E-2.1 Ecophysiological Studies on Canopy in Tropical Forest

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Abstract

(1) Diurnal changes of photosynthesis in leaves of four tree species at the canopy.

Measurements of photosynthesis and stomatal conductance were conducted with leaves of four tropical tree species, *Neobalanocarpus heimii*, *Xanthophyllium amoneum*, *Ptychopyxis caput-medusae* and *Dipterocarpus sublamellatus*, at the canopy in the lowland forest at Pasoh, Malaysia. A canopy walkway was used to access to the canopy level in the crown of 30-40 m tall individuals. The diurnal changes of net photosynthesis and stomatal conductance were determined two consecutive days. The most significant difference of the environmental factors between the two days was vapor pressure difference. The diurnal patterns of net photosynthesis were different between the two days and between the four species examined in the present measurement, though photosynthetic rates of these four species were quite low. Photosynthetic rates increased with increasing PFD (photon flux density) before noon and then declined. This diurnal pattern of net photosynthesis was typical for *D. sublamellatus* and *N. heimii*. The responsibility of net photosynthesis to PFD was not clear in *N. heimii*, probably because of the low stomatal conductance in day time caused by the water deficit. The close to proportional relationship between stomatal conductance and net photosynthesis and similar slopes of the relationship could be detected except for *D. sublamellatus* on the day 1.

(2) Photosynthesis and morphological characteristics of *Elateriospermum tapos* at different insertion levels.

Measurements of photosynthesis and characteristics in *Elateriospermum tapos* grown in the lowland forest at Pasoh, Malaysia were conducted on leaves attached at various height from 34 m of the canopy level to 16 m using a canopy walkway. Photosynthetic rates and stomatal conductance were measured at 34, 26, 21 and 16 m from the ground with a portable photosynthesis system and steady state porometer, respectively. Beside of these measurements, leaves were collected to measure the morphological characteristics from the same levels and seedlings (ca. 1 m in height).

The relative PFD was 28% at 34 m, 14% at 26 m, 8% at 21 m, 4% at 16 m and 2% at 1 m. Leaf sizes increased with lowering height and were almost double of leaves of seedlings suggesting that the difference in leaf characteristics is mainly induced by the differences of PFD at the different levels.

The measured photosynthetic rates were related to the incident PFD. The apparent quantum use efficiencies in leaves at lower levels (16 and 21 m) and higher levels (25 and 34 m) were ca. 0.05 and 0.03, respectively. These results indicate that those leaves attached below the canopy have the photosynthetic characteristics of shade leaves.

Key Words Allometry, Forest canopy, Photosynthesis, Stomatal conductance

1. Introduction

Tropical rain forests are unique among terrestrial forest ecosystems because of their high biodiversity and their low seasonal fluctuations of environmental conditions. The solar elevation angles are high and produce greater average and maximum solar flux than at temperate regions. This depends on the geographical situation of tropical regions that the respective zenith angles of mid-day sun positions at northernmost and southernmost time are 108-114° and 61-66° in a tropical rainforest region, depending on latitude. Annual variation in photo period in this region varies from 1-3 hr. Furthermore, seasonal fluctuations of temperature are also quite low with 2 °C.

The habitat where many organisms are abundant is leafy canopy layer. Under the tropical climatic conditions, the sizes of emergent trees are giant and some tree species reach to 50 m or more. Thus it is difficult to attain the canopy level and elaborate to measure photosynthetic rates of leaves at the canopy level. This is why the knowledge on the photosynthetic CO_2 uptake rates of tropical tree species is limited, especially at the canopy level.

Many measures are applied to reach the tree canopy. The tree climbing method has been extensively used to access the canopy level (Perry, 1978). However, using the climbing method, it is almost impossible to carry instruments and measure photosynthesis at the canopy level. In these days, to overcome these shortcomings, large scaled construction of the canopy observation systems is becoming popular. In 1960, a wooden tower, supported by the trunk of a big tree, was constructed in the Pasoh Forest Reserve, Negri Sembillan, Malaysia under the IBP project. But the main purpose of this tower was to monitor the meteorological factors, since no intensive works were performed on the biodiversity under this project but on the primary production of tropical forest. A unique method was developed by French scientists (Halle and Pascal, 1992). In Barro Colorado Island, Panama the construction crane was set in 1990 (Joyce, 1991) and intensive works for not only photosynthesis measurements but also for the biodiversity of tropical forest. Japanese scientists constructed a canopy observation system in Lambir Hills National Park, Sarawak, Malaysia in 1992-1993 (Inoue et al., 1994). The purpose of this system is also to survey the biodiversity of tropical forest. We constructed a tree canopy walk-way system in Pasoh Forest Reserve in 1992 under the project on tropical ecosystem and biodiversity supported by the Japanese Environment Agency. This canopy walk-way system is constructed from three towers; two towers are 30 m and one is 52 m high. A 20 m long walk-way spans between towers at 30 m high. From this tower, we can access six tree species, *Neobalanocarpus heimii, Xanthophyllium amoneum, Ptychopyxis caput-medusae, Dipterocarpus sublamellatus,* and *Elateriospermum tapos.* In the present study, we used this canopy walk-way and measured morphological characteristics of leaves of *E. tapos* at various height levels. Photosynthesis and stomatal conductance were measured at the forest canopy in *N. heimii, X. amoneum, P. caput-medusae* and *D. sublamellatus* and at various height levels in *E. tapos.*

