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Eclipse Effects on CO₂ Profile within and above Sorghum Canopy

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Abstract: We analyzed the effects of a partial solar eclipse (22 July 2009) on microclimate including vertical gradients of CO₂ concentrations ([CO₂]), so called [CO₂] profile, in a mature sorghum canopy. Together with CO₂ measurement, major photosynthetic drivers of microclimate, light intensity, temperature and atmospheric H₂O concentration ([H₂O]) were also measured simultaneously at the same place and height. [CO₂] at 6.0, 3.2, 2.1, 1.4, 0.7, 0 m above the ground (canopy height was 3.2 m) increased by 5.8, 4.8, 9.0, 7.8, 6.4, 7.6 μmol mol⁻¹, respectively, from 1 hour before the eclipse maximum to the eclipse maximum, during which the incident solar radiation above the canopy dropped by 1473 μmol photons m⁻² s⁻¹. However, it declined by 3.4, 10.6, 10.8, 6.0, 5.4, and 5.8 μmol mol⁻¹, respectively, from the eclipse to 1 hour later, during which the incident radiation increased by 1350 μmol photons m⁻² s⁻¹. The [CO₂] profile during the eclipse was uniform except for higher [CO₂] near the ground. Comparative analysis of the effect of light intensity on the microclimate during the eclipse-induced light decreasing phase (ELDP) and eclipse-induced light increasing phase (ELIP) revealed that [CO₂], [H₂O], temperature and relative humidity (RH) are significantly correlated with the light intensity above the canopy in a nearly linear fashion. Furthermore it indicated that detected less light-reacted canopy photosynthesis at a higher layer within the canopy during ELIP might be due to slower response of stomatal opening (than closing) to the light intensity above the canopy.

Key words: Canopy photosynthesis, CO₂ profile, Eclipse, Microclimate, Sorghum.

On Wednesday, 22 July 2009, a total eclipse of the sun was seen from within a narrow corridor that traversed half of earth. The path of the moon's umbral shadow started in India, and, crosses mainland Asia. Afterwards, the path crossed Ryukyu Islands and curved southeast through the Pacific Ocean where the maximum duration of totality reached 6 min 39 s. A partial eclipse was seen within a much broader path of the moon's penumbral shadow, which included most of eastern Asia, Indonesia, and the Pacific Ocean.

The effects of a solar eclipse on plant behavior have been reported. In general, the effects of an eclipse on plants are related to the light limitation experienced during the phenomenon (Economou et al., 2008). Although in natural environments leaves are exposed to a highly fluctuating light environment ranging from seconds to minutes or even longer interval (Barradas and Jones, 1996), a sudden drop in solar irradiance during a solar eclipse provides a challenge for investigating its impacts on plant behavior (Economou et al., 2008). Deen and Bruner (1933) studied stomatal movements of the gray birch

during the sun eclipse in 1932. Drop of sap flow velocity during an eclipse has been observed in several plants (Lagefoged, 1963; Fernandez et al., 1996; Morecraft et al., 2000; Harberle et al., 2001). Photosynthetic reactions were also assessed during an eclipse. Harberle et al. (2001) assessed photosynthesis and transpiration of trees during the day of an eclipse by using a thermo-electronically controlled cuvette system. Four cereal field crops and three leguminous field crops were also measured for the photosynthesis and transpiration by using a closed portable infrared gas analysis system (Economou et al., 2008). Leaf cuvettes and chambers to assess photosynthetic reactions have been used in a field by many researchers (Field et al., 1982; Collatz et al., 1991; Denmead et al., 1993). The use of cuvette and chamber system enables measurement of diurnal variations of carbon fluxes in terms of environmental response functions (Schulze and Koch, 1969; Collatz et al., 1991; Baldocchi, 2003). However, the physical placement of the cuvette on a leaf or a chamber over a plant may produce biases and artifacts (Baldocchi, 2003). The manual dependency of a cuvette limits the number of

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leaves that can be measured across the domain of a plant canopy within a reasonable time frame, e.g., an hour. It is difficult to sample, with high statistical confidence, the natural variability that exists in photosynthesis; sources of variation include the acclimation of leaf photosynthesis to sun or shade environments and vertical gradients in photosynthetic capacity (Ellsworth and Reich, 1993). The photosynthetic light response curve is usually determined under a controlled environment. However, the drivers that affect this curve may vary diurnally within the air layers of the canopy (Al-Saidi et al., 2009a).

Since a number of abiotic and biotic factors such as turbulent mixing, light, water and plant life form influence the canopy $[\text{CO}_2]$ profiles (McNaughton, 1989; Buchmann et al., 1996, Buchmann and Ehleringer 1998), the sudden dynamic change of solar radiation caused by an eclipse may influence the terrestrial ecosystems and photosynthesis, and subsequently $[\text{CO}_2]$ profiles. Al-Saidi et al. (2009a) recently developed a short sampling time system for measuring vertical gradients of $[\text{CO}_2]$ and $[\text{H}_2\text{O}]$, compared to the previous systems (Xu et al., 1999; Leuning et al., 2000). The scopes of this study are; (1) to describe the gradients of microclimatic fluctuations, mainly during the eclipse (2) to assess canopy photosynthetic reactions to light fluctuation in a fast changing microclimate during the eclipse by comparing the light decreasing phase and light increasing phase.

