canopy closures have different effects on understory plants [25,26]. Li *et al*. founded that the shade could affect the ecological environment of the tea garden, which is beneficial to the tea tree to increase the net photosynthetic rate and improve the photosynthetic capacity [27]. In order to ensure the normal growth of the plants, it is necessary to ensure that the canopy of the upper plants is not too large, so as to provide sufficient illumination for the underlying plants. Studies have shown that the net photosynthetic rate, stomatal conductance, transpiration rate and water use efficiency of *Illicium difengpi* leaves grown under the forest or the open space are basically consistent with the light intensity. However, the net photosynthetic rate, stomatal conductance and transpiration rate of the open land were larger, and the water use efficiency under the forest was greater [28]. Furthermore, *Medicago sativa L*. was planted in apricot forest, and it was found that the photosynthetic rate of *Medicago sativa L*. decreased with the increase of shading degree, and the photosynthetic parameters such as light saturation point, light compensation point and maximum net photosynthetic rate decreased accordingly [29].

It can be seen from the above studies that the parameters of photosynthesis are closely related to the size of canopy closure. However, it has not been studied that the influence of canopy closure on the growth of *Ilex latifolia*. Therefore, the objective of this study was to investigate the effect of canopy closure on *Ilex latifolia* growth interplanted in *Phyllostachys pubescen* forests using the indicators of photosynthetic characteristics of *Ilex latifolia* leaves.

2. Materials and Methods

2.1 Plant Material and Growth Conditions

The study site was located at Hanggai Town of Anji County (30°52′N, 119°36′E), Zhejiang Province, China. The canopy closure of bamboo forests in the experimental area was mainly 0.65-0.75. *Ilex latifolia* seedlings in 2 years old and well-growing were selected as experimental material and transplanted in *Phyllostachys pubescens* forests with different canopy closures. The canopy closure was measured by the system punctuation head-up observation method. Each canopy closure was set up with 3 plots and there were 9 plots in total. The area of each plot was 30 m × 30 m. 100 *Ilex latifolia* plants were interplanted in each plot with an interval space of 3 m. There were three types of canopy closure as 0.56 (T1), 0.72 (T2) and 0.86 (T3) employed in this study.

2.2 Diurnal Changes in Photosynthesis

In August 2018, the experiment was conducted on sunny days. All measurements were carried out using a portable open-flow gas exchange system (Li-6400) during the period of 7:00-16:00. In each plot, five *Ilex latifolia* plants were chosen and five leaves of each plant was selected and measured. The tested leaves were selected from the mid-lower to the middle parts of the sunny canopy in the outer periphery of the canopy. Measurements were all carried out under the natural conditions and the average value was obtained by five replicates. The measurement was done every hour from 11:00 to 14:00 and every 2 hours in other time. Measured parameters included net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration.

2.3 Photosynthetic-light Response Curve

Using the Li-6400 photoresponse automatic measurement procedure, the air CO_2 concentration was set to a constant value of 400 μmol·L^{-1} and the temperature was 22 °C. Red and blue light source were used in the leaf chamber. The photosynthetically active radiation was controlled by the artificial light source which would raise the light intensity from 0 to a level above the saturation point. The set values were 20, 50, 100, 150, 200, 400, 600, 800, 1000, 1200 and 1500 μmol·m^{-2}·s^{-1}, respectively. Parameters of net photosynthetic rate, transpiration rate, stomatal conductance, relative air humidity and leaf temperature were measured simultaneously.

2.4 Statistical Analysis

The data were analyzed via one-way ANOVA according to LSD's test at $p<0.05$ and the sample variability was presented in line diagram with a standard deviation (SD). All data were analyzed using the SPSS (IBM SPSS Version 20.0). The figures were drawn with Excel 2016.

3. Results

3.1 Photosynthetically Active Radiation and Temperature

As shown in Figure 1, the diurnal variation of photosynthetically active radiation in three plots was unimodal. It rose from 7:00 to 13:00 and then decreased after that. Moreover, the peaks of T1, T2, and T3 were 125, 71 and 70 μmol·m^{-2} s^{-1}, respectively. The photosynthetically active radiation of T1 was significantly higher than that of T2 and T2 was higher than T3. Obviously, the photosynthetically active radiation was negatively related to the canopy closure.

Similarly, the change of air temperature was also unimodal. The air temperature ranged from 24 °C to 35 °C during the measurement. There was no significant difference among three groups in air temperature.

