Temporal and Vertical Variations in Photosynthetic Drivers in Mangrove Canopies, Okinawa, Japan

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Abstract: The mangrove is characterized by the subdaily fluctuations of tidal inundation and, importantly, has many sources of CO₂ such as autotrophic and heterotrophic respiration and marine organisms. For these reasons, the mangrove ecosystem would be expected to possess different microclimatic profile characteristics from those of terrestrial ecosystems. The objective of this study is to determine the characteristics of vertical profile of CO₂, H₂O, and air temperature within and above the canopies of mangrove forests at Okukubi River, Okinawa, Japan. The mangrove canopy had low CO₂ concentrations, high H₂O concentrations in air, and variable temperature. Tidal inundation provides a control on microclimatic variation not experienced by dryland forests.

Key words: Air temperature, Carbon dioxide, Mangrove forest, Tidal inundation, Vertical and diurnal variations, Water vapor.

Photosynthesis and respiration are gas exchange processes that influence the assimilation of atmospheric CO₂ and the reassimilation of respiratory CO₂ within the plant canopy (Coyne and Kelley, 1975). The rate of photosynthesis of a leaf is affected both by its environment of surrounding air (Prioul and Bourdu, 1973) and by the location of the leaf within the plant canopy (Wolf and Blaser, 1971). The drivers of photosynthesis, including CO₂ concentration, H₂O concentration, air temperature, and light intensity, vary within plant canopies. Therefore, plant physiologists can participate in the efforts to ameliorate climate change, including atmospheric warming, by investigating such drivers of photosynthesis at the canopy scale with a view to enhancing plant productivity. Enhancing plant productivity, in turn, constitutes one of the most promising methods to decrease the concentration of anthropogenic CO₂ in the atmosphere, particularly plants such as mangroves which have high capacities for CO₂ sequestration.

The gradient method is a measurement system that uses apparatus positioned at various heights in a plant canopy to measure microclimatic variables such as ambient CO₂ and H₂O concentrations, and has been used to quantify vertical profiles of microclimate in various plant canopies, including those of agricultural crops and terrestrial forests. Such measurements of environmental variables are very important for linking the variables that affect photosynthesis under field conditions with the physiology of individual leaves measured under laboratory conditions. For example, the photosynthetic intercellular CO₂ response curve and light response curve are usually determined under controlled conditions, but without actual field measurements the curves cannot be linked to the natural microclimate in plant canopies. Without this link, the dynamics of photosynthesis under actual field conditions (cf. controlled conditions) cannot be properly understood. Moreover, understanding the characteristics of these environmental drivers of photosynthesis under field conditions will assist in the better management of various ecosystems, including terrestrial forests and mangrove forests, in order to enhance plant productivity which in turn will help our management of CO₂ sequestration (Garrett et al., 1978).

Large variations in micro-climatic variables, including CO₂ concentration, have been reported for various herbaceous canopies, such as rice (Ziska et al., 2001), soybean (Baldocchi et al., 1983), and terrestrial forest canopies (Bazzaz and Williams, 1991; Buchmann et al., 1996). However, the gradient method has not yet been used to characterize the vertical profiles or diurnal fluctuations of these environmental variables within mangrove forests in order to provide basic data for researchers of mangrove physiology. The mangrove forest, a coastal wetland ecosystem, is expected to have
a more complex environmental arrangement than other ecosystems such as terrestrial forests. This is because of the fluctuations in air temperature and water vapor resulting from the tidal cycle, and because of additional sources of CO₂ in the form of autotrophic and heterotrophic respiration and the activities of marine organisms.

Given the lack of micro-environmental data for mangrove canopies, the potential importance of mangroves in CO₂ sequestration, and the unique environmental setting of mangroves, the objective of this investigation was to quantify the vertical and diurnal variations in CO₂, H₂O concentration, air temperature, light intensity, and wind speed within mangrove canopies. The results of the study as reported provide important new information about the photosynthetic environment in mangrove canopies.

Materials and Methods

The field measurements were conducted in the mangrove forest at Okukubi River during 22-24 September 2007. The mangrove study site, a protected area since 1994, is located on the Pacific coast of Okinawa Island, on the east side of Kin town and about 70 km northeast of Naha city in Okinawa prefecture, Japan (26°27’N, 127°56’E). The Okukubi River covers the area from downstream Namizato to Kisenbaru and includes Kanna Dam, which is located about 2 km from the river. The river has a variety of habitats from estuarine to tidal flats, containing a wide range of aquatic hemipterans and benthos.

The mangrove species adjacent to the river at the study site included three species of Rhizophoraceae family, Bruguiera gymnorrhiza, Kandelia candel, and Rhizophora stylosa. B. gymnorrhiza was the dominant species at the study site with a mean diameter at breast height of 36 cm. The canopy height ranged between 7 and 9 m with a mean height of 8 m. All leaves were located between 7 and 9 m height. Mangrove tree density was 7.6 trees per 10 m². The soil type was an intertidal sandy soil. During the measurement period, the high tide occurred during two periods, from 0300 to 0600 and from 1540 to 1720. The land surrounding the river is intensively cultivated with the dominant agricultural crops being rice and taro.