Materials and Methods

1. Study site

The experimental field is located at the University of the Ryukyus ($26^\circ 15' \text{N}$, $127^\circ 45' \text{E}$) in Okinawa, Japan, at an altitude of 127 m. The site was about 260 km from the peripheral axis of the eclipse totality, with 92% sun obscuration. The soil of the experimental field was dark red soil (Shimajiri Marji) that is widespread in the Okinawa Islands. Chemical fertilizer was applied twice during the plant growth period.

2. Plant materials

Sorghum [*Sorghum bicolor* (L.) Moench cv. Koutoubun-Sorugo] seeds were sown on 30 April 2009, at a row spacing of 0.6 m and plant density of 5.6 plants m^{-2} . The area of the stands was 165 m^2 , the height of the sorghum stands was approximately 3.2 m in 20 July 2009. Emergence of ear leaf and panicle was confirmed on 10 and 20 July 2009, respectively.

3. Measurements of microclimatic factors

The measurements were conducted on bare land over an area of 300 m^2 and the sorghum stand during 16-19 and 20-29, July.

The vertical gradients of CO_2 concentrations ($[\text{CO}_2]$), H_2O concentrations ($[\text{H}_2\text{O}]$), air temperature and light

intensity within and above canopy were measured according to Al-Saidi et al. (2009a,b) with a modification of sampling height and addition of photosynthetically active radiation (PAR) light sensor bars to measure the transmitted light intensity in the canopy. The system measures the temporal fluctuations and vertical variation in $[\text{CO}_2]$, $[\text{H}_2\text{O}]$, temperature, and light intensity, at six different heights in the canopy (Fig. 1). Six inlet tubes (6×8 mm) were positioned on a steel tower at heights of 0, 0.7, 1.4, 2.1, 3.2 and 6.0 m above the ground at the site. $[\text{CO}_2]$ and $[\text{H}_2\text{O}]$ were measured by sampling air at a flow rate of 17 mL s^{-1} from each height. The sampling apparatus included one infrared gas analyzer (IRGA, 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. This technique enables measurement of fresh air at any of the solenoid valves as the air is switched from one height to another. To avoid sampling pre-equilibrated air in the sample pump and the infrared gas analyzer (IRGA) cell from the previous measurement, for equilibration of temporal measured air, we allowed 20 seconds which is considered to be enough for measured air to reach a plateau state in $[\text{CO}_2]$ in this profile system (Al-saidi et al., 2009a). Consequently, sampling was completed in a two-minute measurement cycle over six heights, that is markedly faster than other systems which require 10 min (Jarvis et al., 1997; Buchmann and Ehleringer, 1998) or even 30 min (Skelly et al., 1996) to complete one cycle of measurements over five heights of a profile. Air temperature was measured using a copper-constantan thermocouple. The thermocouples were positioned near the air inlet at six heights on the tower and shaded to avoid direct sunlight. Photosynthetic photon flux density (PPFD) was measured using two quantum sensor (LI-190SA, Li-Cor) placed on the top of the tower and 3.2 m height. At the other sampling heights, PAR light sensor bars (#s366816, Spectrum Technologies, inc.) were attached parallel to the ground. These sensor bars were calibrated with the quantum sensor (LI-190SA, Li-Cor) outdoor in the day-time before the measurement started, and showed good correlation ($r > 0.997$ in overall sensor bars). Since 6 independent PPFD sensors were embedded in each light sensor bar transmitting mean output by mV, light at a certain height shaded by leaves above a light sensor bar in the sorghum stand was measured with less variance induced by a set position of a light sensor bar. To avoid artificial shade by other sensors and standing pole, we oriented the light sensors to the south and the others behind. The IRGA and all sensors were connected to a

