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# Variation in photosynthetic photon flux density within a tropical seasonal rain forest of Xishuangbanna, south-western China

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**Abstract**: The effects of canopy development, solar angle, and weather conditions on temporal variation in photosynthetic photon flux density(PPFD) at three heights within a tropical rain forest canopy in Xishuangbanna, China, were examined. PPFD was measured every second and stored as 10-min averages from 1 December 2002 to 30 November 2003. PPFD variability was examined at three different temporal scales. Specific days in March, September, and December with clear and overcast sky conditions were selected to separate the effects of leaf area index(LAI) and solar angle on diurnal variability. On both clear and overcast days, mean daily average PPFD was significantly different between March and September at all heights, except 10 m on clear days, suggesting that LAI directly influences PPFD. In contrast, the differences in daily average PPFD among three heights between September and December were likely due to variation in solar angle. In addition, daily average PPFD at all locations were significantly lower under overcast than clear sky conditions in March, September and December. Over the year-long study, the mean daily total PPFD at 21 m, 10 m and 4 m was 2.8, 2.7 and 0.7 mol/($m^2 \cdot d$), which accounted for 9.7%, 9.4% and 2.4% of the daily PPFD above the canopy, respectively. Significant differences in mean daily total PPFD occurred at the same heights among different seasons, and diurnal, day-to-day and seasonal PPFD varied at different heights within the canopy. The possible effects of light variability on physiological and morphological responses of plants are discussed.

**Keywords**: photosynthetic photon flux density; temporal light variability; tropical seasonal rain forest canopy; Xishuangbanna

## Introduction

Photosynthetic photon flux density(PPFD) within forest canopies is intrinsically heterogeneous in space and time. Because some species are genotypically suited for specific light regimes, understanding the heterogeneity of the light regime within a forest canopy is important for assessing vegetation regeneration, growth, and succession (Canham, 1994; Watling, 1997). In addition, many plant ecophysiological processes respond non-linearly to changes in the intensity and temporal variability of PPFD (Vierling, 2000). Therefore, characterizing PPFD heterogeneity may be important in predicting rates of photosynthesis within a forest canopy, which can further help us to understand energy and mass exchanges between the forest and the atmosphere (Baldocchi, 1995; de Pury, 1997; Pearcy, 1997; Kirschbaum, 1998).

Many studies have investigated heterogeneity of PPFD within natural and agricultural canopies(Baldocchi, 1994), but long-term monitoring of light within the tropical forest canopy at very short time interval is rarely done because of the difficulties in placing sensors, the cost of sensors and data-loggers, and the large amount of time required for the frequent downloading and maintenance of instruments. For studies within tropical forests, high time resolution PPFD data have been limited to measurements near ground level (Vallanares, 1997).

Recent work has shown that temporal variation in light may had a significant impact on plant growth(Ackerly, 1997; Robison, 1999). Light variability within the forest canopy is influenced by leaf phenology, solar angle, sky conditions, gap size and its location within the canopy, and canopy depth (Baldocchi, 1994). As a first step towards understanding the potential influence of temporal fluctuation of light on plant growth, it is necessary to characterize this variation. The best method to characterize the variability of light regimes within a forest canopy involves continuous measurements of light over long periods at different heights in order to sample a range of canopy development and sky conditions. However, this has rarely been done in tropical forest ecosystems. A common limitation to most studies is that light measurements were not continuous, only occurred at specific periods during a year (Vierling, 2000).

The aim of this study was to characterize the effects of canopy development, solar angle, and sky conditions on the temporal variation of light in a vertical gradient within a tropical seasonal rain forest canopy. In addition, the potential implications of diurnal, day-to-day and seasonal light variability on plant growth are discussed.

## 1 Description of the study site

This study was conducted in a tropical seasonal rain forest(21°55′39″N, 101°15′55″E, elevation 750 m) in the Menglun Forest Reserve in Mengla County, Yunnan Province. It is a permanent plot dedicated to long-term ecological research managed by the Xishuangbanna Tropical Rainforest Ecosystem Station, the Chinese Academy of Sciences. The mean annual air temperature is 21.7℃ and annual rainfall is 1487 mm, of which 87% occurs in the rainy season (May—October) and 13% in the dry season (November—April). Dense fog layers commonly occur during the dry season and further dividing the dry season into a cool dry-season from November to February, and a hot dry-season from March to April.