Five samples per tree were randomly collected from three trees to determine the nitrogen and carbon percentage of leaves, stems and roots. The nitrogen and carbon percentage were measured with automatic high sensitive N-C analyzer (NC-90A, Shimadzu). Five leaf samples per tree were randomly collected from three trees to determine the mean total chlorophyll content. The leaf samples were washed with distal water and then extracted with 99% ethanol. The samples were stored in plastic box and protected from direct sunlight. After 24 hr, the total leaf chlorophyll content was determined according to the method of Smith and Benitez (1955).

The warmth index, based on the data of 1991-2000 obtained from Okinawa Astronomical Observatory, was 217.8°C mo (Kira, 1991). For the same 10 yr period, the mean minimum temperature of 16.8°C and the mean maximum temperature of 28.8°C occurred in February and July, respectively, and the mean annual temperature was 23.2°C. The mean minimum and maximum air temperatures during the experimental period, as recorded by the Japan Meteorological Agency, were 25°C and 31°C, respectively.

The gradient measuring system used in this study has been fully described in a previous paper (Al-Saidi et al., 2009). Briefly, the system measures the temporal fluctuations and vertical variation in CO₂, H₂O concentration, temperature, and light intensity, for six different heights in the canopy, over a one-minute
Six inlet tubes (6 × 8 mm) were positioned on a steel tower at heights of 0.3, 1.8, 3.8, 5.8, 7.8, and 9.8 m above the ground at the mangrove site. CO₂ and H₂O concentration were measured by sampling air with flow rate of 17 mL s⁻¹ from each height in turn. The sampling apparatus included one infrared gas analyzer (LI-840, Li-Cor), six three-way solenoid valves (USG3-6-1, CKD), one valve for each level, and one stepping relay (G9B-12, Omron). The stepping relay was used to switch between valves so that gases from all monitoring levels were sampled. Two exhaust pumps were used to ensure a simultaneous flow rate of air through all inlet tubes at all levels while the sampling pump was used to suck the air from the actively-monitored level.

Air temperature was measured using a multisensor copper-constantan thermocouple probe. The thermocouples were positioned near the air inlet at six heights up the tower and shaded to avoid direct sunlight. Photosynthetic photon flux density was measured using a quantum sensor (190SB, Li-Cor) placed on the top of the tower. Air temperature, relative humidity, and wind speed were measured by the Server Environmental Monitoring System (Green Kit, ESD) during the period 23–24 September 2007. This monitoring period represented the weather conditions between 1030 and 1800 of the measurement period of microclimatic profiles which was conducted from 1800 on 22 September to 1800 on 23 September 2007. This monitoring system was

Fig. 3. Diurnal variations in CO₂ (left hand diagrams), H₂O (middle), and air temperature (right) within and above the mangrove canopy, measured 22-23 September 2007. The interval between measurements is 10 s for each monitoring height.
malfunctioned during the period between 1800 on 22 September and 0900 on 23 September. The infrared gas analyzer and all sensors were connected to a data-logger (DA-100, Yokogawa) and measured every 10 s for each monitoring height. This short sampling time represents a marked improvement over previous systems (e.g., Xu et al., 1999; Leuning et al., 2000) in terms of the temporal resolution of the data (improved from 10−30 min per 6-height measurement cycle to 1 min).

Results and Discussion

At observational site, the mean leaf nitrogen and carbon percentage were 1.20 ±0.13% and 48.0 ±3.1%, respectively; mean stem nitrogen and carbon percentage were 0.20 ±0.05% and 45.2 ±1.5%, respectively; and mean root nitrogen and carbon percentage were 0.30 ±0.06% and 36.8 ±2.7%, respectively. The mean leaf total chlorophyll content was 258 ±91 mg m−2. Above the mangrove forest canopy, the maximum photosynthetic photon flux density, 1961 μmol m−2 s−1, occurred around 1300. There were partly cloudy conditions around 1000 and again around 1500 (Fig. 1). Between 1030 and 1800, the mean wind speed at the 3 m height in the canopy was 0.26 m s−1 with the maximum value occurring around 1650 (Fig. 2). Between 1030 and 1800, the mean air temperature and relative humidity were 29.5ºC and 70.4%, respectively (Fig. 2). For vertical profiles of CO2, H2O, and air temperature, the 1 min data were averaged and plotted over 3 hr intervals. The concentrations of CO2, H2O, and air temperature differed both diurnally (Fig. 3) and between the different air layers of the canopy (Fig. 4).