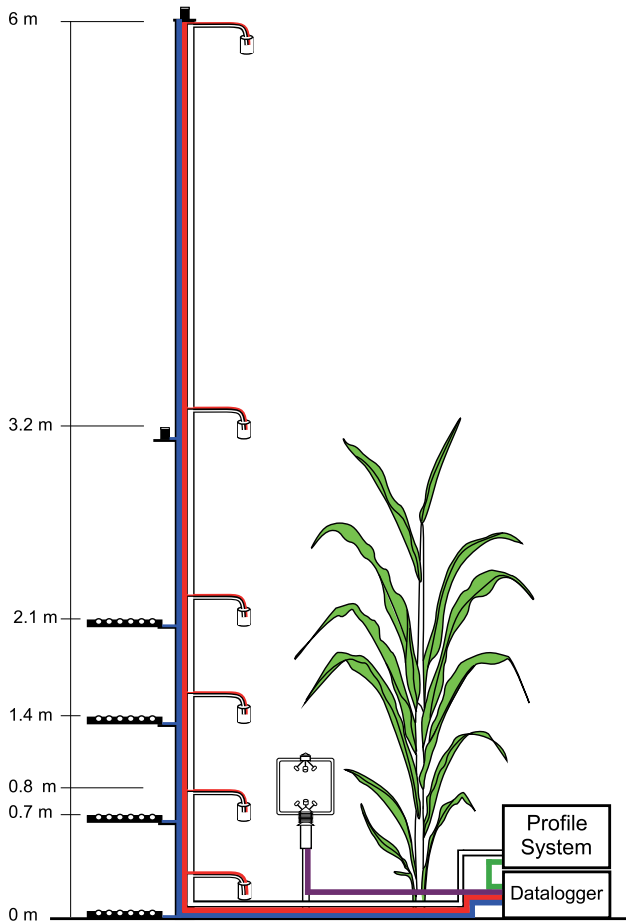


Fig. 1. Schematic diagram of the experimental setup. Sensors for photosynthetic photon flux density (PPFD), inlets tubes for air sampling and wire thermocouple sensors of air temperature were set above (6 m) and within canopy (3.2, 2.1, 1.4, 0.7 and 0 m). Note that 2 sensors for PPFD at 6 m and 3.2 m were both single PPFD sensor, whereas at the other measurement height light sensor bars (6 PPFD sensors per bar) were set. Red, blue, green and purple lines show cables for air temperature sensors, PPFD sensors, an infra-red gas analyzer (IRGA) and a ultrasonic anemometer set within the Sorghum canopy (0.8 m).

data logger (DA-100, Yokogawa). The data from the sensors were sampled every second, and 10 s averages were computed and stored on a computer to coincide with the measurement of $[CO_2]$ and $[H_2O]$. Wind speed, wind direction and ambient pressure in the sorghum stand were measured three-dimensionally by the three-axis ultrasonic anemometer (HD2003, Delta Ohm) set at the center of the three-axis at 0.8 m height and near the steel tower (Fig. 1). Wind speed and direction were measured continuously with a wind monitor (MODEL 05103-47R.M., YOUNG) attached to the top of the solid pole (6.0 m) in the field within 40 m from the sorghum stands. Relative humidity (RH) at each height is calculated from the data obtained by the temperature and $[H_2O]$ measurement at each height, and the pressure measurement by the three-axis ultrasonic anemometer within the canopy, assuming that

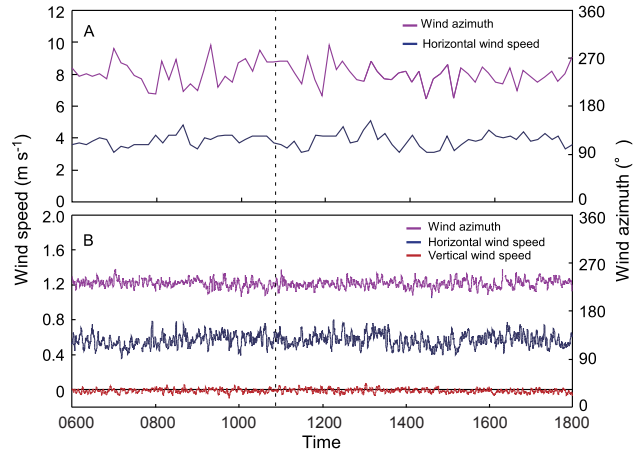


Fig. 2. Wind speed and direction at 6.0 m above the field of the experimental site (A) and within the Sorghum canopy at 0.8 m above ground (B) in the day time of 22 July 2009. Wind azimuth, purple line, indicates the direction of wind flowing horizontally. 0° is adjusted to the geographical north and goes clockwise up to 360°. Blue and red lines show the horizontal and vertical wind speed, respectively. In the vertical wind, plus means the speed of wind flowing upward, while the minus means downward. Data in A were led every 10 seconds and averaged in 10 minutes. Data in B were led every second and averaged in 10 second. Dotted line (1054) shows the time of the eclipse maximum.

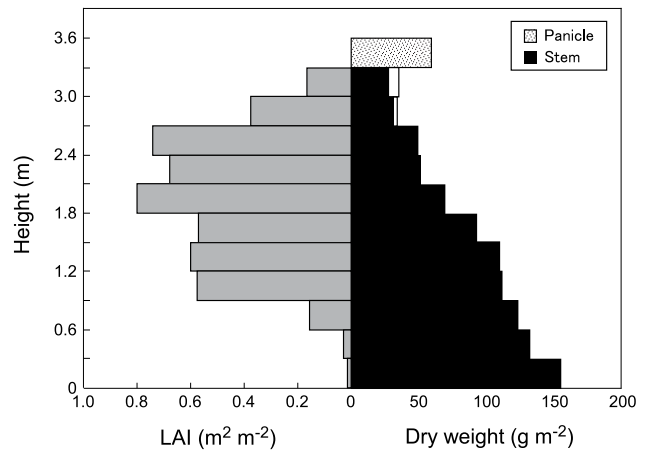


Fig. 3. Distribution of leaf area, panicle dry weight, stems and leaf sheaths in the sorghum canopy at the late ripening period on 30 July 2009.

the pressure variance within the canopy was small. IRGA was calibrated by using nitrogen gas as zero and a standard CO_2 gas containing $400 \mu mol mol^{-1}$ of dry air in both the laboratory and field before and during the measurement, respectively. In addition, the exhaust purge of the profiling system was maintained steadily.