2. Materials and Methods

(1) Diurnal changes of photosynthesis in leaves of four tree species at the canopy.

The measurements of net photosynthesis and stomatal conductance of *Neobalanocarpus heimii, Xanthophyllium amoneum, Ptychopyxis caput-medusae* and *Dipterocarpus sublamellatus* were conducted at the canopy walk-way which is set at the Pasoh Forest Reserve in Peninsula Malaysia. Leaves were considered canopy, since they were exposed to unobstructed sunlight for some part of the day and were greater than 30 m high. The canopy walk-way is constructed from three towers. Two towers are 30 m and one is 40 m high. A 20 m long walk-way spans between towers at 30 m high.

Stomatal conductance was measured with a steady state porometer (model 1600, LI-COR Inc.). Photosynthetic measurements were made with an ADC portable field gas exchange system with its Parkinson leaf chamber, air supply unit, and LCA-2 infrared gas analyzer (Analytical Development Co. Ltd., Hoddesdon, UK).

(2) Photosynthesis and morphological characteristics of *Elateriospermum tapos* at different insertion levels.

For the measurements of leaf characteristics, photosynthesis and stomatal conductance, the canopy walk-way system was used to approach the different height levels and collected leaves of *Elateriospermum tapos* attached at different heights.

Leaves of *E. tapos* were collected at 34, 26, 21 and 16 m from the ground. Beside of these leaves, leaves were collected from seedlings (ca. 1 m in height) After measuring leaf width, leaf length, leaf area, petiole length, leaves and petioles were dried at 80 °C for 72 hr and weighed.

The traditional method to measure the relative PFD inside and outside the plant community is to measure PFD at noon on a cloudy day. In a tropical area, however, it is quite difficult to find those cloudy days. Furthermore, because the heights of tropical trees are great and some tree species reach 40 m or higher, the simultaneous measurements of PFD above and inside or beneath the forest canopy is difficult. To solve this difficulty, we developed a new method.

Photon flux density (PFD) was measured by setting a LI-190 SA (LI-COR) quantum sensor at the height of 34, 26, 21, and 16 m from the ground, where leaves were clustered. Output from the sensor was recorded using a data recorder (model LI-1000, LI-COR) for one minute interval and the diel PFD was computed. Using these data, relative PFD was calculated by;

$$\text{PFD}\ (\%) = \frac{\int Q_a}{\int Q_o} \times 100$$

where Q_a and Q_o are PFD (μmol m^{-2} s^{-1}) at infinite level "a" and above the canopy (40 m from the ground), respectively.

Photosynthesis and stomatal conductance of *Elateriospermum tapos* were measured at the different height level. The measurements of net photosynthesis and stomatal conductance of *Neobalanocarpus heimii*, *Xanthophyllium amoneum*, *Ptychopyxis caput-medusae* and *Dipterocarpus sublamellatus* were conducted at the top of the canopy walk-way (30 m high). Leaves of these species were considered canopy, since they were exposed to unobstructed sunlight for some part of the day and were greater than 30 m high. For *Elateriospermum tapos*, measurements of photosynthesis and stomatal conductance were conducted at various height levels.

Stomatal conductance was measured with a steady state porometer (model 1600, LI-COR Inc.). Photosynthetic measurements were made with a LI-COR LI-6200 portable photosynthesis system with a quarter liter chamber, air supply unit, LI-190 SA quantum sensor and LI-6250 infrared gas analyzer. The measurements of photosynthesis were also performed using an ADC portable field gas exchange system with its Parkinson leaf chamber, air supply unit, and LCA-2 infrared gas analyzer (Analytical Development Co. Ltd., Hoddesdon, UK).

3. Results and Discussion

(1) Diurnal changes of photosynthesis in leaves of four tree species at the canopy.