The concentration of CO2, either within the mangrove canopy or just above it, during daytime or night-time, scarcely ever achieved the value of 385 μmol mol−1 which is the atmospheric concentration of bulk air measured at the Mauna Loa laboratory in Hawaii (Fig. 3). The exception was during high tide at night-time. At 9.8-m height, the mean CO2 concentration was 371 and 367 μmol mol−1 during nighttime and daytime, respectively. From 0900 to 1500 in 23 September 2007, CO2 concentration reached the minimum (365 μmol mol−1) in the mid-canopy layer (7.8 m height), probably due to the consumption of CO2 by photosynthetic activities in the densest part of the canopy. H2O concentration from 0900 to 1200 near ground level was higher than that above the canopy by about 2.5 mmol mol−1. The air temperature fluctuated during the period from 0900 to 1500, especially in the mid-canopy layer. Such diurnal variations in the microclimatic drivers of photosynthesis must invariably produce temporal fluctuations in the rate of photosynthetic activity of the mangrove canopy.

CO2 concentration decreased with increasing height within the mangrove forest canopy (Fig. 4). The unique vertical profiles and overall concentrations of CO2 in the mangrove canopy may be caused by the effects of soil respiration as well as CO2 dissolving in seawater. H2O concentration remained more or less constant, and equivalent to the above-canopy level above a height of 2 m. Air temperatures in the mid-canopy layer were higher than those measured above the canopy and also higher than the near-ground layer, by about 4ºC (Fig. 4). This was probably due to the absorption of long wave radiation by the leaves of the mid-canopy layer, causing the heating of ambient air within the canopy by heat flux. Under
such warmer conditions, the rate of transpirational cooling may increase with increasing air temperature in order to stabilize leaf temperatures. Although the air temperature in the mid-canopy was higher than that above the canopy, the $H_2O$ concentration remained more or less constant (Fig. 4). The leaves of the mangrove tree are characterized by low leaf conductance and water potential (Ball, 1988; Theuri et al., 1999). Under these conditions, stomata may close, preventing the reduction of leaf temperature by transpirational cooling.

In contrast to dryland forest stands, the mangrove stand is characterized by the daily fluctuation of tidal inundation. At the mangrove stand, high tides inundated from 0300 to 0600 and from 1540 to 1720 during 22-23 September 2007. In contrast to high tide during the day, the mangrove canopy during high tides at night appeared to store relatively high CO$_2$ concentrations (Fig. 3). The CO$_2$ concentration increased sharply from 374 to 383 $\mu$mol mol$^{-1}$ during the nocturnal high tide. Although this accumulation of CO$_2$ in the canopy at night may be associated with low wind speed (Brown and Rosenberg, 1970; Minhua et al., 1997), the sharpness of the change in CO$_2$ level suggests that the high tide is a more likely explanation. During daytime hours, the increase in CO$_2$ concentration was observed during high tide, but the increase relatively was lower than that during the night. This increase was between 375 to 380 $\mu$mol mol$^{-1}$. This difference may be due to increased wind speed or the influence of photosynthetic activities during the day, although maximal rates of photosynthesis have been found to be reduced when mangrove plants are exposed to flooding regimes (Ellison and Farnsworth, 1997). In addition, when seawater floods the mangrove stand during high tide, the water temperature beneath the canopy may decrease due to the canopy preventing direct sunlight from falling on the water. When water below the mangrove canopy contains lower CO$_2$ gas pressure than the atmosphere, CO$_2$ will move by molecular diffusion from atmospheric air below the canopy into the water. In consequence, more CO$_2$ will usually dissolve in cold surface water to form carbonic acid, which is transferred from the mangrove stand to the river and eventually to the ocean.

Tidal inundation also has a significant influence on water vapor concentration and air temperature in the mangrove canopy (Fig. 5). The mangrove canopy experienced high water humidity levels because of tidal inundations. During the high tide, the $H_2O$ concentration increased in the canopy while the air temperature decreased. This increase in $H_2O$ concentration is almost certainly due to the saturating effect of the high tide. The air temperature in the mangrove canopy during night-time was lower than that during daytime. As well as the lack of sunlight, this is also because of the effects of tidal inundation, which help to moderate within-canopy air temperature during the night.

**Conclusion**

This investigation has quantified the diurnal and vertical fluctuations in micro-climatic drivers of photosynthesis for a mangrove canopy. The canopy had low CO$_2$ concentrations, humid (but variable) air, and variable temperature. Tidal inundation provides a control on microclimatic variation not experienced by dryland forests. The findings of the study carry two major implications. The first is that these field data concerning mangrove canopy environments should be taken into consideration when attempting to link mangrove productivity with the photosynthetic response of individual leaves in laboratory experiments. The second is that the data, particularly the low CO$_2$ canopy air environment of the mangrove ecosystem as measured, point to the potential importance of mangrove reforestation programs to sequester atmospheric CO$_2$. Investigations into both of these aspects of mangrove forests are currently being conducted.

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