4. Canopy structure

In order to analyze the data obtained by the measurement of fluctuations of the microclimate within the sorghum

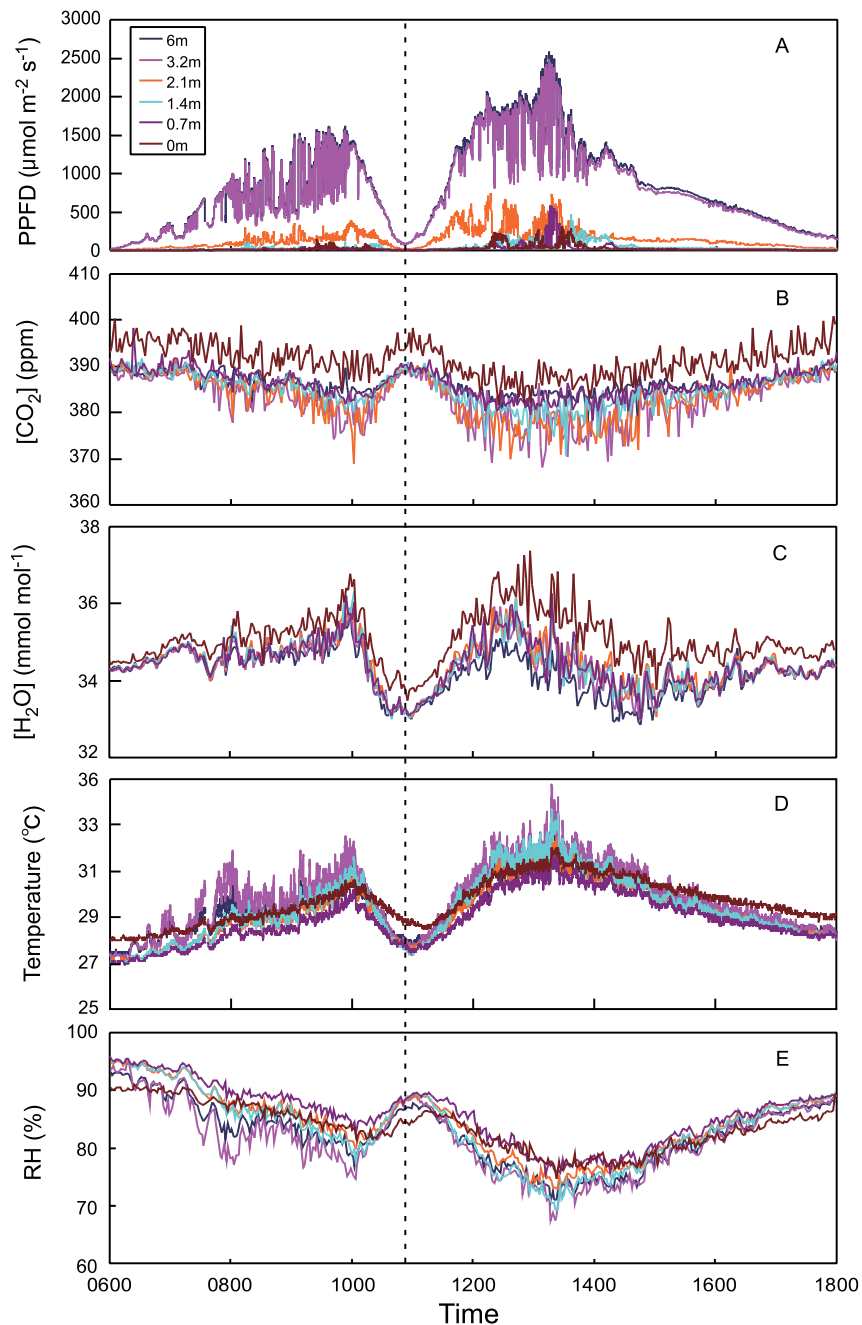


Fig. 4. Time series of measured data of photosynthetic photon flux density (PPFD, A), CO_2 concentration ($[\text{CO}_2]$, B), H_2O concentration ($[\text{H}_2\text{O}]$, C), temperature (D) and relative humidity (RH, E) at various heights within and above the canopy. Dotted line (1054) shows the time of the eclipse maximum.

stand, we used the ordinary stratified method proposed by Monsi and Saeki (1953) by cutting a plant horizontally. A 30-cm-thick segment within the area of 1.2 m by 1.2 m square was used. The measurements were made on 30 July at the same place as the measurements of $[\text{CO}_2]$ profile and other microclimatic factors.

5. Statistic analysis

The relationship between the microclimatic factors with the light fluctuations obtained during the eclipse-induced

light decreasing phase (ELDP) and eclipse-induced light increasing phase (ELIP), was statistically analyzed by analysis of covariance (ANCOVA).

Results

The geographically calculated eclipse maximum was at 1054:10 on 22 July. Throughout the day of measurement, cloud intermittently shaded the field we observed. However, the decrease and increase in solar radiation could be visibly recognized.