The forest structure at the study site can be divided into three general tree layers that are represented by different species. More than 70% of all individuals of trees occur in tree layer C(below 16 m), which has small evergreen trees and juveniles of species from the upper tree layers(above 16 m). Tree layer B, which is between 16—30 m, consists of a mixture of evergreen and deciduous species, such as *Barringtonia macrostachya*, *Gironniera subaequalis*, and *Sloanea cheliensis*. Tree layer A, having a canopy height of over 30 m, is dominated by *Pometia tomentosa* and

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*Terminalia myriocarpa*. Many species of algae, lichens, mosses and ferns comprise the epiphytes communities. The woody climbers, such as *Byttneria integrifolia*, and *Gnetum montanum* are also common at the study site(Zhang, 1995).

## 2 Methods

### 2.1 Light measurements

PPFD was simultaneously measured at three different vertical heights within the canopy. A tower located in the study site was used to place sensors. The sensors were arranged according to the structure of the trees around the tower, considering the fact that the spatial and temporal variability of light within the forest canopy is extreme. The top and middle sensors were placed at 21 m and 10 m respectively, and the lowest sensor was placed at 4 m (LQS70-10SUN, Apogee) above the ground, which was the bottom of the tree canopy. In addition, a quantum sensor(LI-190SB, LI-COR, Lincoln, NE) was installed at a height of 70 m to record above-canopy light. All sensors were connected to a CR-23XTD data-logger (Campbell Scientific Inc., Logan, UT), above- and within-canopy PPFD was measured every second and stored as 10-min averages to detect short-term variability in light conditions (Gendron, 2001). These measurements(10 min averages) were recorded continuously from 1 December 2002 to 30 November 2003, but the time periods from 800 to 1900 h local time were used for our calculation of PPFD.

### 2.2 Data analysis

Daily PPFD was calculated for each sensor by averaging 10-min measurements and then multiplying by total day length (Chazdon, 1984). The percentage of PPFD transmission was then calculated from daily totals for each sensor inside the forest, using data from the 70 m sensor as a reference. Readings of daily measurements were summed monthly, seasonally and yearly for each sensor to obtain the monthly, seasonally and yearly mean daily total PPFD and mean daily percentage of PPFD transmission at each canopy location.

The coefficient of variation(CV) for diurnal PPFD and daily total PPFD at each sensor was calculated, and student's $t$-test was used to compare daily average PPFD or the mean of daily total PPFD among different heights of the forest and among days or seasons.

To characterize the diurnal light variability, representative days in March, September and December (Table 1) were selected to determine the effects of canopy development and solar angle on incoming PPFD. Solar angle was similar for these selected days between March and September, but LAI(Leaf area index) was different since deciduous trees lose more leaves in March and April than during other months. Days in September and December had different solar angles but similar LAI. Both clear and overcast days were selected within each of these three periods(Table 1).

**Table 1 Six selected days over the year**

| Period | Sky condition | Date and Julian day | Solar elevation(degrees) | LAI |
|---|---|---|---|---|
| Hot-dry | Clear | Mar 24(83) | 69.6 | 4.4 |
| | Overcast | Mar 29(88) | 71.5 | |
| Rainy | Clear | Sep 26(269) | 67.5 | 5.8 |
| | Overcast | Sep 23(266) | 68.7 | |
| Cool-dry | Clear | Dec 22(356) | 45.0 | 6.0 |
| | Overcast | Dec 25(359) | 45.0 | |

## 3 Results

### 3.1 Diurnal light variability

On clear days, differences in daily average PPFD were significant between March and September, with values in March being 1.1 and 1.4 times greater than that in September at 21 m and 4 m, respectively. In contrast, the daily average PPFD at 10 m did not differ between March and September. A tree-fall gap approximately 40 m SE of the sample site allowed PPFD to transmit directly to 10 m height from 1030 to 1150 local time due to sun/gap/sensor geometry. However, influenced by the heavy fog during the entire morning, daily average PPFD in March was 87.6% of that in September at 10 m above the ground. In comparison with clear days during September, within-canopy PPFD at three heights in December was characterized by low values and small daily variation. The daily average PPFD was significantly different between September and December at three vertical heights within the canopy(Fig.1, Table 2).