The diurnal changes of net photosynthesis and stomatal conductance in *N. heimii, X. amoneum, P. caput-medusae* and *D. sublamellatus* were determined on 6 and 7 July, 1993. The concurrent changes in incident PFD, air temperature and vapor pressure deficit (VPD) are also shown. The major difference in aerial environmental conditions between the two days was that the level of PFD was lower during the morning of the day 2 in the early morning due to cloud cover. However, the level of PFD of the day 2 was higher in the afternoon as compared with that of the day 1. The diurnal patterns of air temperature were similar on both days, but there was a difference of VPD between the two days and the VPD of the day 2 was higher than that of the day 1.

The diurnal patterns of net photosynthesis were different between the two days and between the four species examined in the present measurement. On day 1, net photosynthesis of *N. heimii* and *D. sublamellatus* reached their maximum in the early morning and declined with time. On day 2, net photosynthesis of *N. heimii* was fairly constant. In contrast to the diurnal pattern of net photosynthesis of *N. heimii*, net photosynthesis of *X. amoneum* and *P. caput-medusae* increased with increasing PFD and the maximum rates were detected when the PFD reached to the highest. On the day 2, however, net photosynthesis of *X. amoneum* did not show the typical diurnal changes and the maximum rate was lower than that of the day 1, though the PFD on the day 2 was higher than that of the day 1.

The diurnal trend of stomatal conductance was similar with that of net photosynthesis. In *N. heimii* and *D. sublamellatus* showed their highest stomatal conductance in the early morning and decreased with time on day 1. On day 2, however, stomatal conductance of *D. sublamellatus* was low in the morning and increased to the maximum at noon and then decreased. In contrast to the diurnal changes of stomatal conductance of *D. sublamellatus*, the stomatal conductance of *N. heimii* showed a similar diurnal changes detected on day 1, though the value observed in the early morning on day 2 was quite low as compared with the value observed on day 1.

Net photosynthetic rates of *P. caput-medusae* showed a typical PFD-photosynthesis curve and no different responses of net photosynthesis to PFD were detected between the day 1 and the day 2. Net photosynthesis of *X. amoneum* also showed a typical PFD-photosynthesis curve, however, the rate detected on the day 2 was lower than that detected on the day 1. In contrast to these relationships between PFD and net photosynthesis, net photosynthesis of *N. heimii* showed higher rates under lower PFD and the rate was fairly constant between 600 and 1600 μmol m^{-2} s^{-1} of PFD.

The individual measurements of stomatal conductance, obtained at PFD's above 500 μmol m^{-2} s^{-1} were plotted against VPD. There was a clear evidence of a partial stomatal closure at higher VPD in *D. sublamellatus*, *P. caput-medusae* and *X. amoneum*. However, no clear relationship between VPD and stomatal conductance was detected in *N. heimii* . Net photosynthesis was also plotted against VPD when PFD was higher than 500 μmol m^{-2} s^{-1}. The response of net photosynthesis to VPD was not clear in the four species measured in the present study.

Net photosynthesis increased with increasing stomatal conductance of the four species detected in the present study. The close to proportional relationship and similar slopes of the relationship of the four species implies an approximately constant and resembeled instercellular CO_2 concentrations between the four.

The present results showed that net photosynthesis rates of canopy leaves of four tropical tree species are relatively lower than those reported in temperate deciduous tree species. Furthermore, no marked differences of photosynthesis between species could be observed. The rates of these four species were comparable with those reported for tropical and temperate evergreen tree species. It is well known that deciduous species have higher rates of net photosynthesis as compared with evergreen ones in a temperate area. In general, the lower photosynthetic rate is reflected by lower stomatal conductance. In the present study, since no remarkable differences of net photosynthetic rates or stomatal conductance were detected between the four species, we could not generalize this concept.

The marked differences of meteorological factors between the two days were VPD and PFD. It is well demonstrated that stomatal conductance is influenced by VPD and decreased by increasing VPD. Photosynthetic CO_2 uptake is known to be influenced mainly by stomatal aperture. Thus net photosynthesis as measured by CO_2 uptake should be lowered by higher VPD. From this speculation, the lower rate of net photosynthesis on day 2 is considered to be caused by higher VPD of day 2 than that of day 1. However, in the present study, we could detect some relationship between VPD and stomatal conductance if data were collected when PFD exceeded 500 μmol $m^{-2}s^{-1}$, but could not detect the clear relationship between VPD and net photosynthesis. No responsibilities of net photosynthesis to PFD should be resulted from the fluctuations of PFD during the measurement. This should be resulted from the time lag of the measuring instruments. It takes more than one minute to measure photosynthesis while less than one second for PFD. Furthermore, photosynthetic CO_2 uptake does not respond to the rapid changes of PFD. From these considerations, we should measure photosynthesis and stomatal conductance simultaneously using one system that includes both instruments for CO_2 and H_2O detectors.