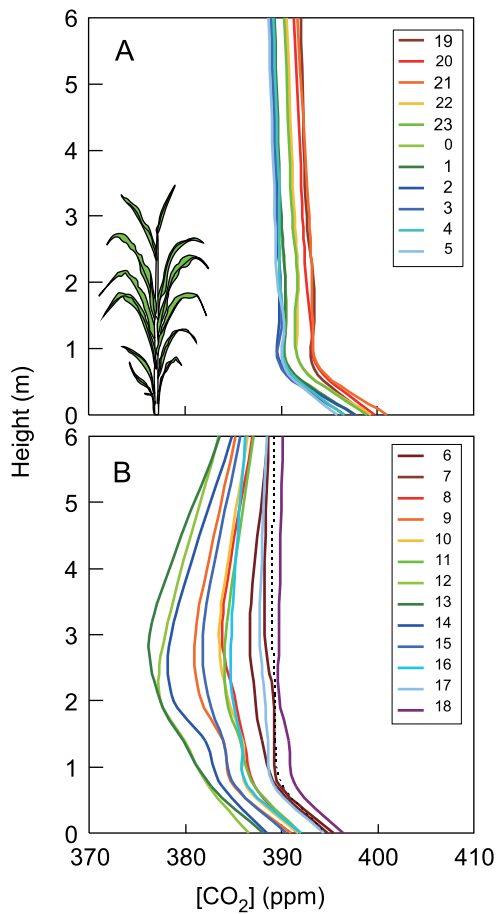


Fig. 5. $[CO_2]$ profiles (A, night and B, day) within and above the canopy measured on 21-22 July 2009. Lines of different colors correspond to the 1 hr means of the every 2-min interval data. Each specific number represents the mean of the following 1 hour (e.g. 6 represents 0600-0659). Black dotted line shows the data obtained during 10 min near the eclipse maximum.

Above the field of the experimental site (6.0 m) and at the measurement site in the sorghum canopy (0.8 m) on 22 July, the wind flowed steadily from the south (Fig. 2A). The mean horizontal wind speed above the field was $3.85 \pm 0.42 \text{ m s}^{-1}$, while the means of horizontal and vertical wind speed in the canopy at 0.8 m were $0.57 \pm 0.07 \text{ m s}^{-1}$ and $-0.01 \pm 0.02 \text{ m s}^{-1}$, respectively. Throughout the day, vertical wind speed was very low (Fig. 2B) within the canopy. LAI at the site of measurement in the sorghum stand was $4.7 \text{ m}^2 \text{ m}^{-2}$ (Fig. 3). Total dry weights of the panicle, stem and leaf per m^2 were 70, 956 and 245 g, respectively. There were also dead leaves from 0 - 90 cm layer at the site, whose dry weight was 46 g. The productive structure of the sorghum shows the typical broad-leaved type characterized by the relatively high proportion of leaves in the higher layers to the low ones. The diurnal change of microclimate parameters during 22 July is shown in Fig. 4. Photosynthetic photon flux density (PPFD) above (6.0 m) and within the canopy (0-3.2 m)

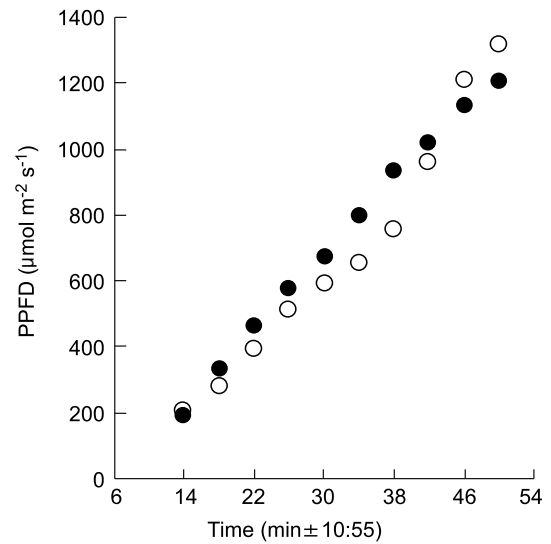


Fig. 6. Time series of light above the canopy during Eclipse-induced Light Decreasing Phase (●, ELDP) and Eclipse-induced Light Increasing Phase (○, ELIP), before/ after 1055, near the eclipse maximum, respectively. Data represent the means of consecutive 4 min readings by the time plotted. The mean velocities of light decreasing and increasing phase, calculated by linearization during ELDP and ELIP are $28.4 \mu\text{mol m}^{-2} \text{ s}^{-1}/\text{min}$ ($r=0.998$), and $30.5 \mu\text{mol m}^{-2} \text{ s}^{-1}/\text{min}$ ($r=0.982$) respectively.

decreased markedly during the eclipse followed by recovery. At the near eclipse maximum (1052:30), the minimal PPFD at 6.0, 3.2, 2.1, 1.4, 0.7 and 0 m was 68, 68, 15, 4, 3 and $3 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Fig. 4a), respectively, although at 1054:10, the time of geographically calculated eclipse maximum, it was 90, 89, 22, 4, 6, $2 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ respectively, which may be due to the slight effect of cloud covered above the canopy sporadically during the day. The PPFD at 6.0, 3.2, 2.1, 1.4, 0.7 and 0 m from the ground were declined by 1473, 1422, 223, 51, 11 and $30 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively from 1 hour before the eclipse maximum (1054:10) to the eclipse maximum. On the other hand, it increased by 1350, 1312, 265, 26, 13 and $16 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively, from the eclipse maximum to 1 hour. Since the leaves occupied at higher layers of the sorghum canopy, a noticeable light extinction occurred from 3.2 m thorough 1.4 m. In addition, the difference of PPFD between the eclipse maximum and before/ after the eclipse maximum became smaller as the measurement height goes deep in the canopy. The same fall and rise fluctuation during the eclipse can also be seen in $[H_2O]$ and temperature (Figs. 4c and 4d). The $[H_2O]$ at 6.0, 3.2, 2.1, 1.4, 0.7 and 0 m from the ground declined by 2.2, 2.2, 2.4, 2.7, 2.5, $2.9 \text{ mmol mol}^{-1}$, respectively. On the other hand, it increased by 1.2, 1.5, 1.6, 1.5, 1.5 and $2.0 \text{ mmol mol}^{-1}$, respectively, from the eclipse maximum to 1 hour later. $[H_2O]$ tended to be low above the canopy throughout the day, while it was relatively high within the