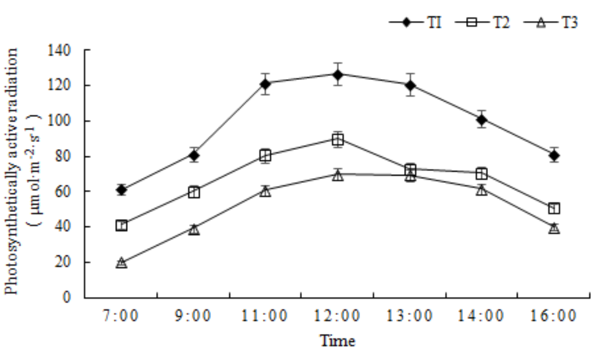

Figure 1. Photosynthetically active radiation in forests with different canopy closures

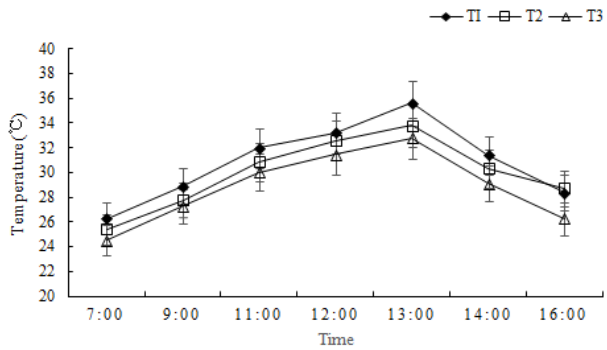

Figure 2. Diurnal temperature variation in forests with different canopy closures

3.2 Diurnal Variation of Photosynthesis

3.2.1 Diurnal Variation in Net Photosynthetic Rate

As shown in Figure 3, we found that the net photosynthetic rate of *Ilex latifolia* was bimodal in diurnal curve of T1. The first peak was 4.99 μmolCO_2·$m^{-2}s^{-1}$ at 9:00 then fell to the lowest at around 12:00. The second peak was 3.40 μmolCO_2·$m^{-2}s^{-1}$, which appeared around 13:00. Moreover, the second peak was significantly lower than the first, indicating a clear "midday depression". However, the curves of net photosynthetic rate of T2 and T3 were unimodal with peaks of 2.95 and 1.96 μmolCO_2·$m^{-2}s^{-1}$, respectively. They all appeared around 12:00.

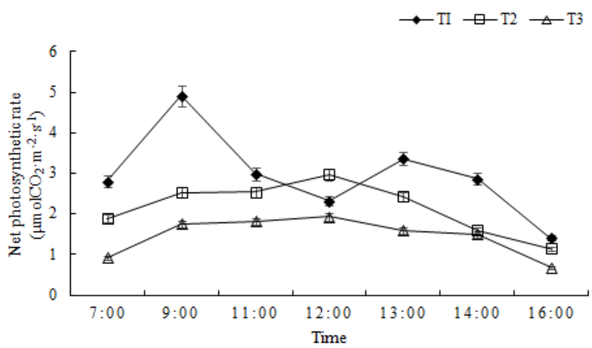

Figure 3. Diurnal variation of net photosynthetic rate of *Ilex latifolia* under different canopy closures

3.2.2 Diurnal Variation of Transpiration Rate

According to Figure 4, the diurnal variation of transpiration rate of *Ilex latifolia* was bimodal. The transpiration rate was at a lower level due to the high relative air humidity in the morning. The transpiration rate of *Ilex latifolia* increased from 7:00 to 11:00 of T1. The first peak was 1.93 μmolCO_2·mol^{-1} at 11:00. Later the transpi-

DOI: https://doi.org/10.30564/re.v2i2.1366

ration rate showed a downtrend to a valley value of 1.82 μmolCO_2·mol^{-1} at 12:00, and then rose to a second peak of 2.08 μmolCO_2·mol^{-1}. After 13:00, the transpiration rate dropped to a lower level. The first peaks of transpiration rate of T2 and T3 were 1.78 and 1.33 μmolCO_2·mol^{-1} at 9:00, respectively. The transpiration rate reached the valley value at 11:00-12:00, then began to rise to a second peak at 14:00. The second peak of T1 was 1.51 μmolCO_2·mol^{-1} while that of T3 was 1.18 μmolCO_2·mol^{-1}, respectively. The net photosynthetic rate in T1 was significantly better than that in T2 and T3. Among the three groups, the transpiration rate of T1 was usually higher than the others.