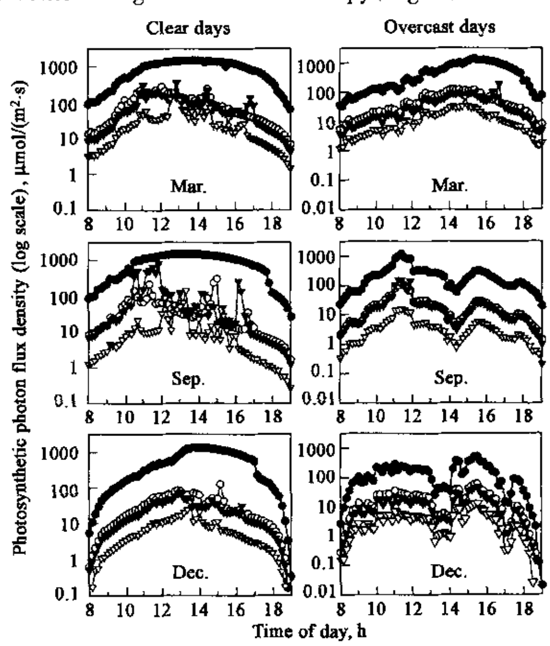


Fig.1 Diurnal patterns of PPFD for above-canopy(closed circles) and within-canopy at 21 m(open circles), 10 m(closed triangle) and 4 m(open triangle) under clear and overcast days in March, September and December

The findings suggest that the differences in LAI play a great role in affecting within-canopy PPFD than solar angle under overcast skies. Differences in daily average PPFD at all three observation levels were significantly different between March and September, while the daily average PPFD recorded at 21 m and 4 m did not differ significantly between September and December(Table 2).

Weather conditions are also important in influencing diurnal PPFD values since the daily average PPFD at the three vertical heights within the canopy were significantly lower under overcast than clear sky conditions in March, September and December(Table 2).

### 3.2 Day-to-day light variability

Daily total PPFD above the canopy ranged from 3.5 to 46.7 mol/($m^2$·d), with a mean of 27.3 mol/($m^2$·d) throughout the year. On sunny days, values greater than 40 mol/($m^2$·d) were recorded above the canopy, which occurred discontinuously from April to August, as a result of the interaction between weather conditions and solar angle. PPFD within this forest canopy can be complex, as shown by high

PPFD days above the canopy not producing high PPFD within the canopy, and vice versa. Our findings show that day-to-day variation patterns of daily total PPFD measured at three vertical heights exhibited different patterns from the above forest canopy, and also differed from each other during the year. Each height experienced one pronounced peak in high light conditions during the year, with the higher daily integral PPFD occurring at 21 m and 4 m during the transitions between April and May and at 10 m during transitions between February and March(Fig.2).

**Table 2 Daily average PPFD(μmol/($m^2$·s)) and coefficient of variation (*CV*; %) at vertical heights in tropical seasonal rain forest under clear and overcast days**

| | | Clear days | | | Overcast days | | |
|---|---|---|---|---|---|---|---|
| | | Mar. 24 | Sep. 26 | Dec. 22 | Mar. 29 | Sep. 23 | Dec. 25 |
| 70 m | Mean | $860.5^{Aa}$ | $832.1^{Aa}$ | $527.4^{Ab}$ | $488.4^{Ab}$ | $239.1^{Ac}$ | $140.8^{Ad}$ |
| | CV | 59 | 62 | 88 | 85 | 100 | 87 |
| 21 m | Mean | $92.4^{Ba}$ | $44.0^{Bb}$ | $30.7^{Bc}$ | $48.8^{Bd}$ | $21.9^{Be}$ | $16.5^{Be}$ |
| | CV | 78 | 125 | 86 | 77 | 111 | 85 |
| 10 m | Mean | $81.5^{Ba}$ | $93.1^{Ca}$ | $21.5^{Cb}$ | $38.5^{Bc}$ | $22.7^{Bb}$ | $11.5^{Cd}$ |
| | CV | 90 | 175 | 82 | 91 | 148 | 89 |
| 4 m | Mean | $31.9^{Ca}$ | $13.1^{Db}$ | $6.9^{Dc}$ | $12.7^{Cb}$ | $3.7^{Cd}$ | $3.3^{Dd}$ |
| | CV | 118 | 172 | 102 | 92 | 97 | 88 |