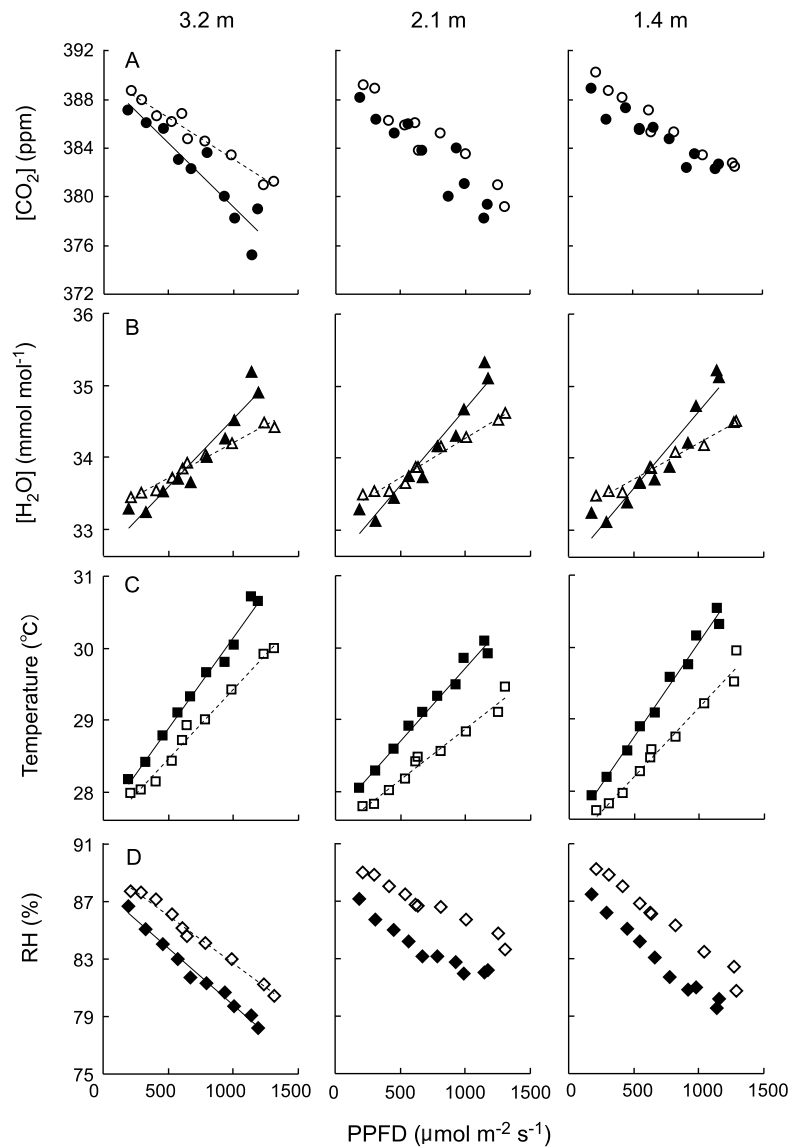


Fig. 7. Influence of light on micro-climatic factors, concentration of CO_2 ($[\text{CO}_2]$, a) and H_2O ($[\text{H}_2\text{O}]$, b), temperature (c) and relative humidity (RH, d) during ELDP and ELIP (shown in Fig. 5). Data correlated to the same plot in Fig. 5, and are averaged in the same manner. Left, middle and right row of the graphs represent the data at 3.2 m, 2.1 m, 1.4 m, respectively. In each graph, closed symbols represent data during ELDP, and opened symbols represent data during ELIP. The regression line (dotted line indicates line of ELIP) shows the significant difference between the slope of regression line of ELDP and that of ELIP (ANCOVA, $P < 0.05$).

canopy, especially in the early afternoon, around the time when a higher PPFD was detected in the day. The temperature at 6.0, 3.2, 2.1, 1.4, 0.7 and 0 m from the ground declined by 2.6, 3.8, 2.6, 2.7, 2.1 and 1.5°C, respectively, 1 before the eclipse maximum to the eclipse maximum while it increased by 1.9, 2.2, 2.0, 2.2, 1.3 and 1.3°C, respectively, from the eclipse maximum to 1 h later (Fig. 4d). The temperature at the higher layers (3.2, 2.1 and 1.4 m) was higher than that at lower layers (0.7 and 0 m) when the PPFD above the canopy displayed a larger

PPFD during the day. At 0.7 m, the temperature was relatively low throughout the day and less fluctuated during the eclipse, whereas the temperature at 0 m showed the least fluctuation and the highest temperature throughout the day. Together with the fall and rise of $[\text{H}_2\text{O}]$ and temperature, the relative humidity (RH) showed a rise and fall during the eclipse (Fig. 4e). The $[\text{CO}_2]$ above and within the canopy increased and decreased as well as RH (Fig. 4e). As close to the eclipse maximum, the $[\text{CO}_2]$ at each height converged except for

Table 1. Influence of light on micro-climatic factors, CO₂ and H₂O concentration, temperature and relative humidity during ELDP and ELIP (shown in Fig. 5). The number in parentheses is the proportion of the slope of the regression line during ELDP to the slope of the regression line during ELIP.