(2) Photosynthesis and morphological characteristics of *Elateriospermum tapos* at different insertion levels.

The relative PFD was 28% at 34 m, 14% at 26 m, 8% at 21 m, 4% at 16 m and 2% at the height of seedlings (1 m). The leaf shape of *E. tapos* is oval. At the canopy level the average leaf width and length were 39.7 mm and 111.9 mm, respectively. Both of these leaf sizes increased with lowering height and these sizes of leaves of seedlings were almost double.

There was a linear relationship between the product of width and length and leaf area.

$$w \times l = 2.056 + 1.336\,LA \quad (r^2=0.991)$$

where w and l are leaf width and length, respectively and LA is leaf area. This relationship was not changed by the height level, but leaf width/length ratio was changed.

The length of leaves decreased with increasing PFD. Leaf area was also decreased with increasing PFD. The average leaf length of seedlings was about double of that in leaves at 34 m high. The difference of leaf length caused by different PFD reflects the decline of leaf area at higher height levels. Leaf area at 26 m and 34 m was approximately half of the leaf area of seedlings or leaf area at 16 m high.

The specific leaf area (SLA) was increased with lowering the level, however, there was no significant difference between leaves at different height levels except seedlings. This result suggests that the thickness of seedlings was thin but leaves attached on the same tree were not influenced by light conditions.

The length of petiole was also different between the height levels. With decreasing the height level, the length of petiole increased. In contrast to the relationship between PFD and leaf length or leaf area, the petiole of seedlings grown at the forest floor was not significantly longer than that of leaves at the lowest height level.

The ratio of leaf length to the petiole length was fairly constant among 21 m to 34 m but the ratio of seedlings was quite high. To identify the characteristics of petiole, the ratio of petiole length to petiole dry weight was estimated. This ratio, named as the specific petiole length, should reflect the mechanical strength of petiole to support the leaf, however, no clear effects of PFD could be detected.

The was a linear relationship between leaf dry weight and SPL on a log-log scale. The SPL had also a linear relationship on log-log scale with leaf length. When slopes of these two relationships are plotted against PFD, both slopes were higher in leaves at higher height levels. This finding indicates that leaves grown under intensive light intensity have higher mechanical strength than those leaves grown under shade condition, though petiole length is shortened by higher PFD.

Photosynthetic rates of *E. tapos* were examined at various height levels. At higher levels, the maximum photosynthetic rates were higher at higher PFD. Judging from these results, those leaves attached on higher levels should have a characteristic of sun leaves, while those leaves attached on lower levels showed a shade type photosynthesis. This trend was clearly shown by plotting the relationship between PFD and photosynthetic rates at lower PFD. Slopes of the relationship between PFD and photosynthesis of leaves at 21 m and 16 m high were higher than those of leaves at 34 m and 25 m. Since the slope, the apparent quantum use efficiency, is a good indicator to know whether leaves are shade type or sun type, leaves attached higher levels are sun type and those at lower levels are shade one.

It is well known that the stomatal conductance is influenced by vapor pressure deficit of the air (VPD). Stomatal conductance of *Dipterocarpus sublamellatus* and *Ptychopyxis caput-medusae* were influenced by VPD and were decreased by high VPD, while those of *Neobalanocarpus heimii* and *Xanthophyllium amoneum* were not. This result may indicate that the former two species are VPD-sensitive and the latter ones are VPD-insensitive.

From the data on seasonal change of precipitation at Pasoh, no clear seasonal changes of precipitation could be detected, however, the precipitation in November is higher than other months. Furthermore, precipitation in August and from December to February is less as compared with other months. Though July should not be dry or less rainy month, we measured photosynthesis on July and November to detect the seasonal changes of photosynthesis.

The diurnal changes of net photosynthesis and stomatal conductance in *Neobalanocarpus heimii*, *Xanthophyllium amoneum*, *Ptychopyxis caput-medusae* and *Dipterocarpus sublamellatus* were determined on July and November in 1993. The concurrent changes in incident PFD, air temperature and vapor pressure deficit (VPD) were also determined. The difference in aerial environmental conditions between the two months was not clear (data are not shown).

Using the data on diurnal changes of photosynthesis and stomatal conductance, the relationship between photosynthesis and stomatal conductance was determined on four species. Photosynthetic rates of *D. sublamellatus* were also determined at two different height levels on July and November and plotted against PFD. However, no clear differences in the relationship between photosynthesis and stomatal conductance could be detected between the two months in any species. This result shows that the seasonal changes in precipitation have no effect on photosynthesis. Furthermore, an age factor, leaves on July should be younger than leaves on November, has no effect on photosynthesis of these four species or leaves are fully matured on July and no senescence should come out on November.