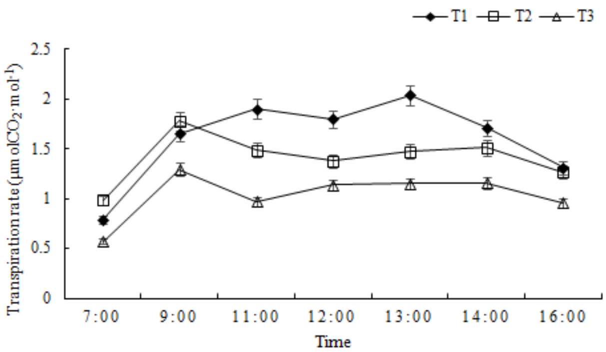

Figure 4. Diurnal variation of transpiration rate of *Ilex latifolia* under different canopy closures

3.2.3 Diurnal Variation of Intercellular CO_2 Concentration

As shown in Figure 5, the daily variation of intercellular CO_2 concentration was V shape which was higher in the morning and evening. The intercellular CO_2 concentration gradually decreased from 7:00 to 11:00, then increased ftom 11:00 to 16:00, but there was no significant difference among the three groups. The daily variation of intercellular CO_2 concentration in all treatments was opposite to the photosynthetically active radiation and the net photosynthetic rate.

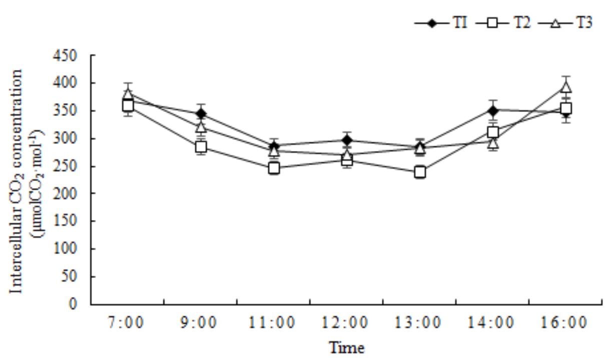

Figure 5. Diurnal variation of intercellular CO_2 concentration of Ilex latifolia under different canopy closures

3.2.4 Diurnal Variation of Stomatal Conductance

The Figure 6 showed that the diurnal variation of stomatal conductance in the leaves of *Ilex latifolia* had a similar pattern of the three treatments, which was bimodal. The stomatal conductance gradually increased from 7:00 to 9:00 as a first peak. The peak values of T1, T2 and T3 were 0.11, 0.10 and 0.07 mol·m^{-2}·s^{-1}, respectively. The stomatal conductance decreased until 12:00. Then it rose and reached the second peak around 14:00, which was 0.08, 0.06 and 0.04 mol·m^{-2}·s^{-1}, respectively. The stomatal conductance of T1 was consistent with the net photosynthetic rate in daily variation. However, the variation of stomatal conductance was not consistent with that of net photosynthetic rate of T2 and T3.

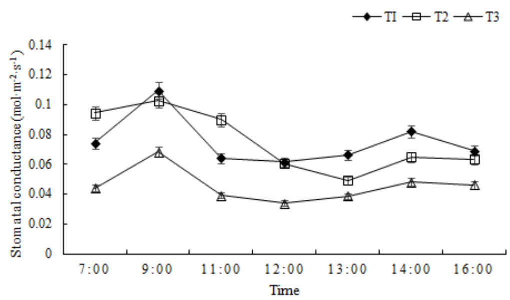

Figure 6. Diurnal variation of stomatal conductance of *Ilex latifolia* under different canopy closures

3.3 Light-response Curve

At 9:00, when the CO_2 concentration was set to 400 μmol·L^{-1} and the temperature was 28℃ , the light-requiring characteristics of *Ilex latifolia* leaves in three groups were different (Figure 7). The net photosynthetic rate showed the highest of T1 and the lowest of T3. The light compensation points of T1, T2 and T3 were 22, 25 and 29 μmol·m^{-2}·s^{-1}, respectively. Moreover, the light saturation points of T1, T2, and T3 were 993, 1115 and 1206 μmol·m^{-2} ·s^{-1}, respectively. Light effective radiation showed that the photosynthetic efficiency of T1 was significantly higher than those of T2 and T3.