Notes: PPFD values within each column sharing a common capital letter or within a row marking the same small letter are not significantly different( $P > 0.05$)

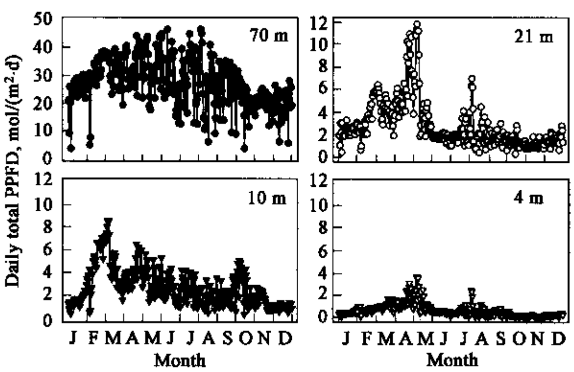


Fig.2 Variations in the daily total PPFD over a year period from December 2002 to November 2003
The dots are the same as Fig.1

Over the one-year study, the mean daily PPFD at 21 m and 10 m was 2.8 and 2.7 mol/($m^2$·d), which represents 9.7% and 9.4% of the daily PPFD above the canopy, respectively. PPFD was always higher at 21 m than that at 10 m when yearly mean daily total PPFD are considered, but it became contrary at 159 d when PPFD was higher at 10 m than 21 m, which is especially conspicuous in February and October. The upper canopy layer partially blocked the solar radiation to the lowest measured height in the forest, as only 0.7 mol/($m^2$·d), or 2.4% of the above-canopy light, was measured at 4 m(Table 3).

### 3.3 Seasonal light variability

Above-canopy monthly mean PPFD was the highest in April and May, and was the lowest in November and December. The monthly mean PPFD at three heights within the canopy showed a clear seasonal pattern during the period of measurement. At 21 m and 4 m, maximum and minimum monthly mean PPFD occurred in April and November respectively; while at 10 m, the increase and decrease of PPFD did not follow the same pattern as found in the above-canopy PPFD. Although the lowest monthly PPFD in December at 10 m coincided with the lowest above-canopy PPFD, no other correspondences were apparent. Unlike other canopy height measurements in this study, the April peak at 10 m did not occur, it was shifted to February, when higher above-canopy PPFD coincided with solar angles more favorable for the direct penetration of radiation (data not shown).

**Table 3 Mean daily total PPFD(mol/($m^2$·d)) and percentage transmission of PPFD(%) at vertical heights for cool-dry, hot-dry, rainy seasons and year-long measurements in tropical seasonal rain forest**

| | | Cool-dry | Hot-dry | Rainy | Year |
|---|---|---|---|---|---|
| 70 m | Mean | $23.6^{Aa}$ | $32.8^{Ab}$ | $27.9^{Ac}$ | $27.3^{A}$ |
| | % | 100 | 100 | 100 | 100 |
| 21 m | Mean | $2.1^{Ba}$ | $5.1^{Bb}$ | $2.4^{Bc}$ | $2.8^{B}$ |
| | % | 8.5 | 15.9 | 8.4 | 9.7 |
| 10 m | Mean | $2.2^{Ba}$ | $4.3^{Cb}$ | $2.5^{Bc}$ | $2.7^{B}$ |
| | % | 8.4 | 12.9 | 8.9 | 9.4 |
| 4 m | Mean | $0.4^{Ca}$ | $1.3^{Db}$ | $0.7^{Cc}$ | $0.7^{C}$ |
| | % | 1.7 | 4.0 | 2.2 | 2.4 |

Notes: PPFD values within each column sharing a common capital letter or within a row marking the same small letter are not significantly different( $P > 0.05$)

The mean daily total PPFD at the same heights were significantly different among seasons. Moreover, at three heights within the canopy, the maximum mean daily total PPFD occurred in the hot-dry season, while the minimum values occurred in the cool-dry season(Table 3).

Differences in mean daily total PPFD were significant among different heights in the hot-dry season; whereas in the cool-dry and rainy season a PPFD inversion appears between 21 m and 10 m, but it was not statistically significant(Table 3).