Measured micro-climatic factors vs. light above the canopy	Sampling height (m)					
	6	3.2	2.1	1.4	0.7	0
CO ₂ concentration	ns	*(1.5)	ns	ns	ns	ns
H ₂ O concentration	** (2.7)	** (1.9)	** (1.9)	** (2.1)	** (2.0)	** (1.6)
Temperature	** (1.4)	** (1.3)	** (1.4)	** (1.4)	** (1.6)	ns
Relative humidity	ns	*(1.2)	ns	ns	ns	ns

Note: *, ** shows significant difference at P<0.05 and P<0.01 level, and ns is not significant difference determined by analysis of covariance (ANCOVA).

the one at 0m that displayed consistently higher concentration throughout the day (Fig. 4b). Apparently, the [CO₂] profile around the eclipse maximum (shown as dotted line in Fig. 5B) displayed the uniformity of the [CO₂] above and within the canopy. It is comparatively different from that at 9-10 or 12-13, before or after the eclipse, which are characterized by low [CO₂] at high layer in the canopy. The [CO₂] profile around the eclipse maximum is rather similar to that at 6 or 18 in the day (Fig. 5B), that at night (Fig. 5A), and that throughout a day on bare land (data not shown). [CO₂] at each height (6.0, 3.2, 2.1, 1.4, 0.7, 0 m) near the eclipse maximum were higher than that at 13-14, when the radiation was the most intense in the day, by 5.4, 12.4, 12.0, 9.4, 7.3 and 6.3, respectively (Fig.5B). [CO₂] at 6.0, 3.2, 2.1, 1.4, 0.7 and 0 m from the ground from 1 hr before to the eclipse maximum (1053-1055) increased by 5.8, 4.8, 9.0, 7.8, 6.4 and 7.6 $\mu\text{mol mol}^{-1}$, respectively. On the other hand, they decreased 1 hour after the eclipse maximum by 3.4, 10.6, 10.8, 6.0, 5.4 and 5.8 $\mu\text{mol mol}^{-1}$, respectively. During the eclipse, light fluctuated as mentioned above. We separate this fluctuation into the eclipse-induced light decreasing phase (ELDP) and eclipse-induced light increasing phase (ELIP), which can be significantly linearized, and show the almost same mean velocity of light change per minute (Fig. 6, ELDP, 28.4 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, ELIP, 30.5 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). The relationship between PPFD above the canopy and each measured micro-climatic factor was investigated (Fig. 7). [CO₂] and RH above and within the canopy showed a significant negative correlation to PPFD in both phase (Figs. 7a and 7d), whereas [H₂O] and temperature at each height showed a significant positive correlation to the PPFD in both phase (Figs. 7b and 7c). Furthermore, this trend showed a nearly linear fashion (Fig. 7). To analyze the effects of light on the microclimate during ELDP versus ELIP, we need to avoid the difference of the settled microclimate in both phases, the slope of the regression line between ELDP and ELIP was compared as a response to the light intensity (Table 1). The difference of the slope was tested by ANCOVA. During ELIP, the [CO₂] at 3.2 m showed a significantly weaker response to

PPFD, compared to that during ELDP (Fig. 7a), and the difference of the slope (the proportion of a regression line's slope during ELDP to that during ELIP) was 1.5 (Table 1). [H₂O] during ELIP rose less than that during ELDP as light intensified (Fig. 7d). The difference of the slope was 2.7, 1.9, 1.9, 2.1, 2.0 and 1.6 at 6.0, 3.2, 2.1, 1.4, 0.7 and 0 m, respectively. The temperature during ELIP showed less increase as light was intensified, and kept lower than that during ELDP throughout the phase (Fig. 7c). The difference of the slopes was 1.4, 1.3, 1.4, 1.4 and 1.6 at 6.0, 3.2, 2.1, 1.4 and 0.7 m. The RH at 3.2 m during ELIP responded weakly to PPFD (Fig. 7d), and the difference of the slope was 1.2 (Table 1).

Discussion

Unlike [CO₂] profiles seen in forests, the [CO₂] profiles obtained in this measurement showed depression in the day time, especially at the time of high solar radiation (Fig. 5B). In agricultural stands, canopy [CO₂] profiles are affected by crop LAI and foliage density (Buchmann and Ehleringer, 1998). Although there is a time gap in the sampling between the microclimatic data on 22 July and the canopy structure data on 30 July, since the panicle had already emerged before 22 July implies the canopy was at the climax of the growth curve at both sampling times. The difference in the distribution of the leaves and LAI was thought to be less involved although the proportion of the panicle to the stem and their biomass might have changed. In dense crop canopies, wind velocity decreases exponentially with decreasing height above the ground, due to increased boundary layer resistance (Baldocchi et al., 1981a and b). Steadily gentler breeze within the canopy than above the field at 6.0 m height throughout the day is considered to be induced by the high LAI (4.7) and canopy architecture that had a relatively high portion of leaves occupied in the higher layers making a thick boundary layer above the canopy (Fig. 2). This boundary layer, the lid above the canopy, may cause the less CO₂ moving across the canopy-atmosphere interface, resulting in a small vertical advection and the vertical gradients of the [CO₂] profile in the day time and the depression of

[CO₂] within and just above the canopy (Fig. 5B).