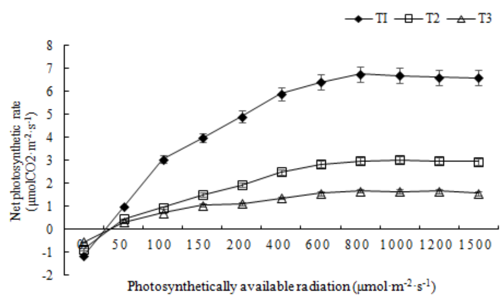

Figure 7. Light-response curves in Ilex latifolia leaves from different canopy closures

DOI: https://doi.org/10.30564/re.v2i2.1366

4. Discussion

Plant growth and yield depend largely on photosynthesis [31,32]. Light is an important energy source and foundation for photosynthesis of green plants [33]. Light intensity regulates plant growth, development and morphogenesis [34-37]. Li *et al*. found that high light stress reduced the stomatal conductance and net photosynthetic rate of *Ginkgo* [38]. Huang *et al*. found that the photosynthetic performance of cherry leaves under low light stress were lower than that under normal light [39]. Canopy closures affects the light conditions (light intensity, light quality) in the forest, even affects the growth of plants [40].

In the natural environment, there are basically two types of diurnal variation curves of plant photosynthesis. One is a unimodal type with the highest photosynthetic rate at noon, and the other is a bimodal type with a valley in the afternoon. The bimodal type has a trough at noon called midday depression [41]. In the study, the diurnal variation of net photosynthetic rate of T1 was bimodal, and there was a midday depression with a significant reduction at noon (Figure 7). The photoinhibition is common in C3, C4 and CAM plants [42-44]. In our study, the diurnal variations of transpiration rate and stomatal conductance were consistent with the diurnal variation of net photosynthetic rate in T1 (Figure 5, Figure 7). This indicated that as the temperature increased, stomatal conductance increased, and the transpiration rate increased as well. In order to reduce the transpiration rate and prevent the loss of more water, the stomatal conductance decreased, the absorption of CO_2 decreased, the net photosynthetic rate decreased of *Ilex latifolia*, and a midday depression occurred.

There were two reasons for midday depression, one is stomatal limitation and the other is non-stomatal limitation [45,46]. According to the classical method proposed by Farquhar and Sharkey [47], the intercellular CO_2 concentration increased, probably due to the increase of leaf temperature at noon, enhanced respiration, and higher photosynthesis effective radiation inhibition of photosynthesis. These results were controlled together by the stomatal and non-stomatal factors.

Comparatively, there was no midday depression of T2 and T3. This indicated that the growing environment of *Phyllostachys pubescens* under the high canopy closure was different from the low canopy closure. When the temperature and photosynthetically active radiation was at a low level, the stomatal conductance was reduced while the change trend was slight, and the net photosynthetic rate was less affected. Therefore, photoinhibition did not occur. Furthermore, the photosynthetically active radiation, transpiration rate, stomatal conductance, and net photosynthetic rate of *Ilex latifolia* leaves of T2 were higher than that of T3 (Figure 1, 3, 4, 7). Chen *et al*. found that the photosynthetic rate of *Camellia* decreased when the canopy closure was too high due to a low light energy captured by *Camellia* under the high canopy closure [48]. In addition, the canopy closure range of the experimental area was 0.65-0.75. In conclusion, according to the photosensitivity characteristics, the canopy closure of 0.72 was more suitable for the growth of *Ilex latifolia* among the three treatments.

5. Conclusions

The photosynthetically active radiation and transpiration rate of *Ilex latifolia* leaves reduced with the increasing of canopy closure of bamboo stands. The photosynthetically active radiation, transpiration rate, stomatal conductance, and net photosynthetic rate of T2 were higher than that of T3. The net photosynthetic rate curve of *Ilex latifolia* of T1 (0.86) was bimodal, with an obvious midday depression. While the net photosynthetic rate curve in T2 and T3 was unimodal. Though the net photosynthetic rate of T1 was higher than T2, it had obvious photoinhibition which affected the plant growth. Overall, canopy closure of 0.72 was more suitable for the growth of *Ilex latifolia*. Different plants have different canopy closures for a better growth. To improve ecological functions and make significant economic benefits, a selection of appropriate canopy closure is necessary for interplantation.

Acknowledgement

The authors thank the financial support from National Natural Science Foundation of China (41671296) and the Department of Science and Technology of Zhejiang province of China (2017C02016).

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DOI: https://doi.org/10.30564/re.v2i2.1366