## 4 Discussion

Because different levels of light variability may have different effects on plants, priority should be placed on the interpretation of diurnal, day-to-day and seasonal variability in PPFD at three heights within the canopy. On a diurnal basis, the different levels within the canopy of the selected days all showed considerable fluctuation in PPFD, among which the 10 m height under the clear conditions in September showed the most extreme light variability, as its CV was 1.9 and 2.1 times that of March and December, respectively. Despite this, there were no significant differences in daily average PPFD between March and September at 10 m height during clear days(Table 2). The effects of fluctuating average daily PPFD or total daily PPFD on plants has been demonstrated in many past experiments; however, grown under similar daily PPFD but different diurnal light variability may also result in different effects on plant performance(Wayne, 1993a; 1993b; Robison, 1999). The CV of the 10-min averages of PPFD within a day is most likely influencing photosynthetic capacity, photoperiodic responses, and canopy display(Ackerly, 1997). Wayne and Bazzaz (Wayne, 1993b) demonstrated that seedlings of *Betula populifolia* and *B. alleghaniensis* grown under similar total daily PPFD, but different CV, differed significantly in leaf-level physiology, biomass allocation, and phenotypic plasticity. For environments with frequent sunfleck events, Gendron *et al*.(Gendron, 2001) found that taking the mean of the difference between two consecutive 10-min averages of PPFD and percentage of PPFD produced higher mean differences. Moreover, this type of light variability may relate more closely to changes in plant traits such as instantaneous photosynthesis, stomatal responses, conductance, and photosynthetic induction rather than CV (Ackerly, 1997;

Gendron, 2001). For example, *Carya ovata* seedlings grown under similar daily PPFD exhibited larger stem biomass, basal diameter and secondary root dry weight in an experiment of short duration sun patch environments when compared to long-duration sun patch environments(Robison, 1999).

On a day-to-day basis, the 10 m height exhibited the lowest CV for daily total PPFD, while the 4 m height was the most variable on a day-to-day basis. Few data are available for detailed comparisons of Xishuangbanna and other tropical rain forests with respect to CV for daily total PPFD. Torquebiau(Torquebiau, 1988) measured PPFD in a mixed dipterocarp forest in Sumatra and showed that the CV of daily PPFD was 49%, 20% and 58% at levels 65%, 28% and 7% of the canopy height, respectively, over the course of 6 d. The CV values in this study site were 75%, 63% and 87% at 64%, 30% and 12% of the canopy height. However, because of the differences of measurement periods, it is hard to conclude if daily total PPFD at different heights within the canopy in our study site were more variable than that at similar canopy heights in Sumatra. Also, the two forests differ in forest properties, such as architecture, which could have substantial influence on PPFD. Plant traits, such as photosynthetic acclimation, leaf morphology, and plant growth, can track day-to-day light variability. For example, in simulations using the tropical pioneer tree species *Heliocarpus appendiculatus*, leaf display was the morphological trait best able to respond to daily variability in light environment (Ackerly, 1997). Gendron *et al*. (Gendron, 2001) suggested that the mean difference between consecutive daily PPFD or daily percentage or PPFD and the CV for day-to-day light variability may provide a useful evaluation of this type of variability and may correlate well with these types of plant responses. However, further research is needed to examine how these different types of light variability characteristics will influence plant growth.

Seasonal variability in PPFD was evident at different heights within the canopy. The 4 m height showed the greatest seasonal light variation, as the mean daily total PPFD in the hot-dry season was 3.2 and 2.0 times that of the cool-dry and rainy season, respectively. The lowest seasonal variation in PPFD occurred at 10 m height, as the mean daily total PPFD in the hot-dry season was 2.0 and 1.7 times that of the cool-dry and rainy season, respectively (Table 3). Seasonal light variability may elicit changes in traits such as photosynthetic acclimation, leaf morphology, plant growth, and growth allocation(Ackerly, 1997). It has been reported that seasonal irradiance controls seasonal variation in net primary production in tropical evergreen forests and should be a strong selective pressure on phenology (Raich, 1991; Wright, 1994). For example, in the lowland tropical rainforest on Barro Colorado Island, daily photosynthetically active radiation was 48% greater in the dry season than that in the wet season, which made drought-tolerant species, such as the canopy trees *Beilschmiedia pendula* and *Jacaranda copaia*, and the sub-canopy tree *Heisteria concinna*, produce leaves and flowers early in the dry season PAR peak(Wright, 1994).

Generally, further research is needed to examine how light measures at differing canopy heights and seasons will influence plant growth in this stand.

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