The difference in the distribution of [CO₂] gradient between that near the eclipse maximum and that before or after the eclipse (Fig. 5B) and the similarity in its profile with that at night (Fig. 5A) and on the bare land implies that a large amount of photosynthetic leaves is a major sink of CO₂ (Han et al., 2003), whose sink strength highly depends on the temporal solar radiation. Absence of light disrupts photosynthetic electron transport, leading to a sudden decline in the measured net CO₂ uptake rate (which closely relates to the CO₂ assimilation process) (Haberle et al., 2001) and consequently the uniform [CO₂] profile above and within the canopy. At the same time, the relatively high [CO₂] at the ground level through diurnal (including the time of eclipse maximum) and nocturnal course implies that soil respiration acted as a constant source of CO₂ throughout the day (Fig. 5). Previous studies on field crops revealed similar canopy [CO₂] changes, showing that soil respiration and turbulent mixing of canopy and boundary layer air were insufficient to offset the photosynthetic demand of highly productive stands (Lemon, 1969; Monteith, 1973; Buchmann and Ehleringer, 1998). The detected greater depression of [CO₂] at a higher layer in the canopy in spite of the high accessibility to CO₂ from the atmosphere may reflect the relatively high sink strength at the higher part of the canopy due to the larger leaf mass and the abundant PPFD availability in the upper canopy.

The linear response of [CO₂] to light fluctuation observed at each height during the eclipse means that the higher sink strength existing in the upper canopy affect the whole canopy level, even just above the ground where a low sink capacity is expected in terms of the scarce leaf mass and light availability (Figs. 3 and 7). The significant difference in the response of [CO₂] to light during ELDP and ELIP can be seen only at 3.2 m. This significant difference is considered to be triggered by the difference in the reaction of the photosynthetic apparatus between the two phases since the [CO₂] profiles in the upper canopy reflected the canopy photosynthetic sink strength the most.

The effect of the temperature on the canopy photosynthesis would be slight because the optimal leaf temperature for photosynthesis of the C₄ plants like sorghum is generally between 30°C and 40°C (Bjorkman et al., 1980). In this temperature range, the photosynthetic rate is considered to vary less within the canopy. In our experiment, however, the leaf temperature was not measured and it is hard to differentiate whether the trend of the [CO₂] response to the irradiance is linear or curved because of its variance (Fig. 7). Thus, the influence of the temperature on canopy photosynthesis is not clear. Throughout the day of the eclipse, the temperature fluctuated in a similar way as the light above the canopy

regardless of the measurement height (Fig. 4a and 4d), which indicates high dependency of the temperature above and within the canopy. The higher temperature at 3.2 m throughout the day may be caused by the heat radiation from the leaves captured relatively high solar radiation than the lower leaves, which can explain the convergence of the temperature at each height toward the eclipse maximum (Fig. 4d). On the other hand, the lower response of temperatures above and within the canopy may be induced by the delay that might be attributed to the buffering reaction of terrestrial radiation, especially the underlying soil in this case (Fig. 4d). To some extent, the temperature response to the eclipse maximum was delayed, especially that at 0 m. The same was found in the data for the eclipse on 29 March 2006 (Economou et al., 2008).

Light energy directly controls the stomatal reaction by its influence on receptor systems in the guard cells (Kaiser and Kappen, 1997). In our experiments, though the RH at 3.2 m showed a weaker response during ELIP than during ELDP, the difference was small (Fig. 7d). The RH response to light tends to be the same, but the overall RH in each height during ELDP was lower than during ELIP (Fig. 7d). In spite of the higher RH during ELIP, [H₂O] during ELIP appeared to change gently, compared to the response during ELDP (Fig. 7b). Changes in stomatal resistance as a response to transient darkness or cloud shading have been observed in several fast-growing herbaceous species (Knapp and Smith, 1990a). In some plant species the stomata reacted promptly, but in others, especially in woody species, stomata were less sensitive to shading (Knapp and Smith, 1990b). As many previous studies (Percy et al., 1985; Chazdon and Percy, 1986; Roden and Percy, 1993; Barradas et al., 1996) showed that photosynthetic assimilation responds more rapidly to decreasing than to increasing irradiance in both laboratory and field experiments. Moreover, the rate of stomatal closure is faster than the rate of opening in changing irradiance (Barradas et al., 1994). Thus, the weaker [H₂O] response to the light fluctuation indicates slower stomatal opening relative to the closing during eclipse, which probably caused interruption of assimilation rate of photosynthesis, consequently the weaker [CO₂] response to light intensity during ELIP.

Conclusion

Relations between the light fluctuation and photosynthetic performance at the leaf level have been studied, but [CO₂] profile measurements during an eclipse have not been reported. The short-sampling profile system in this experiment well described the detailed response of microclimate within and above the canopy to the light during an eclipse. The study revealed a high dependency of the canopy photosynthesis, stomatal response to the

light intensity and its possible regulation on the photosynthesis. In addition, by combining this fast measurement of profiles for [CO₂] and [H₂O] with the other microclimate factors, we can obtain more comprehensive knowledge of the interaction between plants and terrestrial ecosystem.

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